

APPENDIX 1

VARIATION IN SHELL SHAPE

A1.1 Shell shape and environment

Tevesz and Carter (1980a) have recently reviewed the environmental relationships of shell form variability in unionaceans. Walker (1981b) similarly reviewed the subject, and completed analyses of shell form variability appropriate to some Australian hyriids. The review of Eagar (1948) has provided a convenient reference material to the habitat relationships of shell shape in unionaceans. Eagar summarised much early anecdotal literature and collated a number of generalisations that have largely been substantiated by subsequent studies; the observations effectively exemplify the long known fact that the considerable variation inter- and intraspecifically in unionacean shell form, is of a systematic nature. While variation in shell size (including the effect of stunting) is considered in Chapter 6, observations on obesity (width/length), and lateral outline (see later) may be summarised from the work of Eagar as follows:

Variation in obesity

1. In a given species, lake forms are recognisably more obese than river forms.
2. Within a single drainage system, river forms tend to increase in obesity downstream (following Ortmann's (1920) 'Law of Stream Distribution').
3. Obesity tends to be positively correlated with stream size and negatively correlated with water velocity.

Variation in lateral outline

1. Arcuate forms with curved dorsal margins and straight or more typically reflected ventral margins, are generally found in small streams or rivers of swift-flowing water.
2. Shells with curved ventral margins, a long hinge-line, and posterior ends expanded or strongly developed, are more typical of lakes or rivers of relatively slowly flowing waters.
3. Relative height (height/length) is often negatively correlated with water velocity, although positive correlations have been recorded.
4. There is usually some correlation between obesity and relative height of shells.

The functional morphological explanation of Eagar's (1948) conclusions regarding the shape-environment correlations, particularly those in relation to lateral outline, had remained largely speculative until recent studies and reviews by Eagar (1977, 1978). In relation to lateral outline, Eagar's (1977) experiments with Margaritifera margaritifera showed that the functional advantage of the arched dorsal and reflected ventral form lay in the provision of a larger

pedal gape, and associated increase in shell weight. The increase in pedal gape and extra shell weight, allowed a stronger anchorage and increased probing power for the foot in the unstable substrates of stream habitats subjected to strong and turbulent water currents. The lighter shells with curved ventral margins and long (and stronger) hinge-lines, however, were argued to have functional advantage over the heavier, dorsally arched shells, in providing active movement over the surface of the substrate in quieter environments. Thus the two contrasting patterns of growth appear to be consistently related to two contrasting functional activities, each typical of forms from habitats differing in water velocity (Eagar, 1977, 1978).

Eagar (1978) extended his explanations on functional morphologies to provide ecological meaning to Ortmann's (1920) 'Law of Stream Distribution' which states that shell form tends to increase in obesity downstream. Eagar argued that greater obesity provided a functionally efficient means of increasing volume of living tissue, thereby providing improved metabolic and functional activity to these forms from quieter waters. In addition, increased obesity in relatively still waters should enhance buoyancy and prevent shells from sinking into soft sediments that may prevail in quieter waters. Eagar stated that these generalisations would also apply to lake forms, which are recognisably more obese than river forms.

In relation to Eagar's (1948, 1977, 1978) generalisations upon the functional morphology of obesity and lateral outline summarised above, specific contributions made to the understanding of shell form in unionaceans are as follows:

As previously described, Eagar (1977, 1978) provided the first functional explanation of the correlation between stream velocity and lateral outline of unionaceans. Early workers provided no explanation for the observation of increasing height of mussels in the downstream direction of streams (e.g. Grier and Mueller, 1926), although Altnöder (1926) recognised that a correlation existed between dorsal arching in M. margaritifera and increasing stream velocity. Other studies on this species (Clarke and Berg, 1950; Hendelberg, 1960; Bjork, 1962; Roscoe and Redelings, 1964), and various unionids (e.g. Evermann and Clark, 1917) had left the problem largely unresolved, being preoccupied with distinguishing between the variation induced by the environment as opposed to ontogeny. Cvancara *et al.* (1978) thought generally that the lower shells of Anodonta grandis and Lampsilis radiata found in the upper reaches of the Sheyenne River (USA) were better adapted to the current.

Amongst hyriid unionaceans, Dell (1953) recorded that relative height in Hyridella from New Zealand, increased from flowing to still water environments. In the light of Eagar's (1977, 1978) interpretation given to the lateral outline of unionaceans from stream environments, Walker (1981b) recognised two distinct growth patterns of Alathyria jacksoni in the Murray River (Australia) - a 'winged' or straight-hinged form and a 'non-winged' or dorsally-arched form. Each growth pattern was characteristic of mussels from moderate and fast water currents respectively. Walker found that a decrease in relative height generally accompanied development of the dorsally arched shell, but emphasised, however, that this relative dimension showed considerable variation, tending to conceal rather than to reveal the

dual nature of the growth patterns.

Ortmann (1920) first proposed the general 'law' that river forms of mussel species within a single stream tend to increase in obesity downstream. The observation has been substantiated by others (e.g. Ball, 1922; Grier and Mueller, 1926; van der Schalie, 1938; Cvancara *et al.*, 1978), but nevertheless not all species accord to the general rule. Ortmann found evidence for example, that the trends were similar only for species of primitive taxonomic grouping. Similarly the relationship may not always hold for the same species in different streams. Cvancara *et al.* (1978) found that obesity of Anodonta grandis increased downstream in the Sheyenne River but not in the Turtle River, North Dakota (Cvancara, 1970). Although Clarke (1973) reported that A. grandis is a highly variable unionid, other studies have indicated that the mussel is conservative in relation to phenotypic plasticity; it has generally been found to vary little in shape between most habitats (Cvancara and Harrison, 1965; Cvancara, 1972; Green, 1972; Ghent *et al.*, 1978).

Various workers have suggested that the occurrence of less inflated and compressed shells in small streams or headwaters, was an adaptation enabling mussels to orientate themselves better to withstand strong currents (Wilson and Clark, 1914; Grier and Mueller, 1926; Clarke, 1973; Anderson and Ingham, 1978). This explanation of functional morphology is generally complementary to Eagar's (1978) interpretation described above, that explained increasing obesity of mussels from quieter portions of rivers, or from lakes. Matteson (1955), however, recorded various small-stream species as having highly obese dorsal portions and highly truncate posterior ends - just the reverse morphological appearance that might be expected under the prevailing conditions. (See Eagar's (1948) generalisations above.) Matteson proceeded to describe how such a truncate form at least, might enable mussels to burrow deeply into the sediments, thereby assisting in maintenance of a hold in strong currents.

Horn and Porter (1981) summarised the findings of a number of early North American studies comparing flowing water and lake forms of the same species. These studies in addition to that of Anderson and Ingham (1978) reported a greater degree of inflation of forms from lake environments. Clarke (1973) nevertheless, reported that Fusconaia flava was more obese in large streams than in any other environment.

A number of studies have corroborated, partly, the functional explanation given by Eagar (1978) for the higher obesities noted in lake forms of a given species. Ghent *et al.* (1978) argued that the wide ventral angle and lightweight shell of A. grandis were morphological adaptations permitting the animal to present a broad bearing surface to a soft-silt, deep-water substrate on which a mussel of narrower ventral angle might smother. (The thin-shell, and ovoid and slightly winged shape of a form of Velesunio ambiguus recorded from shallow, soft-muddy lagoon environments in southeastern Australia by McMichael and Hiscock (1958) and Walker (1981b), may serve a similar function.) The narrow ventral angle and heavier shell of Elliptio complanata from lake environments conversely, were thought by Ghent and co-workers as being ideally suited to life in hard-sand, wave-swept reaches. Such a shell would allow the mussel to plough

deeper and more supportive furrow paths. Stern (1983) corroborated the findings of Ghent *et al.* (1978), but in relation to a stream habitat, where obese and compressed species were characteristic of mud and sand substrates respectively. Anderson and Ingham (1978) and Tevesz and McCall (1979) also suggested that the moderately inflated and thin shelled form of Lampsilis radiata siliquoidea, would enhance its buoyancy in soft sediments. Tevesz and McCall added, moreover, that the form might permit the retention of enough water between the valves to flush away any shallow silt covering from the siphon areas.

In further relation to stability in the substrates of lake environments, Clarke (1966, 1973) reported that the anterior-beak length/length ratio was highest in specimens of A. grandis from the sandy sediments of large lake habitats. This suggested to Clarke that the large foot volumes inherent in these forms were physically selected for, enabling mussels to maintain their positions in exposed habitats and on shifting substrates. This functional morphology has a similar analogy therefore to that interpreted by Eagar (1977, 1978) for the increased stability in fast-current stream environments offered by the large pedal gape of dorsally arched shell forms.

Shell form in different species nevertheless, does not always appear to respond in the same morphological direction under similar environmental conditions. Clarke (1973) for example, found L. r. siliquoidea to be more obese in large lakes than elsewhere. He suggested that these more obese forms with lower surface to volume ratios might be better able to remain in place without being dislodged by turbulent and shifting currents that occur in lakes during storms. The relative obesity recorded for this species contrasts sharply with the relatively compressed form of E. complanata recorded by Ghent *et al.* (1978) in similar habitats. As mentioned above, a similar contradictory shell form was reported by Matteson (1955) in small-stream species, than had generally been reported for forms in small streams and headwaters.

Sediment type, and water turbulence and flow have not been the only implicated factors determining shell morphology. For Swedish unionids, Agrell (1949) observed that such features as anterior development, relative height and obesity were positively correlated with eutrophication. Amongst factors such as taxonomic differences, stream velocity and sediment type, Cvanacara *et al.* (1978) indicated that nutrient availability could account for differences recorded in relative height and obesity of unionids in the Sheyenne River (USA). Between Canadian lakes, Green (1972) found that factors such as shell height, width and inside volume were apparently conservative variables in relation to measured environmental variables, including sediment type.

The above review has been concerned so far with comparison of growth forms between quite different environments, such as prevail between quiet and still water, and turbulent and flowing water environments. Between similar habitats (e.g. lakes) or within the same habitat, the following findings in relation to a given species have been reported. Between lakes, the results of Green (1972) (above) suggest little variation in unionacean form. Within lakes, Fisher and Tevesz (1976) and Horn and Porter (1981) reported generally no significant relationship between shell morphology and various environmental

variables such as depth and sediment type. Of three species studied by Horn and Porter, however, obesity of one species, Lampsilis sp., was positively correlated with percent organic matter of the sediments. No causal relation was inferred. Both Cvancara (1972) and Ghent et al. (1978) found that shell morphology of A. grandis did not change with depth in respective lake environments, although Cvancara found a significant decrease in height of L. r. luteola and Anodontoides ferussacianus with depth. Again no causal explanation was offered. In central New York state, Harman (1970) noted that E. complanata decreased in obesity from shallow to deeper waters in the Finger Lakes; that A. grandis was relatively higher in the warmer littoral waters than the colder sublittoral and profundal waters of three lakes; and that L. r. radiata had ovate shells in the depths of the Finger Lakes as opposed to a more typical lateral outline in littoral waters.

The above discussions have described the nature and extent of the broad intra-specific variation characteristic of shell shape in unionaceans, from or between a variety of habitats and environments. Surprisingly, present understanding of the forces that manifest this considerable phenotypic plasticity in natural populations, is poor. Although both selection by the environment and direct phenotypic response by unionaceans are implicated, the relative contribution of these forces to shell form is not clear. Tevesz and Carter (1980a) described studies that evidenced phenotypic modifications of shell morphology in unionaceans following the damming of a stream; shell form in the populations from the newly created lakes quickly assumed some of the proportions characteristic of lake-dwelling forms. However, these observations are apparently ambiguous in interpretation because some of the observed influences were apparently related to human interference. Eagar (1978) described transplant experiments of a marine bivalve that had been transferred to new environments. Phenotypic changes of shell shape took place immediately, and in the same direction as those found in shells on the neighbouring sediments. However, in relation to the shell form of stream-dwelling unionaceans at least, Eagar felt that both selection and phenotypic moulding were operative, but that selection by the environment probably played the major role.

Character variation in shell form along ecological gradients, such as occur for example along the length of a stream are termed ecoclines. Ecoclines are clearly distinguishable from character gradients or clines reported over relatively large geographical areas in that the latter are largely independent of local environmental effects. They are most clearly evident when these effects are controlled for by the sampling of similar habitats (Cvancara, 1963; Walker, 1981b). Cvancara (1963) found evidence of a geographical cline in shell character of species of Lampsilis in North America. He observed that relative height and obesity increased toward lower latitudes suggesting that the three subspecific forms may represent only one species. Clarke and Berg (1959) reported a similar geographical cline in subspecies of Lampsilis radiata across central New York state. The claim, however, was refuted by Harman (1970). In Canada, Clarke (1973) observed generally, that northern populations of unionids were often more compressed than southern large-stream counterparts. McMichael and Hiscock (1958) found a cline in the anterior to beak/total length ratio of the hyriid, Velesunio ambiguus. The ratio

tends to decrease in higher latitudes.

Finally, attention must be drawn to the interest that unionacean shell form has held in regards to paleoecological and paleolimnological reconstruction. Analyses of the environmental relationships of the broad variability in shell form of present day species, provide potentially, a useful means of inferring corresponding environmental changes in ancient aquatic ecosystems. The studies of Eager (e.g. 1948, 1977, 1978) are particularly noteworthy in demonstrating how shell form-habitat information may be used to reconstruct the habitat of fossil species.

Nevertheless, with inadequate ecological information on present day shell form - habitat relationships, such paleoenvironmental reconstructions may be incorrect. In a thorough appraisal of the topic, Tevesz and Carter (1980a) concluded that a common shortcoming of most form-habitat studies was that explanations of functional morphology for observed correlations, were largely speculative. This situation has possibly been remedied to some extent by the experimental work of Eager (1977, 1978) (which Tevesz and Carter apparently did not have access to), in regards to interpretation of the lateral outline-stream velocity correlation. However, sufficient diversity of findings in the obesity-habitat relationship have been recorded to suggest that generalisations about the functional morphology of obesity in unionaceans need to be cautiously applied. Obese shells for example, may be adaptive for life on soft muddy sediments, but such forms are not always present in relatively still-water environments upon these sediments (Clarke, 1973; Cvanacara *et al.*, 1978). Thus, reconstruction of the paleoenvironment from fossil forms of this phenotype in various geological strata may be incorrect. As the phenotypic response by different species to the same environmental conditions may differ (e.g. Ortmann, 1920; Cvanacara *et al.*, 1978), reconstruction of paleoenvironments require in the very least, specific information concerning functional morphologies of present day forms of individual species. Even after explaining the adaptive morphology of the various forms, Green (1972) and Anderson and Ingham (1978) warned of the danger in applying present-day results determined for one geographical region, to data from another. Data applied beyond a regional scale may be suspect where geographical clines in shell form exist.

A1.2 Sexual and ontogenetic variability

Only for lampsiline unionids is sexual dimorphism in shell features marked. Reportedly, females of various species are more obese, higher and thicker-shelled, and are distinguishable from males both visually and statistically (Coker *et al.*, 1921; Ball, 1922; Anderson and Ingham, 1978; Kat, 1983d). The obese condition of the female shell is generally most pronounced over the marsupial regions and Coker and co-workers, and Anderson and Ingham thought this condition was an adaptation allowing for large numbers of eggs to be held in the outer gill marsupia. Anderson and Ingham added that the thicker shell of female *Lampsilis* might provide protection as the inflated form of the shell generally would be less resistant to wave action or stream currents.

For other unionaceans (Johnson, 1946; Heard, 1975; Dudgeon and Morton,

1983) including hyriids (McMichael and Hiscock, 1958; Walker, 1981b), females may also be more inflated than males. The dimorphism, however, is far less conspicuous than in lampsiline unionids, and if present at all, may only be detected by statistical testing. Ecophenotypic variation in shell morphology is generally assumed sufficient to mask any tendency for sexual dimorphism in these groups.

Unionacean shell form may be markedly influenced by ontogeny, and bivariate analysis between standard variables generally reveals allometric relationships (Eagar, 1978). Relative height and obesity for example, may either increase or decrease with growth (Eagar, 1948). In relation to obesity, Ortmann (1920) and Ball (1922) recorded that young unionids were more obese than older specimens. Agrell (1949) and Crowley (1957) nevertheless, reported that juveniles of the respective unionids studied, were less obese than full-grown specimens. In stream-forms at least, however, generally a decrease in relative height with age can be expected, with progressive development of dorsal arching of the shell (Evermann and Clark, 1917; McMichael and Hiscock, 1958; Clarke and Berg, 1959; Hendelberg, 1960; Bjork, 1962; Roscoe and Redelings, 1964; Walker, 1981b). Eagar (1948) remarked that changes in one shell dimension appeared almost invariably to be accompanied by changes, possibly compensatory, in other shell dimensions. Agrell (1949) and Hendelberg (1960) for example, reported that relative height and obesity were positively correlated.

Because environmental influences which mould shell form are expressed only in older individuals, such specimens give the characteristic 'reaction form' (Eagar, 1948), and most workers have included only the older shells in their calculations. Indeed several authors have stressed that material should only comprise individuals which have been subjected to environmental influence for a sufficiently long period of time (e.g. Agrell, 1949). van der Schalie and van der Schalie (1950) and Cvancara (1963) added that a source of variability in many shell form-environment studies could be due to using shells of variable age.

In relation to sexual and ontogenetic variability, Tevesz and Carter (1980a) sounded a cautionary note to studies where unionacean shell form was used as an indicator of environmental change. Because of such variability, habitat segregation of different age classes or sexual morphs for example, could result in morphologically distinctive groupings that might be correlated with, but not necessarily causally related to environmental factors. They added that correlation between relative shell dimensions added to the difficulty in distinguishing between fortuitous, rather than causally related, correlations between shell form and environment.

APPENDIX 2

DISTRIBUTION AND ABUNDANCE

A2.1 Factors affecting the distribution of freshwater mussels

A2.1.1 Broad geographical dispersal

Transport by fish in relation to sea level changes, stream confluences, and coastal flooding as well as transport by animals other than fishes have been considered to be important factors in relation to broad geographical dispersal (van der Schalie, 1945; Clarke, 1973; Sepkoski and Rex, 1974; Walker, 1981b). There has been debate as to whether stream confluence is the best explanation for the natural distributional patterns observed (van der Schalie, 1945, 1963) or whether it is only one of several ways by which mussels have dispersed from one drainage system to another (McMichael and Hiscock, 1958; Walker, 1981a). With respect to dispersal by animals, attachment to the feet of, or undigested fish material carried in waterfowl have been suggested as significant dispersal mechanisms of freshwater mussels - particularly of some species within the Australasian region (McMichael, 1958; McMichael and Hiscock, 1958; Walker, 1981a).

Other than the aforementioned means of broader geographical dispersal, other ecological and physiological factors are involved in between- and within-drainage distribution, and that of the microhabitat preferences of a species. Factors involved can be grouped into biotic, hydrological and physicochemical categories. The relationship of the physicochemical environment in determining the range of a single species is poorly understood (Fuller, 1974; Haukioja and Hakala, 1974). Inconsistent or contradictory reports of relative importance of the various factors in determining the distribution and abundance of freshwater mussels have led some (Fuller, 1974; Tevesz and McCall, 1979) to consider that many species have quite broad tolerances for different water types and habitats. Anodonta for example, is an ubiquitous North American genus that is seemingly indifferent of water type (Fuller, 1974; Green, 1980). Nevertheless, other species have a limited geographical distribution and/or apparent habitat restrictions. Margaritifera margaritifera has a holarctic distribution but within its range is restricted to unpolluted and perennial, softwater streams (generally acidic in nature) in localities free of silt deposition (Boycott, 1936; Hendelberg, 1960; Björk, 1962; Roscoe and Redelings, 1964; Stober, 1972; Bauer, 1983). Even for this species, however, there is some doubt as to whether the distribution is limited by water hardness per se, and exceptions to the softwater occurrence have been noted (Boycott, 1936; Björk, 1962). In Middle Europe, the species is considered a glacial relict and physiographic isolation from a former, broader circumpolar distribution has been used partly to explain its apparent stenotopy (Jungbluth, 1978).

A2.1.2 Biotic relations

The most important biotic relationship and chief dispersal phase of freshwater mussels are with the brief parasitic period of the larval glochidium upon fish. As noted by Walker (1981a), few references have

been made to the role of fish in mussel dispersal, mainly because little is known of the host preferences of particular mussel species. Kat (1984), however, presented a thorough review of parasitism in unionacean bivalves. He concluded that the parasitic relation between the mussel and its host fish, would tend to reduce the unpredictability of the freshwater habitat as it applied to the juvenile mussel. Because of their specialised habitat requirements (by comparison with other freshwater bivalves), Kat thought it would be of advantage for unionaceans to form an association with a fish that shared the same habitat requirements, so that dispersal over long distance occurred with much more habitat fidelity.

Apart from their broad ecological tolerances, it is a noted feature of widely distributed and abundant species (e.g. *Anodonta* in North America (Fuller, 1974; Trdan and Hoeh, 1982), *Velesunio ambiguus* in southeastern Australia (Walker, 1981a,b)) that they parasitise a large number of host fishes. In relation to broad geographical dispersal, however, rarely are the ranges of distribution of mussel species and their host fishes the same. Generally the mussel's range is smaller than that of the host suggesting that other factors act to exclude mussels from their potential range (van der Schalie and van der Schalie, 1963; Strayer, 1983). Walker (1981a) made similar comments with respect to the geographical range of waterfowl, considered to be possibly important passive agents of dispersal of Australian freshwater mussels.

Within a drainage system, fish hosts are regarded as especially significant in determining presence or absence of mussels (van der Schalie, 1938). Examples of abrupt cessations in the distributions of both mussels and their fish hosts above barriers such as waterfalls are cited in evidence of this (Fuller, 1974). Isolated but general accounts imply that fish hosts are even more significant in determining local distribution of mussels. The recruitment of young in particular sites of a stream (e.g. eddies, along edges of reed beds) for example is claimed to be directly affected by the habits and activities of fish hosts (Coker *et al.*, 1921; Negus, 1966; Cvancara, 1967, 1970). Cvancara (1970) believed that fish hosts were of more importance than bottom type in determining distribution of mussels in the Red River Valley (USA) as many species of mussels occurred on a variety of substrate types. Differences in the species composition of mussels between localities of a Swedish stream were thought by Norelius (1967) to be related only to host fish distribution at the time of metamorphosis. For lake populations, Kenmuir (1980) thought the local abundances of two species of mussel in tropical Lake Kariba (Zimbabwe) were more directly influenced by the habits of their fish hosts than by any other factor. Finally, Strayer *et al.* (1981) could find no physical or chemical factor to account for the low density of mussels in an oligotrophic lake in New Hampshire (USA) and hinted at fish host limitation, as fish in oligotrophic waters were likely to be scarce.

The relationship between freshwater mussels and their fish hosts in determining mussel distribution is obviously important but poorly understood. As commented aptly by Strayer *et al.* (1981): "It would be desirable to have more information on the role of fish-mussel relations in mussel population dynamics."

Other significant biotic effects upon mussel distribution include mammalian predation. Published accounts describe how muskrats in North America can feed heavily upon mussels and in fact severely restrict the shallow water distribution of some species (reviewed in Fuller, 1974; Strayer, 1983). In both North America (Fuller, 1974) and Australia (Walker, 1981b) consumption by aboriginal man is considered to have had a significant effect on mussel populations in the past.

Other bivalves may affect the local distribution of freshwater mussels. Three lampsiline species occur in Lake Waccamaw, eastern North and South Carolina (USA); the percentage of samples having a lampsiline was increased if other lampsiline species were present suggesting a gregariousness among the three species (Porter and Horn, 1983). While no causal mechanism was suggested by Porter and Horn, clumping of conspecifics was previously thought by Tudorancea and Florescu (1968) to represent an adaptation ensuring successful fertilization. Clumping of conspecifics may result from environmental heterogeneity but also can occur in homogeneous environments, which has often been reported but rarely quantitatively assessed, as done by Kenmuir (1980) and Salmon and Green (1983).

Filter-feeders are generally assumed not to partition the environment for food and space (Kraemer, 1979). Competitive advantage according to Fuller (1974) was no more than a superior reproductive ability of some mussel species. Tevesz and McCall (1979) in reviewing literature concluded that niche widths of unionids were much broader than marine filter-feeders and attributed this to a relative absence of predation and competition in the freshwater environment. Strayer (1981) in explaining the broad microhabitat tolerances of unionids in some Michigan (USA) streams, attributed them in part to the absence of competition in these environments where densities were low and space and food superabundant.

Nevertheless, it is the belief of others, that competitive exclusion between bivalves is real, and that competition is reduced and species diversity greatly increased through both spatial and temporal partitioning of the environment. In evidence, Harman (1972) and Sickel (1980) cite substrate preferences of species in lakes and streams; Green (1971) used multiple discriminant analysis of bivalve lake molluscs in central Canada to show that separation was primarily on a trophic basis; Stern and Felder (1978) and Trdan and Hoeh (1982) cite spatial and temporal differences in encystment of larvae of sympatric unionids on host fishes in evidence of resource partitioning to reduce competition for available hosts. The pattern of distributional segregation of two unionid species in a Swedish lake outlet, led Bronmark and Malmqvist (1982) to conclude that interspecific interactions were suppressing establishment of young conspecifics and the other species in a very productive habitat. Finally, in undisturbed river habitats in North America, Kraemer (1979) argued that Corbicula, an introduced bivalve, competed with indigenous freshwater mussels for substrate.

The final significant biotic factor of consideration is the influence of vegetation on mussel distribution. Invariably, rooted vegetation is reported to have a negative influence on mussels (Coker *et al*, 1921; Boycott, 1936; Pennak, 1953; Tudorancea and Florescu, 1968;

Cvancara, 1972; Fuller, 1974). A number of factors are considered to contribute to the restricted distribution of mussels by vegetation: plants and their decayed material contribute to finer, less consolidated sediments in which to burrow; plants may compete with mussels for bottom space; restrict movement of mussels; interfere with glochidial and juvenile settlement; and effect water movement so modifying the oxygen regime and delivery of food (Coker *et al.*, 1921; Tudorancea and Florescu, 1968; Cvancara, 1972, Bronmark and Malmqvist, 1982). Only Salmon and Green (1983) have reported a positive association of rooted vegetation and mussel distribution and abundance. In the lotic environment under study, they implied that vegetation stabilised the microhabitats of mussels by decreasing water turbulence. In a newly created tropical lake (Lake Kariba, Zimbabwe) the benthic habitat (including a lamellibranch population - *Corbicula*) was markedly enriched after invasion of three plant species (McLachlan, 1969). Significantly, the large freshwater mussel population of the lake (Kenmuir, 1980) was not part of the association. In other lentic studies, only those by Lewandowski and Stanczykowska (1975) and Fisher and Tevesz (1976) have reported no association, positive or negative, between mussel density and aquatic vegetation.

A2.1.3 Abiotic relations

Depth

Quantitative descriptions of mussel distribution and abundance in relation to water depth are comparatively recent (Cvancara, 1972) and follow initiation of SCUBA investigation and the ease and accuracy with which it has contributed to study.

In lakes, the relationship is a predictable one and a preferred depth range is sought by most species, from occurrence in minimum depths of 5-8 cm of water (*Lampsilis radiata siliquoidea* in the Canadian Interior Basin (Clarke, 1973)), to a maximum of between 18-31 m (*Anodonta grandis* in Lake Michigan USA (Reigle, 1967)), and 30 m (*Elliptio complanata* in central New York lakes, USA (Harman, 1970)). Within the preferred depth range, an optimal depth - generally shallow, is reached by most species at which densities are at a maximum and beyond which densities steadily peter out (Okland, 1963; Cvancara, 1972; Haukioja and Hakala, 1974; Lewandowski and Stanczykowska, 1975; Fisher and Tevesz, 1976; Ghent *et al.*, 1978; Kenmuir, 1980; Green, 1980; Strayer *et al.*, 1981). As a general rule found by these same authors, the optimal or preferred depth does not exceed 3 m for species so far studied, although *A. grandis* in Lake Bernard, Ontario (Canada) reaches maximum densities between 2.5-12 m (Ghent *et al.*, 1978) and species in tropical Lake Kariba (Zimbabwe) occur between 3-12 m (Kenmuir, 1980).

Causal factors in the pattern of depth distribution in lakes have generally only been hypothesized. Exposure, temperature extremes, wave action, silt-recirculation and predation are believed to restrict mussels from marginal zones (Coker *et al.*, 1921; Matteson, 1948; Fuller, 1974; Marshall, 1975; Fisher and Tevesz, 1976; Kenmuir, 1980; Green, 1980). Finer, silty and unconsolidated sediments; low dissolved oxygen; decreasing water temperature (thus slowing metabolism, reproduction and growth; less water turbulence to bring and keep in suspension living or dead food material; reduced light

penetration and its effect on living food; increasing water pressure; the absence of fish hosts at depth; and changing water chemistry, with increasing depth - all have been suggested as important factors restricting mussels to relatively shallow waters (Cvancara, 1972; Fuller, 1974; Haukioja and Hakala, 1974; Fisher and Tevesz, 1976; Ghent *et al.*, 1978; Kenmuir, 1980; Strayer *et al.*, 1981).

Surprisingly, little attention has been paid to the role of low dissolved oxygen in explaining the absence of mussels at depth, although the lakes in question are generally claimed to be adequately oxygenated. Coker *et al.* (1921) and Fuller (1974) stress its importance in general statements. Okland (1963) observed periods of inferior oxygen conditions in the deeper parts of Lake Borrevann, Norway but did not draw any conclusions between this and the corresponding absence of mussels. Plover Cove in tropical Hong Kong experiences seasonal deoxygenation of the hypolimnion in the dry season. As *Anodonta woodiana* is distributed in the shallow waters near the margins of this reservoir, Dudgeon and Morton (1983) considered it unlikely that the species would experience the same wide fluctuations in oxygen concentrations. Mussels occur over a wide range of depths (3-12 m) in the waters of Lake Kariba, Zimbabwe, (Kenmuir, 1980); the waters of this lake are adequately oxygenated at most depths but the oxygen levels at greater depths (> 11 m) are thought too low for both mussels and their fish hosts to survive. In man-made impoundments the effects of low dissolved oxygen have received some attention. Bates (1962) attributed the gradually diminishing fauna in the Kentucky Reservoir, Tennessee River (USA) partly to decreasing oxygen tensions. In a similar vein, Isom (1971) attributed the net loss of 60 species of mussels in the Fort Loudon Reservoir (Tennessee R.) to periodic oxygen sag.

Study of the depth distributions of mussels in lotic environments is not as relevant as in lentic environments because, as emphasised by Stern (1983), depth is no more than a reflection of current velocity and substrate type. Thus both Haukioja and Hakala (1974) and Stern (1983) report in lotic distributional studies that bottom type is more significant than depth in determining distribution. Negus (1966), however, found a lake-pattern of distribution of mussels in the Thames River, England. No causal factors were suggested but presumably water turbulence in the central (and deeper) portions was one factor. Both unsuitable bottom type and strong water currents restrict mussels to shallow waters in the Neva River, Rumania (Tudorancea and Gruia, 1968). Similarly, the shallow water occurrence of mussels in the Middle Thames River, Ontario was attributed to advantages of associated low currents (Salmon and Green, 1983). In contrast, mussels in a Swedish lake outlet occurred in largest numbers in the central, deepest portions where Bronmark and Malmqvist (1982) believed reduced chances of desiccation, more food and less vegetation to restrict movement made this environment more favourable. (Water turbulence and velocities in the central portions of the outlet presumably never exceeded levels at which mussels are physically displaced.)

In a manner akin to tropical, monsoonal drainages, the Crapina-Jijila marshes of Rumania receive annual floodwaters from the Danube River. The annual flooding modifies the distribution and abundance of freshwater mussels in the marshes; during the flooding mussels are

widely dispersed, but undertake extensive migrations as the waters subside. Thus, densities are greatest at the end of the subsidence period when waters have contracted. If flooding subsidence is too rapid, mussels may be stranded, severely affecting populations (especially new recruits) in some years (Tudorancea and Florescu, 1968; Tudorancea, 1972).

Finally, in relation to water subsidence and shallow water effects, Marshall (1975) noted that apart from stranding large numbers of mussels in shallow regions, added implications of extreme water level fluctuations typical of impoundments in Zimbabwe are the marked effects on water chemistry. Although the tolerance limits of some species of mussels to high water temperatures have been determined specific evidence of the restriction of freshwater mussels from shallow waters by high water temperatures is lacking. The general statements made earlier are the only references to the effects of high water temperatures upon mussel distribution.

Hydrology

There is a considerable literature on the influence of hydrological factors (water body type, substrate and/or flow regime) on freshwater mussel distribution and abundance. Much of the material is descriptive, and from recent quantitative studies, especially in relation to habitat preferences, some conclusions may be misleading or contradictory.

It is a commonly observed phenomenon that the freshwater mussel fauna of larger streams and lakes with regular water renewal, are more abundant and diverse than of smaller tributaries, ponds or still lakes (Evermann and Clark, 1917; van der Schalie, 1938; Pennak, 1953; Cvancara, 1967; Green, 1972; Sepkoski and Rex, 1974; Kenmuir, 1980). The wider range of available habitats in larger waterbodies and in particular, where there is a continuous and strong current in large streams, are generally thought to enhance faunal development. Boycott (1936) adds that larger bodies of water may also contain more species by virtue of the fact that the chances of importation have been greater.

The effects of current in relation to bringing about faunal enrichment have been ascribed to the constant supply and change in oxygen, food and minerals and to the enhancement of fertilization (Evermann and Clark, 1917; Coker et al., 1921; Boycott, 1936; Pennak, 1953). In the absence of significant flow (that is, in lakes and impoundments, intermittent streams or streams of low discharge), the mussel fauna is often observed to be impoverished, a factor variously attributed to resultant low dissolved oxygen, high water temperatures, desiccation, increased concentration of salts, predation and fewer fish hosts or the restriction of their dispersal at low discharge (Coker et al., 1921; Cvancara and Harrison, 1965; Norelius, 1967; Cvancara, 1967, 1970; Imlay, 1973; Horne and McIntosh, 1975; Kenmuir, 1980; Strayer, 1983). The effect of discharge is considered particularly important in the Crapina-Jijila marshes of Rumania, where mussel recruitment is mainly influenced by flooding of the Danube River. Years of significant and long lasting floods enhance development of mussel populations through phytoplankton blooms (Tudorancea, 1969, 1972).

References to the habitat preferences of different species are numerous but often general in nature, describing broadly (and occasionally specifically) how each species is more commonly found in a particular type of waterbody, or in particular conditions or regions of the waterbody (Coker et al., 1921; Boycott, 1936; van der Schalie, 1938; van der Schalie and van der Schalie, 1950; Cvangara and Harrison, 1965; Clarke, 1973). Quantitative measures of the habitat preferences and specific requirements of species in relation to broad dispersal are uncommon. Studies by Green (1971, 1972) and Strayer (1983), represent the only attempts of defining niche or habitat requirements over a wide geographical range.

Within a particular drainage system, studies on the habitat and microhabitat preferences of species are common, and often diverse in findings - particularly in regard to substrate preferences. Some bottom types are inimical to the establishment and maintenance of mussel communities. Mussels are rarely found on shifting sand or silt, bare rock or unconsolidated muds and silts - substrates in which the foot cannot penetrate and function effectively as a holdfast structure or into which mussels would rapidly sink and asphyxiate (Ellis, 1931; Boycott, 1936; Clarke and Berg, 1959; Marshall, 1975; Fisher and Tevesz, 1976; Strayer et al., 1981; Suloway, 1981). With respect to soft and unconsolidated muds, Kat (1982) found that even though a species might occur in these (e.g. Elliptio complanata), the constant energy expenditure needed to maintain a station effectively lowered the fitness of individuals, as shown by reduced growth rates resulted. Kat regarded these substrates therefore, as low quality microhabitats. Yet it is this degree of tolerance to soft substrates that partly explains the broad distribution of some species of freshwater mussel. Anodonta grandis for example, can live in softer, siltier bottoms than most other species (Evermann and Clark, 1917; Ghent et al., 1978), an adaptation contributing to its widespread occurrence in lakes.

The shape and size of particular species may determine their habitat requirements. The lightweight and ovate shell of A. grandis for example, enables the species to 'float' upon fine silty muds (Ghent et al., 1978). The swollen shell of Velesunio ambiguus may perform a similar function in similar habitats in Australian waterways (Walker, 1981b). Various other reports draw attention to the occurrence of larger and heavy-shelled species in headwaters, large rivers or wave swept shores of lakes in correspondingly coarser substrates, and of smaller and/or thin-shelled species in quieter and siltier, muddy environments (Jewell, 1922; Coker et al., 1921; Clarke and Berg, 1959; Ghent et al., 1978; Horne and McIntosh, 1979). It has been generally suggested that larger and heavier shells assist in maintaining the station of mussels in turbulent environments. Horne and McIntosh (1979) correlated the flow patterns and corresponding type of stream bottom with the distribution of various sized species in the Blanco River, central Texas (USA). Coon et al. (1977) considered that the number of heavy-shelled species in pools of the Mississippi River had increased in recent times as these were probably better able to anchor in the relatively unstable sand substrates that have developed over the same period.

Between the extremes of inimical substrates, from clean sand/soft silt to coarse gravel/stiff clay, Coker et al. (1921) believed there was a

great variety of bottom types that could be used by various species of mussels. Yet they considered that bottom type was of first importance in governing distribution in rivers at least. In more recent studies, bottom type has been considered important in determining mussel distribution and abundance (Harman, 1972; Haukioja and Hakala, 1974; Fisher and Tevesz, 1976; Horne and McIntosh, 1979; Sickel, 1980; Bronmark and Malmqvist, 1982; Stern, 1983; Salmon and Green, 1983) or unimportant (Cvancara and Harrison, 1965; Dean, 1968; Cvancara, 1970, 1972; Green, 1971, 1972, 1980; Tevesz and McCall, 1979; Walker, 1981b; Strayer, 1981; Kat, 1982; Porter and Horn, 1983).

Some apparent discrepancies in conclusions of the above studies can be accounted for and qualified as follows. Absence from inimical substrates and maintenance of location in others - according to the shape and size of species, can account for much of the published work relating to apparent selection of bottom type by different species. Nevertheless, although substrate type is generally recognised as a reflection of the flow regime or local turbulence, emphasis often tends to be placed, in lotic studies at least, on "preference" or "selection" for sediment type per se rather than any regard for the physiological tolerances of species to some condition which is related to relative water movement - such as oxygen availability. A much cited work is that of Harman (1972) who concluded that the type of substrate influenced species distributions of molluscs. While his study dealt mostly with gastropods, in relation to freshwater mussels he considered that their needs were soft but firm substrates in which to anchor. Harman (1972) listed quite specific sediment requirements of several species which in earlier studies in the same region (Clarke and Berg, 1959; Harman, 1970) were reported to be broader. Further, both a progressive increase in mussel species and substrate type were noted in three lakes studied. Harman (1972) admitted, however, an increase in the trophic status over the three lakes that may have contributed to the observed distributional patterns; also, in the largest lake, the dispersive capabilities were much greater.

Other than species size being correlated with occurrences in particular substrates, the study by Bronmark and Malmqvist (1982) concluded that particle size of the sediments was important in determining distributional patterns of Unio pictorum. The presence of the species was positively correlated to particles of size 0.25-0.5 mm; smaller particles were thought to interfere with feeding and respiration while larger particles were believed to interfere with locomotion.

Tevesz and McCall (1979) presented the most convincing conclusions in relation to the bottom type requirements of freshwater mussels. Within the accepted provisions of soft, yet firm substrates, their reviews of past surveys and studies led to the conclusion that the requirements of most species are in fact quite broad. Selection within the variety of bottom types that can be used by the various species, are most readily explained in terms of (a) mussel shape and size and resultant stability of location, and (b) physiological tolerances of various species to varying flow regimes, themselves expressions of oxygen status at least.

In studies of the microdistribution of freshwater mussels in lotic environments, flow patterns have been found to be important

determining factors. The absence of mussels from too vigorous and turbulent currents has been mentioned previously. Where currents are less vigorous, studies have shown relationships between mussel distribution and current strength. Mussels in the Middle Thames River, Ontario were most often found in stable, low current regions where Salmon and Green (1983) considered minimal turbulence, a steady food supply, minimal siltation and enhanced reproduction as optimal conditions for the presence of mussels. Similarly in the Murray River (Australia), Walker (1981b) found mussels grouped in gentler currents along the innermost margins of meanders or in regions of sharp bends where the flow changed abruptly. Otherwise and in presumably stable substrates, the characteristic habitat of various mussel species from other lotic studies, has been found to be along banks, in the centre, or in other sites exposed directly to the current (Evermann and Clark, 1917; Björk, 1962; Cvancara *et al.*, 1966; Simmons and Reed, 1973; Bronmark and Malmqvist, 1982; and earlier references to Margaritifera margaritifera). Such locations are generally believed to provide optimal conditions for extracting food, soluble mineral materials and oxygen from the water; Evermann and Clark (1917), Roscoe and Redelings (1964) and Cvancara *et al.* (1966) reported further evidence of this in the observations that most mussels in their study sites were oriented with siphons directed upstream or directly into the current.

Good evidence of the flow requirements of some essentially riverine mussel species is provided in the observations of the local occurrences in man-made impoundments. Marshall (1975) and Kenmuir (1980) found highest numbers and largest sizes of mussels in Lake McIlwaine and Lake Kariba, Zimbabwe respectively, in the river section of the lakes, attributing the observed distributions partly to increased numbers of fish hosts and to an absence of or nevertheless tolerance by mussels to siltation in the river section. Walker (1981b) considered water flow the single most important determinant of the distribution of the two species of mussel in the Murray River. Vesunio ambiguus occurs in slow-flowing and still waters while Alathyria jacksoni is characteristic of areas of moderate to strong currents. In an irrigation reservoir on the river (Lake Mulwala), A. jacksoni predominates along the old river channel where water continues to flow most strongly while in the surrounding quiet water, V. ambiguus is dominant.

Walker (1981b) suggested that the presence or absence of the above species from particular flow regimes was more directly related to their oxygen requirements. V. ambiguus could survive in deoxygenated water for short periods, while A. jacksoni was intolerant of short period anoxia. Mention has been made of the study of mussels in the Blanco River, central Texas in which Horne and McIntosh (1979) found species distributed according to a correlation between increasing shell size and stream velocity. The authors observed in addition, that the most tolerant species of low dissolved oxygen were found in habitats away from faster water, while the least tolerant were generally confined to swifter flowing habitats. Both studies suggest that much can be learnt of the habitat requirements of freshwater mussels when their oxygen requirements and tolerances to low dissolved oxygen levels are fully evaluated.

Final consideration of the habitat requirements of freshwater mussels must account for the life habits of juveniles. Almost invariably it

is remarked in studies of mussels, that juveniles are rarely found. Apart from the difficulties in collecting small mussels and their rapid growth rates (section 3.2.1), their scarcity is generally attributed to their sensitivities and vulnerability to stresses and predation, or to their quite different habitat requirements (Lefevre and Curtis, 1910; Isely, 1911; Coker et al., 1921; D'Eliscu, 1973; Fisher and Tevesz, 1976; Kenmuir, 1980; Green, 1980).

Bottom type, streamflow and turbulence, and water depth are factors considered of prime importance in determining distribution of juvenile mussels. Isely (1911) found juveniles of various riverine species in fairly swift water from a bottom of coarse gravel. He suggested such environments provided a constant supply of food and oxygen, were frequented by fish and were free from shifting sand and silt accumulations. Negus (1966) found other riverine juveniles along the edges of reed beds and beneath landing stages, in sediments of fine shelly gravel, rich in organic matter. Such habitats were places where fish were known to congregate, and the sediments were silt free. Howard (1922) believed that species generally required clean, silt-free bottoms for survival, yet successfully raised one species (Lampsilis luteola) in crates in the Mississippi River, despite an accumulation of 2-3 cm of silt over the juveniles per week. As the crates were located in current-swept reaches of the river, the influence of adequate oxygen supply is almost certainly implicated in juvenile survival, especially as young mussels generally are known to be more susceptible to low dissolved oxygen levels than adults (Ellis, 1931). Water depth in most environments is mentioned as an important requirement (Isely, 1911; Coker et al., 1921; van der Schalie, 1938; Matteson, 1955; Green, 1980) and young mussels are often reported to occur in shallow waters close to the water margins. Finally, Isely (1911) and Coker et al. (1921) believed that any consideration of ecological factors inimical to mussel life should be directed towards the juvenile habitat as adults could live in environments where young would perish.

Physicochemical limnology

Fuller (1974) has provided the most recent review on the effects of physicochemical parameters on the physiological ecology, and levels for successful maintenance of unionid mussel populations. Most attention has been directed (in the chemical ecology of mussels) on the influences of water hardness and salinity in determining mussel distribution. However, the influence of any chemical factor in determining distribution is poorly understood for there has been scant work on the limits of tolerance of mussels for any chemical parameter.

The availability of dissolved calcium carbonate, important in shell formation, has in the past been considered critical to the maintenance of mussel populations (Coker et al., 1921; Boycott, 1936; Pennak, 1953; Clarke and Berg, 1959; Tudorancea, 1972; Isom and Yokley, 1973). Fuller (1974) agreed that hardness (as CaCO_3) was essential to mussel development but added that no published levels were available at which hardness determined presence or absence of a particular species. Fuller (1974) cited studies which gave limiting levels of various chemical parameters that reflected availability of dissolved CaCO_3 , to the unionid fauna of particular regions, but listed other works which recorded their presence at much lower levels. While the broader

geographical distribution of some species is believed to be determined by hardness (Boycott, 1936; Clarke, 1973), nevertheless other contrary findings are available in the literature - for example, the significance (Coker *et al.*, 1921) or insignificance (Sepkoski and Rex, 1974) of water hardness in determining mussel distribution in the Atlantic slope waters of eastern United States, or more locally its importance (Clarke and Berg, 1959) or unimportance (Harman, 1969; Harman and Berg, 1970) in central New York state (USA). Evidence to show the reliance of a single species upon calcium and/or carbonate availability is very limited. Green (1972) used multivariate statistics to show that the distribution of Lampsilis radiata in some central Canadian lakes was apparently influenced by carbonate availability. The remaining studies pertain to the occurrence in and tolerance of other species to softwaters: Margaritifera margaritifera is found in softwater lakes and streams (referenced earlier); Green (1980) stated that Anodonta in North America commonly occurs in softwaters; and Strayer (1981) argued that lack of calcium (2-3 mg/l) was not a factor limiting the population of Elliptio complanata in Mirror Lake, New Hampshire (USA).

A suggested means by which soft, poorly buffered waters may affect mussels, is indirectly as the result of freely available carbonic acid, which in harder waters combines with calcium in solution to form bicarbonate (Coker *et al.*, 1921; Harman, 1969; Fuller, 1974). Fuller (1974) summarised studies relating to the adverse physiological effects of low pH upon mussels. Apart from observed effects of valve erosion at low pH, however, (Coker *et al.*, 1921; Jewell, 1922; van der Schalie, 1938; Tudorancea, 1972) distributional studies are mixed in findings and suggest if anything, an indifference by species to acidity. In a naturally acid stream in Illinois (USA) (pH 5.6-6.8), Jewell (1922) recorded 9 species, apparently abundant and influenced more by bottom characteristics than by water type. The lack of mussels in the acid-degraded zone of a polluted stream receiving acid drainage in Virginia, was thought by Simmons and Reed (1973) to be caused by effects of siltation and altered fish populations rather than any direct effect of acidity. In river systems on the eastern seaboard of the United States, Sepkoski and Rex (1974) found a significant correlation between hydronium concentration and species numbers, believing the result accounted for the low numbers of species in two rivers of high acidity. The rivers ranged in pH from 4.3 to 5.9, but were, however, also high in chlorides (Johnson, 1970), a chemical factor also believed to be restrictive to mussels (Cvancara, 1967, 1970). Matteson (1955) placed mussels in a strongly acidic lake (pH 4.4-6.1) and noted that their reaction over a period was akin to that of aestivation, with the valves tightly closed. The findings of Jewell (1922) mentioned earlier, however, suggest that residents may behave differently. Harman (1969) thought that in central New York streams, reduced abundances of mussels were not caused by the low levels of water hardness, as much as by the rapid (and detrimental) changes in pH values associated with the soft waters. Finally, other species have been noted to be specifically tolerant of or actually partial to, acid waters: Margaritifera throughout Europe and North America (see earlier references and especially Bauer, 1983); Anodonta in North America is often found under acidic conditions (Green, 1980); and the density of Leptodea ochracea in Lake Waccamaw, North and South Carolina (USA) was found by Porter and Horn (1983) to be negatively correlated with increasing pH.

Of the chemical factors limiting mussels in the Red River Valley in North Dakota and Minnesota USA, Cvancara (1967, 1970) believed chloride content to be ecologically most significant. In the Turtle River, no live mussels were recorded at chloride levels of 87 ppm or more, derived from surrounding saline soils (Cvancara and Harrison, 1965). Sepkoski and Rex (1974) found a significantly negative correlation between dissolved solids and species number of mussels in streams of the Atlantic coast (USA), but could not interpret the result other than perhaps representing low species numbers in the saline drainage systems of Florida. Green (1972) found that part of the ecological separation of Lampsilis radiata and Anodonta grandis in central Canadian lakes had to do with the high sensitivity of A. grandis to sodium chloride. For both species, high NaCl concentration had an apparently deleterious effect on shell deposition. In South America, the distribution of Hyriidae is correlated with salinity, and mussels are absent when salinity exceeds 2500 ppm (Bonetto *et al.*, 1962). Dean (1968) showed a similar restriction of Hyridella drapeta in Victorian streams (Australia) to salinities less than 300 ppm.

In the Murray River, prevailing salinities are generally high from returning irrigation water, but are nevertheless not of sufficient concentration to affect the two resident species, Velesunio ambiguus and Alathyria jacksoni. Both species are thought unlikely to be affected by salinities below 3.5 g/l (Walker, 1981b). Other occurrences in relatively saline waters were recorded for Anodonta woodiana in tropical Plover Cover Reservoir (Hong Kong); Dudgeon and Morton (1983) recorded their initial presence in the reservoir in 1972 when chloride levels ranged between 100-200 mg/l (Morton, 1977).

Imlay (1973) found that unionaceans were highly sensitive to the direct effects of potassium and believed high natural levels (>7 ppm) in waterways were responsible for the absence of mussels from certain regions in North America.

The effect of water depth and flow regime as a reflection of oxygen status and their bearing on mussel distribution has been discussed previously. Apart from the studies already mentioned, the role of dissolved oxygen in determining freshwater mussel distribution and abundance has received relatively little attention other than broad general statements. The factor may be unimportant in large perennial rivers. In other waterbodies its effect may only be felt at critical times of the year, necessitating seasonal measurement and precluding spot, isolated measurements typical of most studies.

Apart from the broad correlations made by Horne and McIntosh (1979) and Walker (1981b) between physiological tolerances to low dissolved oxygen of particular species, and their habitat requirements, Fuller (1974) has summarised enough studies to further demonstrate the broader tolerances of quiet water species over characteristic riverine species. Selected pool species in North America (Amblema plicata and Anodonta spp.) were tolerant of anoxia for at least short periods, other riverine species required 2.5 ppm of dissolved oxygen for survival (Fuller, 1974). Kenmuir (1980) found that Caelatura mossambicensis, a deep pool species in Zimbabwe, could survive dissolved oxygen levels of 2 ppm, but succumbed below this level. Forty seven percent of the mostly fluvial mussels tested by Horne and

McIntosh (1979) were dead after 7 days at dissolved oxygen levels of between 0-0.5 mg/l. Ellis (1931) stated that young mussels were very sensitive to oxygen reduction, and that adults became inactive when oxygen tension was reduced to 20% saturation or less.

Fuller (1974) cited the work of Grantham (1969) who found no mussels in the Mississippi River where dissolved oxygen occasionally dropped as low as 3 mg/l. In the Fort Loudon Reservoir, Tennessee River, dissolved oxygen content of water near the bottom averaged about 3 mg/l with periodic lows of less than 1 mg/l when measured in the summers of 1965-68. The same regions have recorded a catastrophic loss of 60 native endemic mussels since impoundment (Isom, 1971). Kenmuir (1980) recorded no mussels in Lake Kariba at depths greater than 11 metres. Oxygen levels at these depths could fall below 2 ppm, concentrations known to be lethal to the mussels of the lake. The absence of mussels from organically rich pools below a sewage effluent in the Blanco River, Texas (USA) was attributed to periods of slow moving waters which could experience extreme fluctuations in oxygen concentrations (Horne and McIntosh, 1979). In organically enriched streams, Gaufin and Tarzwell (1952) believed that nocturnal deficiency in dissolved oxygen was the critical factor determining the distribution of stream organisms, especially when modified by seasonal flow characteristics (Tarzwell and Gaufin, 1953). Finally, one consequence of anoxia is the production of hydrogen sulphide from decomposition of non-living organic material. While nothing is known of its effect on freshwater mussels, it is at least harmful and toxic to fish (Ellis, 1937).

Reference has previously been made to the evidence for and against the limitation on mussel distribution by food availability, and the trophic separation of bivalves to avoid competition. Other studies have implicated trophic factors as the causes of increased species diversity and abundance in some regions: Clarke and Berg (1959) observed that sandy, shallow and eutrophic lakes in New York state were the most productive with respect to mussel species and densities; Okland (1963) found highest densities of mussels in Lake Borrevann, Norway, in the eutrophic shallows and summarised other work that found that the population density of Anodonta piscinalis in European lakes increased with increasing degree of eutrophy; in coastal streams of eastern United States, Sepkoski and Rex (1974) found a significant correlation between species number and nitrate concentration; and in Lake Kariba, Kenmuir (1980) found highest densities of mussels in waters of highest trophic status.. Whether food limitation is the cause of low densities in oligotrophic waters, however, is questionable. Strayer et al., (1981) argued that food and calcium were not limiting in Mirror Lake, New Hampshire, a soft, oligotrophic lake, but that low mussel densities may have more to do with a corresponding paucity of fish hosts, also likely to be scarce in oligotrophic waters.

Excessive organic enrichment of waterways, however, has adverse effects on mussels. Fuller (1974) summarised the work of Starrett (1971) who found no mussels in the Illinois River (USA) wherever ammonia concentrations exceeded 6.0 ppm. In tolerance tests to ammonia on five species of local mussels from the Blanco River central Texas, Horne and McIntosh (1979) found levels of 5 mg/l ammonia (as $\text{NH}_4^+ - \text{NH}_3$) lethal to 40 percent of the mussels tested in 7 days. This

level of sensitivity was believed in part to explain the absence of mussels from organically polluted sections of the Blanco River. Lewandowski and Stanczykowska (1975) found no mussels in the vicinity of local sewage outflow into Lake Mikolajskie (Poland) at values of 20 mg/l ammonia (as $N-NH_4$).

The effect of turbidity, especially in its severest form, has received considerable attention in relation to freshwater mussel distribution. Cvancara (1967, 1970) suggested turbidity may possibly be important in restricting mussels from the lower sections of some tributaries in the Red River Valley (USA), but added that turbidity in the Red River itself is consistently high but yet large numbers of species apparently thrive in its waters. High turbidities and siltation characterise waters of the Murray River in Australia, yet Walker (1981b) could find no evidence of any adverse effects upon mussels and even suggested that siltation and erosion might conceivably provide more available habitats in the extensive silt-derived substrates. Further, Tevesz and McCall (1979) believed, after reviewing the literature, that the absence of bivalves from soft bottoms had nothing to do with any inability to feed and respire effectively in turbid waters.

In its most severe form however, i.e. unnaturally high turbidities of unnaturally long duration, detrimental and often catastrophic effects upon mussels are observed. Erosion silt is harmful to mussels in a number of ways: it screens out light thereby reducing the food supply; smothers out sedentary biota during periods of sudden inundations following floods; interferes with feeding, mussels remaining closed 75-90% of the time; and retains organic matter, carrying it to the bottom and thereby increasing the oxygen demand immediately above the stream floor (Ellis, 1931, 1936, 1937). Chutter (1969) adds that in regions of seasonal rainfall in South Africa, shifting silt and sand lead to shallowing and a resultant increase in temperature of the bottom waters, thereby indirectly and adversely affecting stream fauna. Wave-induced, silt-recirculation in the shallows of Lake Kariba was believed by Kenmuir (1980) to stifle young mussels and subsequent development of shoals there.

A2.2 Anthropogenic activities

Much attention has been directed to the steady decline of freshwater mussels in waterways since the 1900's particularly in the Mississippi River drainage, where commercial exploitation of valuable species has been greatest and distribution and abundance of many species significantly affected. In the Mississippi drainage, overharvesting and dam construction in particular, have led to serious declines in species abundance and diversity (Fuller, 1974).

The adverse effects of impoundments upon mussel fauna are well documented and include: siltation caused by the obstruction to flow; changes in the fish fauna both within and upstream of impoundments and the elimination of fish migration from downstream; changes from riverine mussel fauna to species typical of quiet waters; increased hydrostatic pressure; and decreases in oxygen tensions (Lefevre and Curtis, 1910; Ellis, 1931; van der Schalie and van der Schalie, 1950; Scruggs, 1960; Bates, 1962; Isom, 1969; Imlay, 1972; Yokley, 1972; Isom *et al.*, 1973; Fuller, 1974; Coon *et al.*, 1977; Kenmuir, 1980).

In Australia, the abundance of Alathyria jacksoni an essentially riverine mussel in the lower Murray River, is thought to have declined in relatively recent times as a consequence of the extensive impoundment of the river in this region (Walker 1981b).

Industrial, municipal or domestic pollution are often mentioned in general statements in studies, as affecting the decline of species in waterways (Coker et al., 1921; Ellis, 1931; van der Schalie, 1938; Clarke and Berg, 1959; Cvancara, 1967, 1970; Green, 1980; Suloway, 1981; Bauer, 1983). Bauer (1983) actually found a positive correlation between mortality rates of Margaritifera margaritifera populations in North Bavarian streams and the degree of organic pollution in the streams. Fuller (1974) reviewed the adverse effects of some pollutants, including wood product wastes, organic enrichment, acid mine wastes, and some heavy metals upon freshwater mussels. Other comprehensive studies and reviews on the effects of pollutants include acid drainage in the North Anna River (Simmons and Reed, 1973) and organic enrichment in the Blanco River, central Texas (Horne and McIntosh, 1979). The specific findings of these studies have already been discussed (section 5.1.1.3).

Finally, the introduction of the Asian clam, Corbicula manilensis, into North American waterways during the 1930's (Kraemer, 1979) has led a number of investigators to wonder as to whether it has contributed to the decline of native mussels through competition (Bates, 1962; Isom, 1968; Isom and Yokley, 1968; Coon et al., 1977; Horne and McIntosh, 1979). Anatomical, ecological and physiological factors that have contributed to the broad tolerances to stresses, rapid colonisation and abundance of C. manilensis have been summarised by Kraemer (1979) and Horne and McIntosh (1979). Kraemer (1979) argued, however, that while Corbicula abounds in heavily managed waterways where substrates are altered and often unstable, in relatively unmanaged rivers, the species does not show the same runaway distribution and biomass, and lives in a competitive role with indigenous mussels.

A2.3 Freshwater mussels as ecological indicators

Freshwater mussels are particularly well suited as indicators of palaeoenvironments, the activities of early man, or of present day water quality for a number of reasons: mussel shells preserve well; mussels often have particular habitat needs; shell size and shape are usually very responsive to the surrounding environment; mussels are sedentary; they absorb simple compounds directly from the water or feed from the basic trophic levels; they are long-lived and, being continually exposed to their environment, integrate variable water conditions (Tuthill, 1967; Cvancara, 1967; Green, 1972; Horne and McIntosh, 1979).

In relation to palaeoenvironments, mussels in North America at least have been used in deciphering drainage history. Mussel distribution has been used to interpret post-glacial stream confluences: van der Schalie (1939) for example used as evidence, the strength of commonness of mussels in both the Tennessee and Alabama Rivers to indicate that both rivers were once connected, mussels being carried across the divide by fishes during the period of confluence. Cvancara (1967) suggested mussels may be useful in indicating historical

changes in river discharge in the Red River Valley (USA). As some species are peculiar only to larger rivers of the valley, their presence in terrace sediments suggests a greater discharge in a particular river at some previous time. Similar rationale can be made for other species indicative of smaller rivers or tributaries (Cvancara, 1967). Lee and Wilson (1969) used the differences in Sr/Ca ratios of recent shells and ancient midden shells to indicate historical changes in palaeohydrologic conditions. Ecotypic shell forms have been suggested as offering reliable palaeohydrologic and palaeolimnologic data on at least a regional basis: in normally smooth-shelled species, rough growth interruption lines may indicate water temperature rises and/or declining water levels (Tuthill, 1967); as prediction of environment from Lampsilis radiata shell morphology in central Canadian lakes is possible, Green (1971) suggested the analysis of shell shape of fossil shells could be made to predict and describe the environment in which particular strata were laid down.

The distributions of some Australian mussel species were cited by Iredale and Whitley (1938) and later McMichael and Hiscock (1958) in support of a 'fluvifaunula' concept - that the principal drainage divisions in Australia supported more or less distinct assemblages of river animals. Walker (1981a) reviewed the idea and arguments. He concluded that the degree of overlap of species appeared too great to warrant the recognition of separate zoogeographic provinces and hence mussels in Australia did not provide effective support for the fluvifaunula concept. Of interest, however, is the correspondence between the ranges of a few mussel species and the geographic boundaries of the fluvifaunular provinces. The range of Velesunio angasi, one such species, nearly coincides with the Leichhardtian province (Walker, 1981a).

As the niches of some North American bivalves have been found to be trophically defined, their potential use and value as indicators of both past and present trophic stages of lakes has been suggested independently by Green (1971) and Clarke (1979).

Finally, in relation specifically to present day environments, interest has been held in recent years in the assessment and value of freshwater mussels as biological monitors of water quality. The topic has been reviewed by Fuller (1974), Horne and McIntosh (1979), Walker (1981b; 1984) and Simpson (1982). Present knowledge as to their value as indicators of pollution in chemical terms is growing and this forms a large part of the work on Velesunio angasi in the Northern Territory (Allison and Simpson, in press). Freshwater mussels apparently have great value as indicators of the "biological recovery zone" (Simmons and Reed, 1973) or at least as indicators of nonpolluted waters. Simmons and Reed (1973) noted that species diversity indices of benthic invertebrates were insensitive to the detection of pollution below a point source into the North Anna River, Virginia (USA), owing to the dominance of insect species. However, the molluscan fauna, including 3 freshwater mussel species, did not re-establish itself for some distance below the pollution source, and Simmons and Reed (1973) considered these organisms therefore more sensitive pollutional indicators and used them to mark the downstream area of full biological recovery. Horne and McIntosh (1979) reaffirmed an earlier suggestion of Ingram's (1957), that mussels may have value as

indicators of nonpolluted waters as their presence indicates at least high dissolved oxygen and other associated physicochemical conditions of clean waters. The absence of formerly present "clean water" species was argued to be a more significant indication of polluted waters than the presence of known pollution resistant forms. Mussels in the Blanco River, Texas, sections of which are organically enriched, are known to be sensitive to low dissolved oxygen levels to varying degrees (Horne and McIntosh, 1979).

APPENDIX 3

POPULATION DYNAMICS

Considerable attention has been devoted to study of the dynamics of freshwater mussel populations. Early work on determining population parameters of freshwater mussels focussed mainly on age and growth, important basic requirements for understanding the ecology of commercially valuable species (Lefevre and Curtis, 1910; Isely, 1914; Coker et al., 1921; Ellis, 1931; Chamberlain, 1931). More recently, as the dominance of freshwater mussels in the total benthic biomass of many freshwater ecosystems has become increasingly realised, their likely importance in the links of food chains and influence in energy and nutrient budgets, has attracted attention. As the basis for assessing the functional role of freshwater mussels in ecosystems (chiefly by way of secondary production estimates), thorough knowledge of the structure of mussel populations has been an important prerequisite (Okland, 1963; Negus, 1966; Tudorancea and Florescu, 1968; Tudorancea and Gruia, 1968; Magnin and Stanczykowska, 1971; Tudorancea, 1972; Lewandowski and Stanczykowska, 1975; Coon et al., 1977; Green, 1980; Kenmuir, 1980; Strayer et al., 1981). Otherwise, study of aspects of the population dynamics of important or formerly valuable commercial species of freshwater mussel, has identified terminal populations and even elucidated factors affecting their decline in regions severely affected by anthropogenic activities and changes (Ellis, 1931; Scruggs, 1960; Hendelberg, 1960; Isom, 1969; Coon et al., 1977; Bauer, 1983).

By far the bulk of relevant information on freshwater mussel populations has been devoted to methods of aging (see below, section 6.3), as this information is a basic prerequisite for determining other population parameters such as growth, population structure, recruitment, mortality and annual production. A notable feature of this considerable literature, however, is a dearth of studies that have validated the aging technique (section 6.3.2). Because of this, several authors have doubted and contested the longevities recorded for some populations of mussel. Margaritifera in particular, from inferences from its growth rate is reported to live from 60 to 100 years in both Europe and North America (early studies summarised in Comfort, 1957; Hendelberg, 1960; Stober, 1972). Even though Altnöder (1926) had earlier shown growth lines of M. margaritifera in one German population to be annual from direct observations of growth over the course of one year, Thompson et al. (1980) questioned the accuracy of estimates of its longevity in general, because growth rate is known to be highly variable between individuals of this species so that large specimens might merely be fast-growing. On the basis that other unionids rarely lived beyond 10-15 years, Dudgeon and Morton (1983) similarly, contested Stober's (1972) reported longevity of 67 years for a north American population of M. margaritifera.

In relation to the accusations by Thompson and co-workers just cited, Comfort's (1957) observations support the claims that generally, large shells represent high growth rates rather than extreme age. Thus while growth rates between individuals are generally noted to be highly variable, an inherent feature of unionid populations (Tevesz and Carter, 1980a), nevertheless much of the variation in growth may be accounted for sexually or by way of broad aspects of the

environment. Tevesz and Carter (1980a) recently reviewed some of these environmental relationships of shell growth in unionacean bivalves.

Prior to discussing factors that may cause variability in growth within a particular species, differences in growth rates between different mussel groups at least, are reported to be related to shell form. Heavy shelled forms (e.g. subfamilies Ambleminae and Megalonaiadinae) often grow more slowly than thin shelled forms (e.g. Anodontinae and Lampsilinae) (Isely, 1914; Grier, 1921 in Stansbery, 1961; Coon *et al.*, 1977).

Few studies have explored the possibility of growth rate differences between the sexes of individual species of freshwater mussel. Tevesz and Carter (1980a) noted that Lampsiline unionids generally, are often markedly sexually dimorphic in shell features including size. Chamberlain (1931) for example, showed that female Lampsilis anodontoides in North America are faster growing in the sexually active phase of life. Judging from the growth data, however, differences are apparently minor. Female Anodonta piscinalis in Finland similarly grow faster with the onset of maturity, but according to Haukioja and Hakala (1978a), differences are so minimal that measurements for both sexes can be pooled in growth studies.

In temperate regions generally, growth is invariably reported to decline or cease during winter in response to declining temperatures (section 6.3). While drought may cause growth cessation in warmer climates (McMichael, 1952), Tevesz and Carter (1980a) suggested that high amounts of suspended solids during Wet season flooding in tropical regions might conceivably arrest growth. Very little information is available on growth of freshwater mussels in the tropics, but at least Kenmuir (1980) has suggested that seasonal differences in growth rates of mussels in Lake Kariba, Zimbabwe are probably related to food availability. Thus temperature and trophic degree are at least two environmental determinants implicated in shell growth.

Within habitats, growth patterns of freshwater mussels have been shown to vary with several environmental factors, of both biotic and abiotic nature:

Density effects on mussel growth are reportedly few, and mixed in findings. Kat (1982) found some evidence that growth rates of Elliptio complanata in stream environments were greater for each size class, at or below observed densities as opposed to densities greater than those usually observed in the stream. Conversely, however, Kenmuir (1980) recorded the largest (and presumably faster growing) mussels in Lake Kariba, in regions of highest density suggesting to him that no competition for resources was evident amongst mussels of the lake.

Reports of substrate effects on growth are ambiguous in interpretation. Brönmark and Malmqvist (1982) found that growth rate of Unio pictorum decreased immediately downstream of a Swedish outlet. While fine sediment particles increasing downstream, could explain the observed growth patterns in that these may interfere with feeding and respiration, food quality (as measured by chlorophyll a) was also

found to decline downstream. Kat (1982) showed that growth rates of E. complanata were reduced on muddy substrates. He believed such sediments reduced feeding efficiency of mussels, as a constant energy expenditure would be required in order that they retain their position. It was conceded, however, that muddy substrates reflected reduced flow regimes and that weaker currents probably supported less nutritive material (Kat, 1982). In Lake Erie, growth of Amblema plicata inhabiting fine-grained sediments in deep water is reduced. Such environments according to Stansbery (1970) reflect reduced currents, these affecting growth rates.

In lakes, growth rates of mussels are invariably reported to decrease with depth (Okland, 1963; Reigle, 1967; Stansbery, 1970; Haukioja and Hakala, 1978a; Ghent et al., 1978; Strayer et al., 1981; McCuaig and Green, 1983). Ghent et al. (1978) found that stunting of Anodonta grandis was smoothly progressive, and that the predictable effect was consistent with similar and expected gradual declines in food supply and/or water temperatures with depth that might suppress metabolic rates. Similarly, stunting in relation to more exposed lake habitats is an unequivocal observation (Coker et al., 1921; Brown et al., 1938; van der Schalie and van der Schalie, 1950; Stansbery, 1961; Green, 1972; Clarke, 1973; Tevesz and Carter, 1980a). Brown et al. (1938) suggested that either wave action alone may produce the stunting effect, as mussels would require a continuous effort to stay in place; food supply or availability may be reduced over exposed habitats; or that stunting might be due to a series of factors associated with degrees of wave action or exposure.

Between habitats or sites, again growth rates may vary considerably (e.g. Margaritifera, Altnöder, 1926). Much of the variation, however, can be explained by limnological factors, in particular, temperature, trophic status and water hardness. In streams, M. margaritifera in Germany (Altnöder, 1926), A. grandis in the Sheyenne River, USA (Cvancara et al., 1978) and Alathyria jacksoni in the Murray River, Australia (Walker, 1981b) generally grow more rapidly in a downstream direction. While trophic status might be expected to increase downstream (Cvancara et al., 1978), Walker (1981b) suggested that increasing temperatures recorded downstream in the Murray River would impart a longer growing season on mussel populations, which may account for differences in growth rates. In the Thames River, higher growth rates of Anodonta anatina at one site were attributed by Negus (1966) to artificial heating of the river there by effluent from a nearby power station, which caused earlier breeding in the local population and provided it with a longer growing season. Coker et al. (1921) believed that the limiting factor of growth in thick shelled species particularly, was not so much the organic food supply as the mineral food supply. Björk (1962) for example, attributed higher growth rates of M. margaritifera between populations in two streams in southern Sweden to both higher trophic degree and increasing water hardness. Similarly, Clarke (1973) observed that streams in the Canadian interior basin that flowed through limestone often supported larger specimens than elsewhere.

Higher growth rates of mussels between different sites of the same lake have been attributed to higher water temperatures (Cvancara, 1972) and/or increasing eutrophy (Harman, 1970; Cvancara, 1972; Kenmuir, 1980). Between different but neighbouring lake populations

in North America, Green (1980) found evidence that calcium availability was the cause of growth rate differences of mussels. Okland (1963) on the other hand, attributed higher growth rates between the mussel populations in two Norwegian lakes, to higher summer temperatures in the shallower lake, in addition to higher levels of domestic sewage there.

The type of environment that mussels inhabit may have profound influences on their growth. Lake populations of a given species are generally noted to be smaller than their counterparts in nearby streams (Evermann and Clark, 1917; Coker *et al.*, 1921; Brown *et al.*, 1938; Harman, 1970; Clarke, 1973; Walker, 1981b), while both individuals in, and species associated with small streams or creeks are smaller than those in large rivers (Clarke, 1973; Tevesz and Carter, 1980a). Coker *et al.* (1921) believed the disparities in growth between rivers and lakes were caused by the deficiency in mineral and organic food in lakes over rivers, where currents kept food matter in suspension. While Brown *et al.* (1938) maintained that the more favourable conditions ascribed to streams could not be supported with limnological facts, presence of currents appear nevertheless to be implicated. Walker (1981b) found for example, better growth of Velesunio ambiguus in the Murray River proper or impoundments on the river in which there was regular water renewal, over populations in still waters. Clarke (1973) noted that mussels in general reached their largest sizes in rivers close to and draining lakes. This may be a trophic phenomenon in that draining waters immediately downstream of lakes (Brönmark and Malmqvist, 1982) and impoundments (Fuller, 1974) are generally noted to be nutrient enriched compared to waters further downstream. Harman (1970) recorded greater growth of individuals of a given species in central New York in nutrient-rich streams as opposed to growth in the cold, deep and nutrient-poor Finger Lakes. Finally, Evermann and Clark (1917) attributed the stunted populations of mussels in Lake Maxinkuckee (USA) not to food (apparently abundant), nor to the absence of current, but to close inbreeding and the absence of "new blood" in the populations.

The effect of temperature on growth rates of freshwater mussels is most effectively observed in latitudinal comparisons. Comfort (1957) states that in mollusc species in general with wide climatic ranges, individuals from colder climates are longer-lived and slower growing than those from warmer climates. Thus the growth rate of Margaritifera margaritifera is noted to be considerably higher in southern Swedish localities (Björk, 1962) than in northern, arctic sites (Hendelberg, 1960). Stober (1972) suggested the even faster growth of M. margaritifera in Montana (USA) over Swedish populations could in part be due to the lower latitudes of his site. Negus (1966) thought that growth of Anodonta anatina in the Thames River was less than that recorded in Norwegian lakes, as summer temperatures were higher in Norway. Populations of Anodonta and Lampsilis in extreme northern, peripheral populations in Canada grow very slowly and Clarke (1973) noted that the maximum sizes reached, were much less than those in more southerly populations. Chamberlain (1931) noted that the growth rate of Lampsilis anodontooides in North America was higher in southern and middle portions of its range than in northern portions and that further south, higher average temperatures coupled with the longer growing season were two likely factors producing greater growth

rates.

A final observation in regard to growth rates are their relations to longevity. As noted by Comfort (1957) above, slower growing molluscs tend to be longer-lived. Segerstrale (1961) noted in relation to the marine bivalve, Macoma baltica for example, longer-lived populations in the deepest localities, were accompanied by a slowing of growth rate with increasing depth. In relation to freshwater mussels, M. margaritifera is not as long lived in southern Sweden as in northern Sweden, a factor attributed by Björk (1962) to faster growth and pearl fishing that shorten its lifespan. Okland (1963) suggested the lack of older mussels in the shallows of Lake Borrevann might be due to the shortening of life attained when growth was accelerated by, for example, higher temperatures. Haukioja and Hakala (1978a) found evidence of growth-selective mortality in some freshwater mussel populations. However, while mortality was observed to be higher in individuals that grew faster, in other populations there was evidence that selective mortality operated on slow growers and in other populations still, did not operate at all.

A feature of long-lived animal and plant populations is the irregular nature of their age distributions (Krebs, 1978). Thus invariably, the age structure of freshwater mussel populations in various freshwater ecosystems is reported to be uneven, and characterised by dominant year classes and long-lived individuals - the result of irregular and considerable year to year variation in recruitment, and low adult mortality (Negus, 1966; Haukioja and Hakala, 1978b; Walker, 1981b; and Strayer et al., 1981). An inherent feature of the age structure of freshwater mussel populations, is the absence of the very youngest age group. This imparts to age frequency distributions a bell-shaped nature. Where intermediate age groups of mussels are most abundant (Brown et al., 1938; Lewandowski and Stanczykowska, 1975; Smith, 1976; Coon et al., 1977), populations are generally regarded as stable (Krebs, 1978). For most age distributions of molluscs, however, the mode is skewed to the left hand part of the curve (Zaika, 1973), and the predominance of younger age groups indicates increasing populations. This type of age distribution is noted in many freshwater mussel populations (van der Schalie and van der Schalie, 1963; Tudorancea and Florescu, 1968; Tudorancea and Gruia, 1968; Tudorancea 1969, 1972; Magnin and Stanczykowska, 1971; Kenmuir, 1980). In other populations, the mode of the dominant age groups may occur in the right hand part of the curve indicating declining populations. This has been reported in exploited (Hendelberg, 1960; Bauer, 1983) and even unexploited (Stober, 1972) populations of Margaritifera margaritifera in Europe and North America, and in populations of mussels following impoundment or embankment (Scruggs, 1960; Tudorancea, 1969, 1972). No freshwater mussel populations have been found in which there are gradual and regular decreases in numbers from juvenile young-of-year to the oldest age group, indicating regular recruitment from year to year.

Age structures of course, are affected by birth and death rates. In relation to recruitment, the notable and reported absence of young mussels in most freshwater environments generally, and suggested or implicated causes have been discussed previously (sections A2.1.3 and 3.2). While some causes of juvenile scarcity have been briefly reviewed by Lewandowski and Stanczykowska (1975) and Kat (1982), for

the sake of completeness, causes have been attributed as follows: to small sizes and consequent sampling biases against the young; high growth rates of juveniles; different habits and habitat preferences than adults; whereas adults are generally clumped, juveniles may be dispersed considerably after leaving the host fishes; irregular year to year recruitment; and pollution and other adverse anthropogenic changes to the environment that juveniles may be particularly sensitive to.

With respect to the present study, variation in year to year recruitment and the habitat preferences of juveniles were of particular interest. Literature relating to spatial patterns of recruitment has been previously described (section A2.1.3). While the unevenness of the age distributions of mussel populations indicates considerable differences in annual reproductive success (Lewandowski and Stanczykowska, 1975; Haukioja and Hakala, 1978 a, b), there has been little attempt at demonstrating temporal variations in recruitment patterns related to environment. Both density dependent and independent factors, however, have been suggested as important regulating factors in freshwater mussel populations.

Fish breeding activities coinciding with release of glochidia were thought by Okland (1963) and Negus (1966) to be important factors leading to successful recruitment. Okland's observations are of interest in that a particularly dominant year class was observed in only two of the three stations studied in Lake Borrevann (Norway) - the only stations where breeding behaviour of the host fishes was observed, thus demonstrating how localised successful recruitment can be. Droughts and floods have been held responsible for annual reproductive success or failure. Bimodality of the length frequency distributions of Alathyria jacksoni populations along middle tracts of the Murray River, were attributed by Walker (1981b) to high mortality and absence of recruitment during a severe drought in 1967 and 1968. Similar troughs in size distributions suggested that recruitment was poor in 1975 and 1976 when widespread and prolonged flood in the river apparently adversely affected recruitment. In the Nera River (Rumania) too, young age classes of Unio crassus are uncommon in upstream stations but predominate lower downstream; Tudorancea and Gruia (1968) believed young mussels were swept away from the upper reaches to be carried into the quieter waters further down. In the Crapina-Jijila marshes of Rumania, however, recruitment of mussels is enhanced by flooding from the Danube River, and in the absence of flooding mussels fail to breed; strong year classes and successful recruitment of Unio tumidus in fact could be traced back to years of high floods in Crapina populations (Tudorancea, 1969, 1972).

Odum (1971) writes: "There is evidence that populations have a "normal" or stable age distribution towards which actual age distributions are tending. Once a stable age distribution is achieved, unusual increases in natality or mortality result in temporary changes, with spontaneous return to the stable situation." Amongst the evidence, Odum cites the suppression of reproduction for several years following unusual survival of year classes of some fish populations. Both Kenmuir (1980) and Brönmark and Malmqvist (1982) believed mussel populations could be regulated in a density dependent fashion. Brönmark and Malmqvist (1982) observed high densities of mussels in a Swedish lake outlet. Such habitats were high quality in

terms of food, oxygen and substrate availability, and scarcity of young was attributed by these authors to suppression of establishment by adults. Kenmuir (1980) similarly observed few young mussels where adult densities were high, but where adult populations had been devastated by earlier drawdown in Lake Kariba, large concentrations of young and rapid recolonisation were observed. Thus recruitment rates in stable and long-lived mussel populations might be expected to be very low, by virtue of the fact that age distribution influences natality in populations (Odum, 1971).

The long life-span of freshwater mussels generally, suggests low adult mortality (Comfort, 1957; Strayer *et al.*, 1981). Nevertheless, apart from physiological longevity, death may occur prematurely in freshwater mussel populations from a number of causes. Some of the factors have been discussed previously (Appendix 2), but again for the sake of completeness, the various causes of mortality have been attributed as follows: life spans may be growth selective (see above); while various predators of freshwater mussels have been recorded, muskrats and aboriginal man are thought to have severely reduced the shallow water distribution of some species in Europe and North America (section A2.1.2). In Australia, water rats (Dean, 1968; Fisher, 1973; Walker, 1981b) and various species of birds (Vestjens, 1973; Fisher, 1973) have been observed to prey upon freshwater mussels, while aboriginal man in the past at least, must have been an important and significant predator (Walker, 1981b); droughts, drawdown in impoundments or rapid subsidence of waters may devastate mussel populations through effects of desiccation, anoxia or direct exposure to predators (Björk, 1962; Okland, 1963; Tudorancea, 1969, 1972; Marshall, 1975; Kenmuir, 1980; Walker, 1981b); winds and high wave action during storms may throw mussels up onto shores where survivors may become food for various predators (Tudorancea, 1969, 1972; Walker, 1981b); and adverse anthropogenic changes such as pollution, impoundment, siltation and overharvesting may similarly devastate populations (section A2.2). In addition to these causes, density dependent affects have been suggested as inducing early mortality in mussel populations. In the Nera River (Rumania), high densities of mussels downstream were believed by Tudorancea and Gruia (1968) to shorten the life span of Unio crassus populations; in evidence the population here comprised mostly young individuals, in relatively poor condition (according to flesh weights) when compared with other stations.

As in recruitment patterns, attempts at interpreting age distributions in relation to significant and devastating mortality effects in the past have been few. In the Crapina-Jijila marshes, a past two year period of high winds and wave action (that throw juvenile mussels onto the shores), was believed to be responsible for the low numbers of two corresponding age classes in the age distributions of mussels (Tudorancea, 1969). Bimodality in the length frequency distributions of Alathyria jacksoni in middle tracts of the Murray River was shown by Walker (1981b) to be caused by a severe two year drought in the river during 1967 and 1968. A. jacksoni is intolerant of both dehydration and anoxia (Walker, 1981b). Mortality rate of all the age classes in populations of Margaritifera margaritifera in streams of North Bavaria, was shown by Bauer (1983) to rise steeply with increasing degrees of organic pollution.

Because of the irregularity in recruitment and long life spans of freshwater mussel populations, few attempts at estimating mortality rates have been made (Negus, 1966; Haukioja and Hakala, 1978 b; Green, 1980; Bauer, 1983). While mortality is generally easier to estimate in the older age classes, it has been suggested (Green, 1980) and found (Negus, 1966) that mortality rates at intermediate ages are lower or negligible in comparison to the oldest part of the population, but at the earliest ages are also probably high (Tudorancea, 1972; Green, 1980). With respect to sexual differences in mortality rates, in populations of freshwater mussels in which growth selective mortality worked against slow growers, Haukioja and Hakala (1978a) found that males suffered higher mortality than females. Elsewhere, changing sex ratios with age have been interpreted as modification or transformation of sex (Tudorancea, 1969).

In relation to physiological longevity, the life spans of light-shelled species throughout the northern hemisphere are remarkably and consistently similar. Species of the subfamilies Unioninae, Anodontinae, Lampsilinae generally live from 10 to 15 years in Europe (Boycott, 1936; Crowley, 1957; Björk, 1962; Okland, 1963; Haranghy *et al.*, 1964; Negus, 1966; Norelius, 1967; Tudorancea and Gruia, 1968; Tudorancea, 1969; Lewandowski and Stanczykowska, 1975), North America (Chamberlain, 1931; Pennak, 1953; Magnin and Stanczykowska, 1971; Coon *et al.*, 1977) and tropical Asia (Dudgeon and Morton, 1983). Coon *et al.* (1977) noted that heavier shelled mussels of the subfamilies Ambleminae and Megalonaiadinae in North America, however, in addition to their slower growth rates, often live longer than mussels of the previously mentioned subfamilies. Thus, species of Elliptio may live from 16 to 20 years (Ghent *et al.*, 1978; Strayer *et al.*, 1981), Quadrula from 20 to 50 years (Lefevre and Curtis, 1910; Comfort, 1957), Pleurobema over 30 years (Scruggs, 1960) and Megalonaias from 25 to over 50 years (Comfort, 1957; Coon *et al.*, 1977).

Light-shelled mutelids in tropical Lake Kariba in Africa have comparable age spans to similar shell forms in the northern hemisphere, of between 10 and 12 years (Kenmuir, 1980). Similarly, in Australia, the lighter shelled Velesunio ambiguus is estimated to live to 11 years along the Murray River, and the heavier shelled riverine mussel, Alathyria jacksoni, 29 years - again comparable estimates to figures recorded for similar shelled forms in Europe and North America (Walker, 1981b).

Vastly different estimates for the life span of Margaritifera margaritifera throughout its circumboreal range but also within countries, however, have been reported. In North America, two populations in central Massachusetts (USA) were reported to live from between 19 and 23 years (Smith, 1976), while in Montana, maximum ages of 67 years were found (Stober, 1972); in southern Sweden M. margaritifera was believed to live from 19 to 24 years (Björk, 1962) and up to 116 years in arctic Sweden (Hendelberg, 1960); and in North Bavaria maximum ages amongst five rivers studied ranged from between 60 and 110 years (Bauer, 1983). While exploitation, pollution and growth-selective mortality have been used to explain differences in the longevity of M. margaritifera (Björk, 1962; Bauer, 1983), doubts over its extreme longevity (mainly because of the aging technique),

have been previously mentioned. There is little doubt that the aging method needs to be validated for each regional population of Margaritifera studied. Even though growth has been shown to vary considerably in this species regionally, it is curious that extreme age per se should be questioned, given that bivalves generally are long-lived and that some marine species may live beyond 100 years (Jones, 1983). Shells of Arctica islandica for example, have been reported with up to 150 growth increments, apparently annual in nature (Thompson et al., 1980).

Apart from studies of growth in relation to habitat and environmental patterns, other aspects of the population structure of freshwater mussels in relation to habitat have been little studied. With respect to distribution of the sexes, Cvancara (1972) noted no apparent trend in sex ratio with depth evident in Lampsilis radiata luteola populations in Long Lake, Minnesota (USA). In relation to size and age distributions, different habitat requirements of young mussels have already been discussed. Within habitats generally, for example, juveniles are often found in shallower waters than adults (section A2.1.3).

Kenmuir (1980) found that mussels increased in size (and presumably age) with increasing depth in Lake Kariba. While more young were recruited in the shallows than elsewhere, drawdown and exposure increased mortality in the shallows or prompted migration of older individuals to deeper waters; mortality due to predation and siltation was argued to be higher in the shallows than elsewhere (Kenmuir, 1980). In Lake Borrevann, Okland (1963) not only found younger Anodonta piscinalis individuals in the shallows (0.4 m) but also in deeper waters (6 m) while the oldest mussels were found at intermediate depths (3-5 m). Okland suggested that the lack of old shells in the shallows might be due to: the unstable environment of the shallows that increases mortality (e.g. ice, drought, wave action, or predation); selective mortality of the faster growing individuals in the shallows; local recruitment effects that may favour the shallows; and dispersal to greater depths with age). He thought the occurrence of younger mussels at greater depths might be a result of periodic oxygen depletions that either shorten the life-span of mussels here or induce migrations upwards towards more favourable habitats. Conversely, in Lake Mikolajskie, Lewandowski and Stanczykowska (1975) found reverse trends to those of Kenmuir (1980) and Okland (1963) in size distributions. Smaller individuals of A. piscinalis occurred at intermediate depths, while larger mussels were found in the shallows and deeper regions. Unio tumidus individuals on the other hand, became smaller with depth. No explanation for the observed distributional patterns was provided by the authors, and interpretation is made even more difficult as habitat related growth rates were not studied. A final observation in relation to size distributions in lakes is that of Green (1980) who found that the size of Anodonta grandis in a small arctic lake was more related to slope of the bottom than to depth, with mean length decreasing with decreasing slope. No causal explanation was offered.

Within microhabitats of streams, a vertical stratification of age classes has been observed with larger and older mussels in a superficial position, and smaller and younger mussels occurring deeper in the sediments (Björk, 1962; Tudorancea and Gruia, 1968). Little

comparison has been made of age distributions within habitats otherwise. Between sites of the Nera River, however, as mentioned earlier, Tudorancea and Gruia (1968) thought age distributions were influenced by currents, with juveniles being swept away from upstream into quieter reaches downstream.

The structure of mussel populations at any given time and place may of course be considerably altered or modified where movements and migrations of individuals are significant. Early thoughts on freshwater mussel movements reached the conclusion that adult mussels rarely if ever moved about, especially in the absence of suitable stimuli and hence that mussels probably lived close to the place that they first settled (Lefevre and Curtis, 1910; Evermann and Clark, 1917; Coker et al., 1921; Ellis, 1931). The only significant movements were believed to be associated with the rapid migrations possible in the parasitic stage upon fish, and that otherwise locomotion played a minor part in the distribution of mussels (Coker et al., 1921; Pennak, 1953). In transplant studies, Isely (1914) found very little evidence of migration in various stream species. While he noted that lighter-shelled species were considerably more active than heavier-shelled mussels (also noted by Lefevre and Curtis, 1910), he also believed that they probably would not migrate far from the point where they dropped from the fish.

Recent thought in relation to total movement over a lifespan is mixed in conclusion. In stream populations, Strayer (1981) found only 2.2% of mussels associated with trails in the substrate that would suggest recent movements. He thought most mussels would not move about much. Salmon and Green (1983) argued, however, that by nature of the instability of the lotic environment, mussels would be expected to move about to some degree in response to various stimuli such as raising or falling water levels. Frequent reports of considerable fluctuations in community composition and population densities suggested to Kat (1982) a considerable degree of mobility of adult mussels. Kat himself observed high rates of migration of Ellipectio complanata in stream environments and thought it conceivable that movements of mussels whose fish hosts had small home ranges might be greater than the larval dispersal distance upon the fish. Ghent et al. (1978) observed random horizontal movements of mussels in Lake Bernard (Canada), but that relatively large proportions of time (up to 30%) were spent engaged in such movements.

An undisputed claim of most observers is that juvenile mussels are much more active than older mussels (Evermann and Clark, 1917; Coker et al., 1921; Kat, 1982), a phenomenon believed to be related to the active searching by juveniles for suitable habitats after dropping from the host fishes (Lefevre and Curtis, 1910; Isely, 1911; Howard, 1922).

Freshwater mussels may respond to various stimuli. Movements may be initiated by pressure, temperature or light (Coker et al., 1921). Bright light for example stimulates movement to deeper waters away from the shallows and their associated hazards (Fuller, 1974). Flooding induces a movement to shallow waters, while receding waters stimulates withdrawal of mussels to deeper waters (Coker et al., 1921; Björk, 1962; Tudorancea, 1972; Fuller, 1974; Kenmuir, 1980; Salmon and Green, 1983). Coker et al. (1921) suggested the stimulus to move to

shore during floods was an accommodation to light conditions as floodwaters are invariably turbid. At other times, mussels may exhibit a positive geotaxis (Matteson, 1948) and actively seek and find their optimum depth when they are experimentally displaced (Isely, 1914; Matteson, 1948). Imlay (1972) however, observed little response of displaced mussels when the displacement occurred either in the wrong season or was artificial. Siltation is one such unnatural event and rather than mussels not responding quickly enough to its smothering effects (Ellis, 1931), Imlay believed the unnatural coverings (that may occur at an atypical season) probably do not trigger the natural response mechanism of mussels for digging themselves out. (The implications of Imlay's study invoke a cautionary note to studies and experiments whose results rely upon the responses of mussels following artificial displacement).

Some environments are apparently more conducive to activity in mussels than others. Evermann and Clark (1917) observed for example that mussels were generally quiescent in deeper lake waters. Margaritifera margaritifera was found to be more active over sandy sediments in streams (Björk, 1962). Brönmark and Malmqvist (1982) believed that large sediment particles would probably have a restrictive influence on mussel locomotion. Less movement was observed by Elliptio complanata on muddy substrates than sandy ones in streams, as these sediments are not exposed to the currents and mussels must therefore rely on their own efforts to move (Kat, 1982). Other mussels may affect the migratory behaviour of individuals, and in displaced mussels at artificially high densities in comparison to lower densities, Kat (1982) observed most movement of and distances travelled by individuals.

During winter in temperate regions, freshwater mussels generally become inactive and bury deeper into the sediments (Isely, 1914; Evermann and Clark, 1917; Matteson, 1948; Pennak, 1953; Stansbery, 1961; Roscoe and Redelings, 1964; Walker, 1981b). While Evermann and Clark (1917) and Coker et al. (1921) observed migrations to deeper waters prior to winter, van der Schalie (1938) and Pennak (1953) claimed these responses were related to receding water levels during autumn rather than decreasing temperatures. Lewandowski and Stanczykowska (1975), however, observed migration of lake Unio tumidus populations into shallow waters with the approach of summer.

Other seasonal patterns of movements, mainly in depth distribution, have been noted by various authors. Seasonal, but unspecified movements of Anodonta spp. have been noted by Salmon and Green (1983). Regular shoreward migrations by spawning mussels of various species have been observed (Ellis, 1931; Yokley, 1972; Brönmark and Malmqvist, 1982). Such reproductive behaviour is believed to be correlated with the increased chances of parasitising host fishes, also noted to be more active in the shallows at these times (Ellis, 1931; Yokley, 1972). Tudorancea (1972) observed both active autumnal migrations associated with reproduction and spring feeding migrations in populations of Anodonta piscinalis in the Crapina-Jijila marshes.

A final and important consideration in the literature relating to the study of the population dynamics of freshwater mussels, is the recent interest in their value as indicators of environmental impact and of past and present environments.

On the basis that unionids can be accurately aged, Tevesz and Carter (1980a) reviewed the potential ways in which unionids may be usefully employed to monitor environmental change. Baseline information available on population dynamics (e.g. age structures, mortality rates) could be used to compare new information with, and to test for, possible perturbations in the environment brought about by pollution or other anthropogenic activities. If the typical period of the year of mortality for individuals of a population could be ascertained for example, it might be possible to tell whether "kills" were natural or man-induced.

Tevesz and Carter (1980a) cited Negus' (1966) study in which she showed the close correlation between increasing growth rates of Anodonta anatina as reflected by relative widths between annuli, and water temperatures. Such information might make unionaceans useful as relative palaeothermometers (*ibid*) or as indicators of thermal pollution (McCuaig and Green, 1983). Similar information is available for marine bivalves, and Jones (1983) suggested such records may prove useful in monitoring environmental disturbances (natural or man-made) or in interpreting past and present climates at sites uninhabited by man.

Lampsilis radiata and Anodonta grandis are unionids with wide geographical distributions in North America and about which much ecological information is known including growth rate differences related to natural environmental variability. As such, McCuaig and Green (1983) considered these unionids valuable research organisms, and showed how growth rate parameters derived from aging studies could be used to test hypotheses about changes in the environment such as long-term temperature changes, or presence of pollutants.

APPENDIX 4

REPRODUCTION

A4.1 Gonadal development and structure of the breeding population

In the Unionidae for which much information is available, the sexes are separate; some species are occasionally or simultaneously (i.e. consistently) hermaphroditic (Pennak, 1953). Among the hyriids and mutelids of the southern hemisphere, there is no indication from the available literature to suggest other than the dioecious condition.

Apart from limited dimorphism in shell shape and size amongst freshwater mussel taxa (Appendices 1 and 3 respectively), the sex is most precisely determined by the nature of the gonads which are imbedded in the upper part of the foot, and which ramify much of the visceral mass. In addition, the sex of most individuals can be determined by morphology of the marsupial demibranchs i.e. one or both pairs of gills of the female that are modified as marsupia in which the developing young are incubated and mature (Heard, 1975). In the hyriid Velesunio ambiguus for example, Walker (1981b) distinguished males and females by the anatomy of the innermost marsupial gill. In non-gravid females, the marsupium was recognisable as a slightly thickened portion of the gill whilst in gravid females, was noticeably extended and swollen with developing larvae. The inner gills of males resembled the outer gills of both males and females. Walker (1981b), however, could not distinguish females from males by this method. For dioecious species in which a gravid condition for the female is the norm, the sexes may be easily distinguished for much of the time by gill morphology alone (van der Schalie and van der Schalie, 1963). Kat (1983d) states of other species, nevertheless, that microscopic examination of the demibranchs may be needed to discriminate non-breeding males from females.

Kat (1983d) in a study of hermaphroditism among unionids, was impressed with the stability of the dioecious system of reproduction. Not only is the occurrence of simultaneous hermaphroditism infrequent (the predominant mode of reproduction for only 6 out of 220 North American species), but among the proportion of predominately dioecious species in which hermaphroditic individuals are encountered (30 out of 101 examined) such incidence is low (Kat, 1983d).

For unionaceans that reproduce predominately as hermaphrodites as well as separate sexes, are reported species for which ratios of males, females and hermaphrodites in various populations vary considerably. Thus, regional differences have been recorded of the sexual composition of a simultaneous hermaphrodite, Anodonta imbecilis in North America (van der Schalie, 1970; Heard, 1975); the ratios of males, females and hermaphrodites of Anodonta cygnea in Britain are constant for, but vary between populations (Bloomer, 1930, 1934, 1935, 1939); in Italy A. cygnea is reported to be dioecious (Giusti et al., 1975); and whilst Margaritifera margaritifera is normally dioecious throughout its holarctic range (e.g. Smith, 1979; Bauer, 1979; Young and Williams, 1984a), a North American population was found by Heard (1970) to be hermaphroditic. Heard (1975) found a variety of sexual strategies among several anodontine species studied over North

America, showing that hermaphroditism was not phylogenetically determined. Nor have different reproductive modes been found to be consistently related to habitat type per se (Heard, 1975; Kat, 1983d). Both van der Schalie (1970) and Heard (1975), although recognising that hermaphroditism had selective value under particular environmental conditions, could not demonstrate any environmental factor that indicated a causal relation with sexuality. Dudgeon and Morton (1983) thought it appropriate to consider the sexual strategies of these bivalves as a balance between the tendency for hermaphroditism and sexual separation. They cited the study of Coe (1941) who believed the sex differentiating mechanism of bivalve molluscs to be so delicately balanced between the two sexual tendencies, that relatively slight differences in environmental conditions could be potent in determining which of the two aspects would be realised.

The study of Anodonta imbecilis by Kat (1983d) has been the first to propose hypotheses to account for the selective value of different reproductive modes in freshwater mussels from a variety of habitats and population densities. Kat believed dense populations in reservoirs and sparse populations in streams for example, were subject to fundamentally different sexual selection pressures acting on ratios of allocation to male and female gonadal products. Several hypotheses to account for the considerable variability in the ratio of male:female gametes produced by A. imbecilis were presented, based on population density, nutrient and sperm availability, mode of fertilisation and limitation of brood space.

Among populations of predominately dioecious species, Kat (1983d) found occasional hermaphroditism to be generally associated with the presence of digenean trematodes within the gonads. Kat suggested that these parasites could secondarily or directly alter levels of sex determining hormones in the infected individuals. However, trematode parasitism was not implicated as the cause of occasional hermaphroditism by either van der Schalie (1970) and Heard (1975) for other populations and species investigated. Developmental errors in sexual determination though, have also been implicated as the cause of such hermaphroditism (Coe, 1943; van der Schalie, 1970; Kat, 1983d).

Occasional hermaphroditism and variable sex compositions among freshwater mussel populations have been linked to possible forms of sex reversal. Amongst the evidence of this is cited seasonal and age specific variations in sex ratios, and exceptions to the normal correspondence of visceral sex and marsupial demibranch morphology. Apart from occasional and simultaneous hermaphroditism, Coe (1943) recognised a further three types of sexuality less common to bivalves: (a) consecutive sexuality, in which there is a single change in the functional sexuality of the individual (usually male to female); (b) rhythmical consecutive sexuality, where the initial phase is male, followed by a series of alternating female and male phases throughout life; and (c) alternative sexuality, in which adults function seasonally as separate sexes. In an extensive study of hermaphroditism in British populations of Anodonta cygnea, Bloomer (1934, 1935, 1939) found that the morphology of the outer, marsupial demibranch did not always correlate with visceral sex amongst various populations, suggestive that individuals changed sex at least seasonally (alternative sexuality). Hermaphroditism was not confined

to any particular age of animal in some populations (Bloomer, 1935) but in others, the gonads functioned as males at first maturity (consecutive sexuality) (Bloomer, 1939).

Tudorancea (1969, 1972) found age and seasonal variations in the sex structure of Unio tumidus and U. pictorum in the Crapina marsh of Rumania. Males predominated in the youngest and oldest age divisions, while females were most common at intermediate ages. During the breeding season females were the dominant sex while for the rest of the time, males predominated. Both phenomena were suggestive to Tudorancea of consecutive and rhythemical consecutive sexuality respectively.

For populations of Anodonta woodiana in Plover Cove, Hong Kong (Dudgeon and Morton, 1983) and Margaritifera margaritifera in streams of Scotland (Young and Williams, 1984a) individuals were found to be either male or female throughout the size range of the species with no suggestion of changing sex with age. Similarly Heard (1975) concluded that sex reversal was absent from several North American populations of Anodonta, noting that visceral sex (or the dominant gonad of hermaphrodites) consistently correlated with morphology of the marsupial demibranchs, regardless of season and age of mussels. In a North American population of M. margaritifera, however, Smith (1979) noted a slight male over female dominance in the youngest age classes. However, as males matured earlier than females, no protandric tendencies were suspected.

Kat (1983d), nevertheless, found the primary gonads of two normally dioecious unionids and one simultaneous hermaphrodite to be spermatogenic. He believed sex determination among dioecious species to be controlled by hormonal levels, with juveniles tending toward maleness due to low levels of sex-determining hormones; true males continued with such low levels while the female condition resulted from high levels. Kat attributed the higher variability in male:female ratios of gonadal tissue amongst female hermaphrodites to the higher hormonal levels hypothesised to determine the female condition. The observed early-maleness in above-mentioned studies therefore (Bloomer, 1939; Tudorancea, 1969, 1972) accord with Kat's (1983d) hypothesis of protandry amongst unionids. In bivalves generally, Coe (1943) observed in normally dioecious species that occasional hermaphroditism commonly occurred in the young at the first reproductive season, and that in cases of alternative sexuality, the male phase was often indicative of immaturity. Protandry of the type proposed by Kat (1983d) for at least the unionids he studied, would place these species in the category of consecutive sexuality.

In considering sex ratios of all individuals from a population averaged over time, the literature shows that there may be predominance of males (van der Schalie and van der Schalie, 1963; Tudorancea, 1969; Yokley, 1972; Walker, 1981b; Zale and Neves, 1982a) or females (Boycott, 1936; Smith, 1979; Kenmuir, 1980; Dudgeon and Morton, 1981; Young and Williams, 1984a). However, no author has provided evidence to show that sex ratios vary significantly from 1:1 in any population of freshwater mussels studied.

Age at sexual maturity for freshwater mussels is invariably reported as either the earliest age at which the gonads mature or at which

gravid females are found (Presumably the lag between gonadal maturation and spawning for most species, nevertheless, is no more than one breeding season.) Haukioja and Hakala (1978b), however, reported age at maturity as the time at which half the females had glochidia in the gills for the first time. Table A4.1 summarises the available literature concerning age at maturity. From these studies some generalisations can be made. Amongst temperate species investigated, thicker-shelled and slower growing species (e.g. *Quadrula* spp., *Pleurobema*) are slower to mature than the thinner-shelled and faster growing species (e.g. anodontines and lampsilines). Tropical species (Seshaiya, 1969; Kenmuir, 1980; Dudgeon and Morton, 1983) by comparison mature at a very early age reflecting presumably, the equitable and higher water temperatures sustained for gonadal maturation and rapid shell growth. Conversely, *Margaritifera margaritifera*, is the slowest freshwater mussel known to reach maturity reflecting presumably the circumboreal range of this animal and consequent slow development and growth.

Gametogenesis in unionaceans from temperate climates is typically continuous throughout the year, though brief periods of inactivity may occur immediately after spawning, while the process usually proceeds at a slower rate over the winter (Matteson, 1948; van der Schalie and van der Schalie, 1963; Stein, 1969; Yokley, 1972; Giusti *et al.*, 1975; Heard, 1975; Smith, 1979; Zale and Neves, 1982a; Jones and Simpson, in prep.) While gametogenesis is most intense during the summer months, spawning, a more or less short and synchronised event in temperate species, occurs during the warmer months ranging between early spring and early autumn. Water temperature is generally assumed to be the cue responsible for initiating spawning.

In tropical climates, gametogenesis has been studied in Indian (Lomte and Nagabhushanam, 1969; Ghosh and Ghose, 1972; Nagabhushanam and Lohgaonker, 1978) and east Asian (Dudgeon and Morton, 1983) unionids. While spermatogenesis is reportedly continuous throughout the year, inactive phases in oogenesis as occur in temperate species have also been reported, and this is related to the cooler winter temperatures. Spawning in *Anodonta woodiana* occurs in the spring (Dudgeon and Morton, 1983) but for the Indian unionids studied, nevertheless, spawning for individual species is protracted, extending over most of the warmer months.

The period over which sperm are present in the testes, is invariably reported to be much broader than that over which ripe ova are present in the ovaries. This has been interpreted as meaning that sperm are released over a timespan that overlaps ovulation in females, thus ensuring successful fertilisation (e.g. Matteson, 1948; Dudgeon and Morton, 1983).

A product of atypical spermatogenesis (i.e. where typical meiotic stages are absent) in bivalves are multinucleate structures termed sperm morulae. They are reportedly widespread in unionids (van der Schalie and Locke, 1941; Bloomer, 1946; Smith, 1979) and hyriids (Heard, 1975; Jones and Simpson, in prep.) and are seasonal in appearance, being present in male follicles prior to spermiogenesis. Coe and Turner (1938) believed most sperm morulae underwent cytolysis prior to the period of typical spermatogenesis. Heard (1975), however, contested this, and provided some evidence to show that the

Table A4.1 Age at gonadal maturity and/or first gravidity reported for the species of freshwater mussels studied worldwide to date.

SPECIES	Region	Authority	Age at gonadal maturity	Age at first gravidity
<u>Margaritifera margaritifera</u>	Scotland	Young and Williams (1984a)	-	12
<u>M. margaritifera</u>	Sweden	Bjork (1962)	20	-
<u>M. margaritifera</u>	U.S.A.	Smith (1979)	7 (male)	-
North American unionids	"	Pennak (1953)	1-8	-
<u>Anodonta grandis</u>	U.S.A.	van der Schalie and Locke (1941)	2	-
<u>A. imbecilis</u>	"	Stansbery (1967)	2	-
<u>A. imbecilis</u>	"	Coker <u>et al.</u> (1921)	2	-
<u>Anodonta</u> spp.	"	Heard (1975)	-	4-6
<u>A. piscinalis</u>	Finland	Haukioja and Hakala (1978b)	-	2-3
<u>A. woodiana</u>	Hong Kong	Dudgeon and Morton (1983)	1	-
<u>Villosa nebulosa</u>	U.S.A.	Zale and Neves (1982a)	3	-
<u>V. vanuxemi</u>	"	"	"	-
<u>Medionidus conradicus</u>	"	"	"	-
<u>Lampsilis fasciola</u>	"	"	"	-
<u>L. luteola</u>	"	Coker <u>et al.</u> (1921)	2	-
<u>L. (Proptera) laevissima</u>	"	"	1	-
<u>Actinonaias ellipsiformis</u>	"	van der Schalie and van der Schalie (1963)	3	-
<u>Amblema plicata</u>	"	Stein (1969)	4	-
<u>Pleurobema cordatum</u>	"	Yokley (1972)	<4	-
<u>P. cordatum</u>	"	Scruggs (1960)	6	-
<u>Plagiola donaciformis</u>	"	Coker <u>et al.</u> (1921)	2	-
<u>Quadrula</u> spp.	"	"	4-8	-
<u>Lamellidens</u> spp.	India	Seshaiya (1969)	2	-
<u>Unio tumidus</u>	Rumania	Tudorancea (1969)	3-4	3-4
<u>Caelatura mossambicensis</u>	Zimbabwe	Kenmuir (1980)	-	1
<u>Velesunio ambiguus</u>	Australia	Walker (1981b)	-	3-4
<u>Alathyria jacksoni</u>	"	"	-	3-4
<u>Aspatharia wahlbergi</u>	Zimbabwe	Kenmuir (1980)	-	2-3
<u>Mutela dubia</u>	"	"	-	1-2

structures completed metamorphosis to provide spermatozoa.

A final factor in relation to gonadal development, is the effect upon the reproductive potential of freshwater mussels of parasitism by digenean trematodes. Invariably, their presence in the viscera is reported to result in partial or complete castration. Kat (1983d) reported up to 85% infection of Lampilis radiata by trematodes in some of the North American populations he studied. Over 30% of individuals of Villosa vanuxemi examined by Zale and Neves (1982a) were similarly infected, and many of the older mussels were found to be rendered functionally sterile. van der Schalie and van der Schalie (1963) reported lower infection rates in Actinonaias ellipsiformis (<2%) while in the hyriid Velesunio ambiguus, parasitism is apparently uncommon (<1%) (Angel, 1961)

Noting that the oldest mussels were reproductively active, displaying normal gametogenesis and gravidity, Scruggs (1960), Stansbery (1967), Heard (1975) and Kenmuir (1980) concluded that no post-reproductive (cessation of reproduction) or senility phase (decline in reproductive activity) occurred in the respective populations of freshwater mussels studied. In studies of aging in European populations of Anodonta cygnea and Unio pictorum, however, Haranghy et al. (1964) noted that variability in the ovary increased with age, while no changes were noted in the gonads of males. In the ovaries of some females, large numbers of mature oocytes were found; in others, mature oocytes were hardly observed; while in others again the ovaries were disorganised and atrophied. Thus while the processes of spermatogenesis and production of apparently viable oocytes continued even in quite old mussels, Haranghy et al. (1964) concluded that for the most part, a post-reproductional period could be assumed for the two unionids.

A4.2 Larval production

The unfertilised eggs of freshwater mussels, having found their way from the ovaries to the water tubes of the marsupial demibranchs, are fertilised by sperm taken in through the inhalent siphon. While the eggs of most species are fertilised more or less at the one time, spawning in some unionids, e.g. Unio spp. (Lillie, 1895; Tudorancea, 1969), Pleurobema cordatum (Scruggs, 1960; Yokley, 1972), is intermittent and all stages of development may be found in the marsupia of individuals at a given time. Evermann and Clark (1917) noted that gravid females were fewer than expected in lake populations of freshwater mussels compared to those from neighbouring rivers, as more opportunities of fertilisation of ova were available in flowing waters. Other studies, nevertheless, report that unfertilised eggs are rarely found in populations of mussels (Coker et al., 1921; Matteson, 1955; Wood, 1974a; Smith, 1976). The number of developing larvae brooded in the marsupia has been estimated to range generally from between several thousand and 3 million, depending upon the species and size of the animal (Coker et al., 1921; Pennak, 1953; Kenmuir, 1980). Gestant females from Scottish populations of Margaritifera margaritifera, however, can harbour from between 3-4 million larvae (Young and Williams, 1984a), while individually up to 17 million young may be produced.

Amongst unionids and margaritiferids, the marsupia may comprise all four gills, the two outer gills, or only special parts of the outer

gills, depending upon the species (exobranchiate condition, Lefevre and Curtis, 1912), while they are contained in the inner gills only (endobranchiate condition) amongst the southern hyriids and mutelaceans.

In relation to larval development, Lillie (1895) gave a detailed account of the anatomy and morphology of developing and mature glochidia of Anodonta and Unio. The study of Matteson (1948) and the more detailed work of Wood (1974a) corroborated Lillie's observations for Elliptio and Anodonta species respectively. Otherwise, numerous workers have studied the seasonal and developmental continuum of embryogenesis in only a cursory manner for the purposes of determining the period of fertilisation, the period and duration of incubation, and number of annual broods of respective mussel populations (e.g. Scruggs, 1960; Yokley, 1972; Heard, 1975; Smith, 1976; Trdan, 1981; Kenmuir, 1981a; Zale and Neves, 1982a).

The duration of larval development, from fertilisation to glochidial maturation is relatively constant amongst species of freshwater mussels, as embryonic development occurs chiefly during the warmer months. Studies have shown in fact, the dependence of embryonic development upon temperature (Matteson, 1948; Yokley, 1972; Wood, 1974a). Development during spring and summer is very rapid (Lefevre and Curtis, 1912), maturation for example being completed in 2 weeks in Quadrula spp. (Lefevre and Curtis, 1912), 4 weeks in Elliptio complanata (Matteson, 1948) and from 16-45 days in Margaritifera margaritifera (Harms, 1909; Smith, 1976). Maturation during late summer and autumn is slower, for example 8 weeks of Anodonta (Wood, 1974a) 7-8 weeks for the four lampsilines studied by Zale and Neves (1982a) and 9 weeks for the hyriid Cucumerunio novaehollandiae (Jones and Simpson, in prep.). Amongst tropical species studied, maturation is completed in 4 weeks in Anodonta woodiana (Dudgeon and Morton, 1983) and 3-5 weeks for species from Lake Kariba (Kenmuir, 1981b). Even in tropical species, maturation during the cooler winter months is reportedly delayed (Kenmuir, 1981b).

In temperate regions of North America (Lefevre and Curtis, 1912; Coker *et al.*, 1921; Pennak, 1953; Clarke and Berg, 1959; Clarke, 1973; Kat, 1984) and Europe (Harms, 1909; Negus, 1966; Tudorancea, 1969, 1972; Wood, 1974b; Haukioja and Hakala, 1978b; Dartnall and Walkey, 1979), general breeding patterns are well known. Two broad reproductive patterns are recognised according to the length of time over which larvae are brooded in the female marsupia. Long-term or bradytictic breeders, spawn during mid-late summer. The glochidia develop during autumn and early winter, but are not released from the marsupia until the following spring and early summer. Short-term or tachytictic breeders, spawn in early spring and release glochidia in late summer and early autumn. The anodontine and lampsiline unionids generally belong to the first category of breeders while amblemine unionids, and margaritififerids belong to the second category.

Among the tachytictic breeders, Unio spp. (Negus, 1966; Tudorancea, 1969) and Pleurobema cordatum (Scruggs, 1960; Yokley, 1972) bear all stages of larval development in the marsupia during summer, and as embryogenesis proceeds so rapidly, multiple release of glochidia is possible each year.

Of the tropical species of freshwater mussel, Seshaiya (1969) found glochidia in the marsupia of Lamellidens during July and August, and again during December, indicating annual production of at least two broods of larvae at extremes of season. The African mutelids Mutela bourquignati (Fryer, 1961) and M. dubia, and unionid, Caelatura mossambicensis (Kenmuir, 1981a) breed throughout the year in tropical Africa, spawning and brooding repetitively (Kenmuir, 1981b). Aspatharia wahlbergi, however, in Lake Kariba breeds seasonally, Kenmuir (1981a) finding gravid individuals only during the summer months. Kenmuir (1981b) attributed repetitive spawning to the warmer environment of tropical waters that presumably stimulated spawning and breeding activity in mussels. Winter lulls in the breeding intensity of repetitive spawners were also noted by Kenmuir (1981b). Kenmuir (1981a) suggested that flowing water may be needed to stimulate breeding in A. wahlbergi, a known riverine mussel. Dudgeon and Morton (1983) reported seasonal breeding of Anodonta woodiana in Plover Cove, Hong Kong, with late spring spawning followed by glochidial release until mid summer. Dudgeon and Morton suggested that cooler autumn and winter temperatures might slow glochidial development in Anodonta from temperate regions, thereby contributing to the bradytictic condition (i.e. brooding of glochidia overwinter). The short incubation period in A. woodiana (one month) was believed to result from much higher winter temperatures sustained in Plover Cove.

Seasonal variations of glochidial release amongst the bradytictic Anodonta over a broad geographical range - Britain (Negus, 1966; Dartnall and Walkey, 1979), Italy (Giusti et al., 1975) and North America (Heard, 1975; Wiles, 1975), were attributed in part by Giusti et al. (1975) to result from temperature variations that may stimulate differential release over a wide latitudinal gradient. Giusti et al. (1975) stressed the importance of determining the exact period of appearance of glochidia upon fish in order to draw conclusions concerning the duration of reproductive cycles. Monitoring glochidial release by periodic examination of host fishes and by drift in fact, is assuming increasing importance in evaluating seasonal breeding cycles of unionaceans (Giusti et al. 1975; Wiles, 1975; Dartnall and Walkey, 1979; Porter and Horn, 1980; Trdan, 1981; Zale and Neves, 1982a; Dudgeon and Morton, 1983; Young and Williams, 1984a).

Of the hyriids of temperate Australasia, distinct seasonality in breeding cycles has been reported only for Cucumerunio novaehollandiae (Jones and Simpson, in prep.). This species breeds in autumn in southeastern Australia. Otherwise, breeding may be more protracted. The glochidia of Hyridella drapeta (Atkins, 1979) for example were observed on fish throughout the year. Except for the months when no fish were available for examination (between May and September), glochidia of Velesunio ambiguus were always present on their fish hosts (Hiscock, 1951). However, peak infections on the hosts of H. drapeta were noted during spring (Atkins, 1979), while inspection of the marsupia of V. ambiguus by Walker (1981b) showed two peaks in glochidial production, one in spring and another in late summer and early autumn. Alathyria jacksoni showed similar patterns to V. ambiguus in larval production (Walker, 1981b). McMichael and Hiscock (1958) suggested breeding of Hyridella was seasonal in southeastern Australia, occurring from spring through to summer. Jones and Simpson (in prep.) substantiated this claim for three sympatric Hyridella species, further adding that a series of synchronised, repetitive

breeding cycles were likely for H. australis during the warmer months. Percival (1931) found 'ripe' glochidia in the marsupia of H. menziesi from New Zealand, from the end of November to the end of January.

The Australasian hyriids therefore, appear to have broader breeding periods than counterparts in northern temperate regions, and all have the potential to produce more than one larval brood per year. This may possibly reflect the milder and more equitable climates of the southern temperate latitudes. Latitudinal variations have been previously implicated (e.g. Kenmuir, 1981a,b; Dudgeon and Morton, 1983) as having some effect on reproductive patterns of freshwater mussel groups.

Apart from the great variety recorded in the periods of gametogenesis, glochidial incubation and release among the different species of freshwater mussels (Dudgeon and Morton, 1983) considerable temporal and spatial variations in breeding patterns have also been reported at the intraspecific level. Connor (1909) and Porter and Horn (1980) observed that the time of breeding of individuals of the same species from the same location varied from season to season, attributable by Connor (1909) at least, to climatic variation. Over a broad geographical range, Margaritifera margaritifera has been reported to produce one (Smith, 1976; Young and Williams, 1984a) or two (Wood, 1974a; early North American studies cited by Smith, 1976) broods of larvae each breeding season, while Bjork (1962) noted regional differences in glochidial release in Sweden. Haukioja and Hakala (1978b) also noted variation in reproductive timing among Finnish populations of Anodonta piscinalis. North American populations of A. imbecilis may complete one or several cycles throughout the breeding season. Presumably climatic differences account in part for these disparities observed in breeding patterns between the various localities. On a more regional scale however, A. peggyae in Florida may complete two cycles in the year in lakes or only one in streams (Heard, 1975). In Zimbabwe, differences in breeding patterns of freshwater mussels between Lake Kariba and Lake McIllwaine were attributed by Kenmuir (1981b) to temperature variations. Within the same stream, the differences in water temperatures between upstream and downstream sites may result in variations in timing of respective breeding cycles (Walker, 1981b; Young and Williams, 1984a; Jones and Simpson, in prep.). Even within the same lake, Porter and Horn (1980) recorded unexplained variations in the time of breeding of mussels between different zones, in the same season.

Heard (1975), recording two sympatric and congeneric Anodonta that had completed one and two annual breeding cycles respectively, concluded that breeding cycles might not be influenced entirely by conspicuous environmental factors such as water temperature and presence or absence of current. In relation to glochidial release at least, a number of workers have drawn attention to the correspondence of time of release of glochidia and the habits and activities of the host fishes; or among sympatric species different periods of release may have resulted from competitive interactions amongst each other for a limited number of hosts (e.g. Kat, 1984). Fish relations thus, are other factors that may influence the seasonal breeding patterns of freshwater mussels.

A further factor that has received little attention, is the effect of

adverse environmental conditions (other than low water temperatures) upon the reproductive cycle of freshwater mussels. The lack of consideration is even more surprising given the known sensitivities of gravid females (see below) and that potentially stressful environmental conditions (e.g. high water temperatures, periods of high or low discharge, turbidity) may in certain environments be highly seasonal.

Numerous authors have noted that gravid freshwater mussels are sensitive to sudden changes in water temperature, rough handling, toxic substances, starvation and especially oxygen deficiency and imperfect aeration of the water, responding under these conditions by aborting eggs and larvae (e.g. Lefevre and Curtis, 1912; Coker *et al.*, 1921; Allen, 1921; Matteson, 1948, 1955; Hiscock, 1951; Tudorancea, 1969; Yokley, 1972; Young and Williams, 1984a).

In relation to low dissolved oxygen concentration, resultant abortion is assumed to occur in order that the gills may be more effectively employed for respiration. Lefevre and Curtis (1912) noted a correlation between the number and portion of gills used as marsupia and susceptibility to abortion. Species using all four gills (e.g. Quadrula) were notoriously sensitive to disturbances and imperfect aeration of the holding water; species of Anodonta, however, using only two gills and possessing other structural modifications of the gills to enhance water circulation, rarely aborted under these conditions. Gravid Lampsilis ventricosa were shown by Matteson (1955) to be more sensitive than nongravid individuals to anoxia. He determined a mean threshold for the gravid mussels at which abortion occurred at approximately 1.8 mg/l dissolved oxygen higher than nongravid ones. Allen (1921) cited studies that showed that the volume of water siphoned in the gravid condition was much less than in the nongravid condition. Allen showed that the feeding processes of freshwater mussels were similarly hindered in gravid females. He indicated that the modifications made in the marsupia were adaptations for water circulation about the eggs and larvae, sufficient for the aeration of these but not of the mother. Thus the gravid gills are unable to meet all the demands (brooding, feeding and respiration) made upon them (Allen, 1921).

In relation to field conditions, Matteson (1955) observed abortion in gravid Lampsilis ventricosa in spring, in unseasonably warm, shallow waters.

A4.3 Glochidial release and parasitism

Kat (1984) recently presented a thorough review of parasitism in unionacean bivalves mainly as it applies to the North American and European fauna. A survey of glochidial hosts of the North American unionaceans as well as a review on the subject had earlier been collated by Fuller (1974). Walker (1981b) also presented a synopsis of the subject and completed studies appropriate to hyriid unionaceans. While no better review of the literature is possible at this stage, the following survey provides an adequate background for the studies presented here.

The mature glochidium, free from the vitelline membrane is a bivalved shell which, depending upon the group, may or may not bear teeth or

hooks at the tip of each valve. A thin tissue of mantle cells lines the inner surface of the valves and some of these cells possess fine sensory hair-like projections. The two valves are cross-banded by a single adductor muscle and in some groups enclose a long and sticky larval thread.

The glochidia of Australian hyriids are uniformly subtriangular and toothed but variation in size and shape between species is not as slight as originally thought by McMichael and Hiscock (1958), Atkins (1979) and Walker (1981b). Jones and Simpson (in prep.) noted that the glochidia of Cucumerunio novaehollandiae and Hyridella australis are much smaller than those of species previously described, and those of the former species possess a unique shell sculpture. With the addition of H. depressa, all three species also bear either a pair of hooks on each valve (C. novaehollandiae and H. australis) or a single bifurcated hook (H. depressa). The glochidia of other Australian species described, bear single, individual hooks upon each valve. Larval threads have been reported on the glochidia of H. drapeta (Atkins, 1979) and Velesunio ambiguus (Hiscock, 1951; Walker, 1981b). Walker (1981b) reported that the glochidial shell margin of V. ambiguus is marked by fine ridges, thought to assist in attaining a firm hold on host tissue. With respect to the genus Velesunio at least, Walker (pers. comm.) has found no observable differences in morphology and morphometry between species.

Studies of glochidia have shown morphology and morphometry to be of useful taxonomic importance. Glochidial morphology has been used to distinguish broad groups of freshwater mussels (Parodiz and Bonetto, 1963) while morphometry has been used to distinguish congeners and even conspecifics (Wiles, 1975; Rand and Wiles, 1975). Rand and Wiles (1975) noted, however, that identification of glochidia to species within a genus was still a formidable problem wherever congeners occurred. Variation in size (Tudorancea, 1972; Walker, 1981b) and structure (Porter and Horn, 1980) observed between glochidia from the same parent moreover, does not make the task of separating morphologically similar larvae of congeners any easier. McMichael and Hiscock (1958) considered that the larval stages of Australian hyriids would be of limited value taxonomically. However, the larvae of Hyridella in southeastern Australia differ sufficiently (Jones and Simpson, in prep.) to suggest that differentiation of species within the genus may be a relatively simple procedure.

While all unionaceans with known life histories exhibit a period of obligate parasitism on a vertebrate host, Anodonta imbecilis at least, has been reported to complete development to the juvenile stage in the marsupial demibranchs (Howard, 1914) or to be discharged by the mother to parasitize fish in the usual manner (Heard, 1975; Stern and Felder, 1978). Walker (1981b) cites an unconfirmed report that an isolated population of Velesunio ambiguus could also apparently pass through metamorphosis in the parental marsupia.

Water temperature may be the direct stimulus required for release of glochidia from the parent, a number of workers having recorded diurnal, day to day, and seasonal fluctuations in numbers of planktonic or parasited glochidia as a function of temperature variation (Tudorancea, 1972; Atkins, 1979; Dartnall and Walkey, 1979; Zale and Neves, 1982a; Dudgeon and Morton, 1983; Young and Williams,

1984a). Fish habits, have assumed increasing importance in determining the seasonal timing and duration of glochidial release. While Coker *et al.* (1921) and Young and Williams (1984a) have drawn attention to the correspondence of host fish activity and temperature cycles, release of glochidia has been shown to coincide with host fish migrations (Davenport and Warmuth, 1965), breeding activities of the host fishes (Yokley, 1972; Zale and Neves, 1982a, b; Kat, 1984) and the seasonal presence of the fishes over mussel beds (Zale and Neves, 1982a, b). Seasonal differences in timing and duration of glochidial release amongst sympatric species are thought by some authors to be indicative of selection to avoid competition for fish hosts (Stern and Felder, 1978; Trdan and Hoeh, 1982; Dudgeon and Morton, 1983; Kat, 1984).

While the glochidia of lampsiline unionids are discharged into the water through minute pores in the marsupial gills, other unionaceans discharge glochidia through the exhalent siphon. Various behavioural mechanisms and structural modifications are used by some lampsilines by which females enhance successful attachment of glochidia upon the hosts. Mimicry of the mantle flaps is used by these species to imitate the appearance and pulsating actions of prey items of fish; disturbance of the structures by predatory host fishes results in the release of glochidia by the female (Evermann and Clark, 1917; Harman, 1970; Clarke, 1973; Kraemer, 1979; Zale and Neves, 1982b). Otherwise, glochidial attachment to the host may be enhanced by the suspension of glochidia in a network of mucous threads (Matteson, 1948, 1955; Yokley, 1972; Atkins, 1979). Host fishes may even be attracted to these suspended particles as food items (Yokley, 1972; Dartnall and Walkey, 1979). Other devices are available for assisting glochidial attachment: glochidia may descend through the water in an opened condition, thus slowing downward movement (Matteson, 1955); the larval thread itself may act as a dragline or by its long and sticky nature aid in direct attachment (Wood, 1974b).

The refrigerated glochidia of Anodonta grandis remained viable for approximately 8 months according to Trdan and Hoeh (1982). Under normal field situations, however, glochidia may survive up to 14 days in the plankton (Pennak, 1953; Telda and Fernando, 1969; Fuller, 1974). The viability of the glochidia of Alathyria jacksoni and Velesunio ambiguus spanned from 50% of the glochidia dead after 5 days at 25° C, to 15 days at 12° C (Walker, 1981b).

Although the glochidia of a number of unionacean species have been shown to parasitise and successfully metamorphose from tadpoles (Seshaiya, 1941; Walker, 1981b); these species normally parasitise fish. The only known host of Simpsoniconcha ambigua in North America is the salamander, Necturus maculosus. This is the only documented exception to the rule that parasitism and subsequent glochidial metamorphosis is normally completed upon a fish host.

One or more species of fish are host to the unionacean glochidium. Strict species specificity in which the parasite is limited to only one host - e.g. Elliptio complanata (Matteson, 1948), Simpsoniconcha ambigua (Howard, 1951), Anodonta implicata (Davenport and Warmuth, 1965), Pleurobema cordatum (Yokley, 1972), Villosa vanuxemi (Zale and Neves, 1982a), appears to be exceptional. While the maximum number of reported hosts for any unionacean glochidium exceeds 30 (for A.

grandis - Trdan and Hoeh, 1982), using Fuller's (1974) review on the number of parasitic relationships elucidated up to then, Kat (1984) estimated that North American species averaged 4.5 hosts each. From this figure, Kat concluded that host specificity in unionaceans was low, proposing that this was the result of an inability to predict the exact identity of the fish that would come into contact with the discharged glochidia.

Australian hyriids apparently observe little host specificity. Walker (1981b) recorded a variety of native fish endemic to the Murray River drainage that served as hosts for Velesunio ambiguus (10 fish species) and for Alathyria jacksoni (8 species), while larval metamorphosis could be completed on several exotics. Atkins (1979) similarly reported that the fish, native to the respective study areas are the normal hosts of Hyridella drapeta (2 endemics and 1 exotic) and H. depressa (2 endemics). The intensity of infection reported for H. drapeta ranged from 1-36 glochidia per fish, and for H. depressa, 6-37. Percival (1931) noted high infections of up to 6 glochidia on the two recorded host fishes (individuals of which were less than 1 cm in length) of H. menziesi.

While host specificity may be low, some fish groups serve disproportionately as hosts to freshwater mussels. Hosts occurring in sympatry with mussels may observe heavy infections. Thus, nesting and territorial centrarchids (Fuller, 1974; Zale and Neves, 1982, a, b; Kat, 1984), molluscivorous fish (Surber, 1912; Fuller, 1974; Kat, 1984) or bottom feeding or dwelling fish in general (Surber, 1912; Lefevre and Curtis, 1912; Percival, 1931; Giusti et al., 1975; Kenmuir, 1980) may be heavily infected and host many different species of mussel.

Generally, the intensity of glochidial infection upon host fishes is reportedly low (Surber, 1912; Evermann and Clark, 1917; Coker et al., 1921; Darnall and Walkey, 1979; Trdan, 1981; Young and Williams, 1984a). Only 8.9% of the 3671 fish examined by Coker et al. (1921) during the warmer months for example, were infected. The mean number of glochidia per infected fish was 125 while the range was 1-416. From his own studies and reviewing previous work, Trdan (1981) noted a negative correlation between the number of species serving as hosts for glochidia of particular unionids, and the infection rate (percent infected and intensity). Where host specificity is high, Trdan proposed that ecological and behavioural factors became important in the initial host-parasite contact, leading to conditions which support a high intensity of infection, a high percentage of the population infected, or a combination of both. Darnall and Walkey (1979) also drew attention to factors such as viability and dispersal of discharged larvae, behaviour of larvae and hosts, and whether or not glochidia are released en masse, in influencing the intensity of infection upon host fishes. Mussel density (Stern, 1978; Bauer, 1979; Kat, 1984) and the immune reaction of the host that strengthens with repeated infections (Fuller, 1974; Stern, 1978; Kat, 1984) are also factors of influence.

Attachment to the host tissues relies mostly on chance, but both tactile and chemical stimuli trigger glochidial attachment (Lefevre and Curtis, 1912; Wood, 1974b; Young and Williams, 1984b). Glochidia cannot discriminate between proper and unsuitable hosts at initial

attachment and the well developed immune response reacts to slough off glochidia after 4-7 days (Kat, 1984) if these are attached to unsuitable hosts.

Glochidia are ectoparasites on the fins, gills and body surface of fishes. Hooked or toothed glochidia generally attach to the exterior or strong and exposed parts of the fish host (such as the fins) whereas hookless glochidia generally parasitise the soft and fine gill filaments. There are many recorded exceptions to this rule, however (Wiles, 1975; Giusti *et al.*, 1975; Meyers and Millemann, 1977; Atkins, 1979; Dartnall and Walkey, 1979; Zale and Neves, 1982c). However, Dartnall and Walkey (1979) concluded that availability of larvae, fish size, type of food selection and feeding behaviour might interact to determine the distribution of the glochidia on fish hosts. Giusti *et al.* (1975) found for example that the gills of bottom feeding, host fishes harboured more glochidia of Anodonta cygnea (larvae of the hooked variety) than predatory fishes.

Of the toothed, Australasian hyriids, the glochidia of Velesunio ambiguus (Hiscock, 1951; Walker, 1981b) and Alathyria jacksoni (Walker 1981b) chiefly parasitise the fins and general body surface of their hosts, and few instances of gill infestation were recorded in field collections. General body surface parasitism has been observed for Hyridella menziesi (Percival, 1931), although the glochidia of other Hyridella species may attach to both gills and general body surfaces (Atkins, 1979). The glochidia of H. drapeta apparently attach exclusively to the gills of host fishes (Atkins, 1979).

Among sympatric unionaceans, Stern and Felder (1978) observed the glochidia of two different species concurrently parasitising different areas of the same fish host (fins and gills). They thought this mechanism may have evolved to reduce competition for the same host in sympatric species.

Encysted glochidia appear as small, semi-opaque tubercles on the host tissues. Qualitative changes involving organogenesis occur during encystment but only in a few species (Surber, 1912; Wiles, 1975; Young and Williams, 1984b) do the glochidia increase in size while still encysted.

A summary of the periods of parasitic duration upon host fishes, reported for a wide range of freshwater mussel taxa distributed worldwide, are summarized in Table A4.2. From these data, it is apparent that for temperate unionaceans under summer conditions, the parasitic period generally lasts from 10-30 days. Although factors such as nutritive condition of the host (Lefevre and Curtis, 1912) and larval maturity (Coker *et al.*, 1921; Zale and Neves, 1982b) may modify the time of metamorphosis, temperature is considered to be the most important factor determining the duration of the parasitic period. Thus, Lamellidens from tropical India has a very short parasitic stage, lasting in the prevailing warm waters for only several days (Seshaiya, 1969). The glochidia of Margaritifera margaritifera overwinter on fish in Scotland (Young and Williams, 1984b) and in two of the five populations studied by Bauer (1979) in Bavaria. Bauer found that the time at which glochidia completed development (before or after winter) was genetically determined rather than determined by environmental factors. In Massachusetts (USA) however, temperatures

Table A4.2 Duration of the parasitic period upon host fishes (and amphibia) in relation to temperature, reported for the larvae of species of freshwater mussel studied worldwide to date.

Species	Region	Authority	Duration of parasitic period (days)	Temperature (°C)
<u>Margaritifera margaritifera</u>	Scotland	Young and Williams (1984a)	290	?
<u>M. margaritifera</u>	Bavaria	Bauer (1979)	c. 14-270	?
<u>M. margaritifera</u>	U.S.A.	Fustish and Millemann (1978)	84	12
<u>M. margaritifera</u>	"	Smith (1976)	36	?
<u>M. margaritifera</u>	"	Roscoe and Redelings (1964)	28-35	?
<u>Anodonta grandis</u>	"	Trdan and Hoeh (1982)	6	21
<u>A. imbecilis</u>	"	"	8	21
<u>A. californiensis</u>	"	D'Eliscu (1973)	26-27	20
<u>A. cygnea</u>	Europe	Harms (1909)	80	8-10
"	"	"	12	20
<u>Villosa nebulosa</u>	U.S.A.	Zale and Neves (1982b)	38-105	16.5
"	"	"	10-21	24.7
<u>V. vanukemi</u>	"	"	28-49	16.7
"	"	"	8-17	25.0
<u>Medionidus conradicus</u>	"	"	10-20	16.0
<u>Lampsilis fasciola</u>	"	"	30-47	19.2
<u>L. radiata siliquoidea</u>	"	Coker <i>et al.</i> (1921)	12-28	?
<u>L. r. siliquoidea</u>	"	Tedla and Fernando (1969)	98	?
<u>Symphynota costata</u>	"	Lefevre and Curtis (1912)	74	10
<u>S. complanata</u>	"	"	14-16	16
"	"	"	9-13	17.8
<u>Elliptio complanata</u>	"	Matteson (1948)	18	?
<u>Simpsoniconcha ambigua</u>	"	Howard (1951)	210	?
<u>Pleurobema cordatum</u>	"	Yokley (1972)	14-18	21
<u>Unio sp.</u>	Europe	Harms (1909)	26-28	16-17
<u>Lamellidens spp.</u>	India	Seshaiya (1969)	3	29-30
"	"	"	6-8	24-25
<u>Velesunio ambiguus</u>	Australia	Hiscock (1951)	22-23	20-22
<u>V. ambiguus</u>	"	Walker (1981b)	22-24	18
"	"	"	16-18	25
<u>Alathyria jacksoni</u>	"	"	22-24	18
"	"	"	16-18	25
<u>Mutela bourquignati</u>	Uganda	Fryer (1961)	25	24-25
<u>M. dubia</u>	Zimbabwe	Kenmuir (1980)	21	25-28

? Not reported

may be sufficiently high over the warmer months that glochidia of M. margaritifera develop quickly enough to achieve full development and drop off the hosts before or after the summer peak in temperature (Smith, 1976). Similarly the glochidia of Lampsilis radiata siliquoidea from Minnesota (USA) are released from the hosts in late summer, but may overwinter as parasites in cooler regions (Trdan, 1981).

APPENDIX 5

FOOD INGESTION, CONDITION AND ANNUAL PRODUCTION

A5.1 Food ingestion

There is difference of opinion over many aspects of the feeding ecology of freshwater mussels, particularly in regard to the potential food items that are ingested and that may be assimilated and whether or not mussels are selective in the types of particles ingested.

All freshwater mussels are suspension feeders, and interspecific differences in feeding among the various species are apparently minimal (Evermann and Clark, 1917; Coker *et al.*, 1921). Bronmark and Malmqvist (1982), finding no significant difference in the size distribution of particles ingested by two sympatric unionids, argued that suspension feeders should be generalists where variability of the food resource is high and predictability low.

A variety of observations on the food of mussels, however, has accumulated. Some have claimed or observed that the food is of plant origin: Evermann and Clark (1917) recorded mud and algae in the guts of unionids but noted that the food of lake mussels comprised more algae and organic material than the chiefly mud component found in river mussels; Coker *et al.* (1921) thought detritus formed the main bulk of the food of freshwater mussels, and observed that vegetable food was preferred to animal substances; the food of Margaritifera margaritifera was recorded by Hendelberg (1960) as consisting mainly of vegetable detritus; and finally Clarke (1973) states broadly, that all Unionidae are phytophagous filter-feeders. Others believe any suspended material will serve as food for mussels: Allen (1914) thought the gut contents comprised any finely divided, living or decaying tissue; nutrients including fats in solution according to Coker *et al.* (1921) may be assimilated; Allen (1921) stressed the importance of nanoplankton including bacteria in the diet of mussels; Churchill and Lewis (1924) recorded that the stomach contents included microscopic animal and plant forms, and debris or detritus resulting from the decay and disintegration of such forms; the food of mussels according to Pennak (1953) consists of zooplankton, phytoplankton and organic detritus; and according to Fuller (1974), the diet consists primarily of detritus and animal plankters - he considered that algae were commonly overestimated as food value.

Fuller's (1974) conclusion above was no doubt influenced by observations such as those of Coker *et al.* (1921) that much of the algae and diatoms passing through the digestive tract of freshwater mussels remained intact and unchanged by the digestive processes. This has been observed not only in other studies of freshwater mussels (Allen, 1921; Churchill and Lewis, 1924), but for corbiculaceans (Gale and Lowe, 1971), other freshwater forms (e.g. Dreissena polymorpha - Ten Winkel and Davids, 1982), and marine bivalves as well (e.g. Coe and Fox, 1944; Jorgensen, 1975; Hildreth, 1980). In accordance with this observation, it is well known that certain forms such as diatoms and some flagellates are immune to digestive enzymes by nature of their resistant tests or cellulose cell walls. However, Allen (1914, 1921) concluded that ingestion was continuous but digestion discontinuous and dependent upon demand for nutrition; he showed that

apparently resistant diatom species frequently found undigested, were digested when fed to starved mussels. It is of further significance that in terms of utilisable energy, living phytoplankton in the diet of filter- and deposit-feeders has been found to be superior to both bacteria and detritus (Moore, 1975; Jorgensen, 1975). Wallace *et al.* (1977) added that the high oil or fat content of diatoms may contribute significantly to the nutrition of filter feeders.

With respect to the food of juvenile freshwater mussels, Matteson (1948) noted that none of the common items of the adult diet were seen to be ingested by the young. He thought it possible that the young might utilise considerable quantities of bacteria and dissolved organic material. Howard (1922), however, stated that the food of juveniles appeared to be similar to that of the adult, namely microscopic plants and animals. For the marine oyster, *Pinctada margaritifera* at least, Nasr (1984) noted that the variety of food increased as the oyster grew older.

In other freshwater bivalves, very few zooplankters have been observed in the diet, which generally comprises algae and detritus (Gale and Lewis, 1971; Wallace *et al.*, 1977; Stanczykowska, 1977). A similar situation may apply to the diet of marine bivalves (e.g. Fox, 1936; Nasr, 1984).

Controversy still exists as to whether bivalves exercise selectivity over ingested particulates. Based mainly on comparisons of stomach contents to the suspension in surrounding waters and the direct observation of various particles on the exposed pallial surfaces, various interpretations have been advanced. In relation to freshwater mussels, Allen (1914) concluded that selection is exercised at the inhalent siphon, palps, and mouth, mussels avoiding most material with no food value and rigidly excluding injurious substances. While the apparent absence of sand and silt from the stomach contents was indicative of selection to Allen (1914, 1921), the inorganic debris present in the ingested materials examined by Coker *et al.* (1921) and Churchill and Lewis (1924) suggested to these authors an absence of selection. Coker *et al.* (1921) noted further, that the stomach contents corresponded to the composition of the surrounding plankton, in type and proportions. Rejection of potential food items was thought by the preceding authors to be accomplished not by ciliary sorting but by ceasing to feed when unwanted substances were present. Churchill and Lewis (1924) felt that everything small enough (whether of nutritive value or not) and not active enough to escape was ingested by mussels; from the heterogeneous mass, the alimentary canal digested and absorbed what it could with the rest passing on. Nevertheless, on Allen's (1914) results, it has been assumed by some, that freshwater mussels exercise some selection over ingested food materials (Pennak, 1953; Clarke and Berg, 1959). Bronmark and Malmqvist (1982) in feeding experiments upon freshwater mussels, noted that the particle size distribution of a charcoal slurry found in the guts of two unionids was significantly smaller than that in the surrounding waters, indicating a sorting and selection capability.

Amongst other freshwater forms, corbiculaceans apparently exhibit very little selection (Gale and Lowe, 1971; Wallace *et al.*, 1977; Hornbach *et al.*, 1984). Gale and Lowe (1971) noted, however, that fewer diatoms were represented in the guts of *Sphaerium transversum* than in

water samples, while the dominance of a few forms of diatoms in the guts of Pisidium (Neopisidium) conventus suggested possible selection to Heard (1963). Dreissena polymorpha according to Ten Winkel and Davids (1982), may select for the size and type of algae ingested, but the selection apparently fails when the animal is starved. According to various authors, marine bivalves may (e.g. Fox, 1936; Bernard, 1974; Hughes, 1975) or may not (e.g. Winter, 1978; Nasr, 1984) exercise active selectivity over ingested materials.

Various environmental factors may influence feeding in bivalves. Some freshwater bivalves have diurnal rhythms of feeding (Jorgensen, 1975; Winter, 1978; Walz, 1978; McCorkle *et al.*, 1979). Notably, the hyriid Velesunio ambiguus observes the greatest number of shell openings during the night (3-6 a.m.) (Hiscock, 1950). With increasing food concentration, bivalves generally increase their ingestion rate; a threshold value is reached, however, beyond which the rate remains constant (Winter, 1978). In practice, nevertheless, ingestion (and therefore growth) is normally submaximal and tends to vary with food levels (Jorgensen, 1975). Ingestion rates also increase with increasing temperature (Winter, 1978) and in freshwater bivalves feeding may cease in winter (Matteson, 1955; Gale and Lowe, 1971). In both freshwater (Gale and Lowe, 1971) and marine bivalves (Riisgard and Randlov, 1981) feeding may be suppressed during periods of low dissolved oxygen. Hornbach *et al.* (1984) observed that filtration rates of the sphaeriid Sphaerium striatinum peaked in association with reproductive condition of the animal rather than with levels of food or temperature.

A5.2 Condition

Studies of body weight variations (i.e. condition) in freshwater mussels are few, and generally cursory in nature. Using shell length versus dry weight regression equations, Cameron *et al.* (1979) found generally no differences between sexes or sizes of mussels, and only minor variations of body weights with season in some unionids studied. Golightly and Kosinsky (1981) observed similarly, that the length/weight relationships for other unionids species were similar between locations and seasons. Using a condition index based upon flesh weights in relation to shell length of Anodonta piscinalis to depict the availability of resources at a certain time and place, Haukioja and Hakala (1978b) recorded, however, that annual variations in condition were considerable. No factors influencing the observed fluctuations were elucidated.

In a more thorough investigation, Huebner (1980) studied seasonal body weight fluctuations of A. grandis and Lampsilis radiata using length/dry weight regression equations. Body weights fluctuated seasonally and both species peaked in condition in spring. Huebner accounted for seasonal weight changes according to whether or not females were brooding larvae, by differences in food availability and quality and by possible disparities between tissue and shell growth. Other than the period when higher body weights were recorded for females brooding glochidia in the marsupia, differences in body weights between the sexes were absent. In other studies, Tudorancea (1969) observed that flesh weights of Unio tumidus were higher in the Crapina than the Jijila marshes of Rumania; using a condition index, Tudorancea and Gruia (1968) observed that condition of U. crassus in

the Nera River (Rumania) was highest where densities were minimal and vice versa. In the latter study, Tudorancea and Gruia thought that the poor condition of mussels measured at high mussel densities was due to poor nourishment (presumably from competition amongst individuals for food at least).

In studies of other freshwater bivalves, Stanczykowska (1964) observed very small body weight variations of Dreissena polymorpha within European lakes, but considerable variations between lakes. As in the Nera River for U. crassus, condition of D. polymorpha was highest where densities were lowest, and vice versa. Stanczykowska pointed to the deleterious influence of overcrowding. In later studies, Stanczykowska (1977) recorded seasonal weight increases of D. polymorpha at the time of gonadal development, while between lakes, the main factor affecting variability in body weight was attributed to trophic conditions. Higher trophic conditions either felt directly, or indirectly through higher water temperatures and lowest mussel densities (i.e. a reduction of competition), resulted in higher body weights of mussels. Stanczykowska noted that algal blooms of specific, unpalatable algae could inhibit food intake and result in a decline in body condition in some populations of D. polymorpha. The same phenomenon has been reported in marine bivalves by Pieters et al. (1980).

In contrast to freshwater forms, condition cycles in marine bivalves are well known. Generally condition peaks in summer and falls in winter, in association with gonadal maturation and spawning respectively (e.g. Hughes, 1970; Peddicord, 1977; Comely, 1978; Newell and Bayne, 1980; Hickmann and Illingworth, 1980). Several authors have drawn attention to the correspondence between food availability (as measured by algal concentrations) and condition (Taylor and Venn, 1979; Newell and Bayne, 1980; Pieters et al., 1980; Hickman and Illingworth, 1980). Thus bivalves time the resource-consuming phase of reproduction to coincide with periods when food resources are abundant.

Hickmann and Illingworth (1980) and Shafee (1980) noted, however, that seasonal changes in condition were quite complex, and resulted from a variety of factors including food, temperature and metabolic activities of bivalves. Hickman and Illingworth (1980) observed generally, that mean condition and latitude were negatively correlated in marine bivalves, and that broadly, temperature and condition were inversely related. Dudgeon and Morton (1983) thought that in organisms generally, high prevailing temperatures would cause an increase in respiration (i.e. maintenance costs), thereby reducing energy available for somatic growth.

High suspended solids have also been implicated as the cause of poor condition in marine bivalves. Peddicord (1977) found that condition of Rangia cuneata was lowest on mud substrates. The mud per se was thought to have no effect upon condition, but the high suspended solids prevailing above the substrates were thought to necessitate frequent cleaning of the filtering apparatus. Peddicord thought that considerable energy might be consumed in filtering the solids, compacting them into pseudofaeces and ejecting them. He suggested that clams probably reduced or ceased their filtering activities during periods of high turbidity to conserve the energy required to

sort and reject particles.

Noting that condition decreased with increasing size, various authors have concluded that the same bivalve species exhibit a senility phase (e.g. Comely, 1978). Hickman and Illingworth (1980) thought that the lower condition observed in larger individuals of Perna canaliculus, might be caused by the increased energy needed for basal metabolism; this requirement would result in less food available for somatic growth. Amongst freshwater mussels, Haukioja and Hakala (1978b) noted that condition of Anodonta piscinalis over a number of populations correlated negatively with length of the reproductive life span.

A5.3 Annual production

Production, or the rate of tissue elaboration of organisms, is in terms of ecosystem functioning, the means by which energy is made available for transmission from one trophic level to another (Waters, 1977). Production and biomass studies allow an evaluation of the roles of the constituent species of a community. Considerable interest therefore has been expressed in the annual turnover ratio, i.e. the ratio of production to standing stock (P/B), as a means of assessing the contribution made by organisms to the functioning of ecosystems. Generally, for a given group of organisms, the P/B ratio is reasonably constant and according to Waters (1977) for aquatic organisms, is usually independent of environmental factors such as water fertility and temperature. Annual P/B ratios are most clearly a function of voltinism (life spans), and expanding and/or short-lived populations observe a high ratio as opposed to overcrowded, stunted and long-lived populations that may observe a much lower ratio. The ratio therefore, decreases with increasing life span, because growth rates are high in the early years.

Known biomass, annual production and P/B ratios of freshwater mussels (shell free, dry weight) from various ecosystems are summarised in Table A5.1. The P/B ratios as expected (Waters, 1977) are relatively constant for the group, and variations are apparently related to the age distributions of the respective communities. (Ratios may be expected to be inversely related to the individual life span of mussel populations.) From Table A5.1, low P/B ratios (as discussed below) are typical of freshwater mussel populations. Thus, although the standing crop of freshwater mussels may be very high, the annual production is reportedly low especially in comparison to the total macrobenthic production. The low P/B ratios observed, have been variously attributed to the long-lived nature of mussel populations and the consequent accumulation of large amounts of organic matter over a number of years (Negus, 1966; Tudorancea and Florescu, 1968; Magnin and Stanczykowska, 1971; Lewandowski and Stanczykowska, 1975; Strayer et al., 1981). Except for predation in the earliest age classes (Negus, 1966), the low ratios indicate that freshwater mussel communities play a trivial role in the ecosystem, in terms of their contribution of biomass and energy to the predators of the trophic level above.

Short-lived corbiculaceans, by contrast with freshwater mussels, are an important food source to animals in higher trophic levels, and observe much higher P/B ratios, generally in the range 1-4 (e.g. Hamill et al., 1979). Marine bivalves also contribute significant

Table A5.1 Annual production, biomass, and turnover (P/B) ratios reported for freshwater mussel communities from various freshwater ecosystems worldwide.

Ecosystem	Biomass (g/m ²)	Production (g/m ² /year)	P/B	Source
Thames River (UK)	12.1	2.1	0.17	Negus (1966)
Lac Saint-Louis (Canada)	0.71	(0.07)*	(0.10)	Magnin and Stanczykowska (1971)
Lac des Deux Montagnes (Can.)	8.6	1.7	0.20	"
Crapina pool, Danube River (Rumania)	4.8	1.1	0.23	Tudorancea (1972)
Mikolajskie Lake (Poland)	0.20	0.07	0.35	Lewandowski and Stanczykowska (1975)
Mississippi River (USA)	3.26	0.482	0.15	Coon <i>et al.</i> (1977) (<i>Amblema peruviana</i> only)
Lake Kariba (Zimbabwe)	2.55	0.876	0.34	Kenmuir (1980)
Mirror Lake (USA)	0.05	0.006	0.12	Strayer <i>et al.</i> (1981)
"	0.74	0.057	0.08	" (shells)

* Value apparently incorrect according to Strayer *et al.* (1981).

biomass and energy to predators of the trophic level above, and ratios may range from 0.15 to 2.6 (Hibbert, 1976). Production in the freshwater bivalve Dreissena polymorpha in Europe, is low, but P/B ratios are higher than those observed for freshwater mussels, ranging from 0.42-0.65 (Stanczykowska, 1977).

While predation upon freshwater mussels (including D. polymorpha) is thus generally unimportant, nevertheless, mussels may contribute in other profound ways to the functioning of ecosystems. Firstly, mussel flesh (consumed by predators, scavengers or decomposers) has a very high caloric content to pass on to other trophic levels (Tudorancea and Florescu, 1968). Negus (1966) reasoned that mussels dying each year in a population with regular recruitment would provide an amount of mussel flesh approximately equal to annual production as food for bottom feeding fish, scavenging invertebrates and decomposers. In addition, a small amount of organic material (approximately 2.8%, Cameron et al., 1979) present in the shells would also return to the ecosystem on decomposition.

At high densities, the filtration ability of mussels has been estimated or argued to be significantly important to the nutrient cycles of ecosystems and to the general circulation of materials in aquatic environments. Filtration, and biodeposition of faeces by mussels abundant in organic matter, are thought to provide significant cleansing and purification of waters (Tudorancea and Florescu, 1968; Lewandowski and Stanczykowska, 1975); and significant acceleration of the breakdown of nitrogenous wastes to provide nutrients for plankton and other benthic fauna (Tudorancea and Florescu, 1968; Lewandowski and Stanczykowska, 1975; Walz, 1978; Stanczykowska, 1978; Kenmuir, 1981c). Lewandowski and Stanczykowska (1975) added that movements of mussels present at high densities may be important in stirring and mixing the bottom sediments. Mussels may also play an important role in the calcium cycles of some aquatic environments (Green, 1980).

Finally, Waters (1977) emphasised that production estimates in themselves are important as indicators of the general well-being of an ecosystem. Pre-disturbance estimates of production for example, may provide baseline data upon which to monitor the effects of environmental perturbations, natural or anthropogenic. Anthropogenic effects may include pollutants - thermal, organic or inorganic; sedimentation; or any other general alteration of the habitat.

APPENDIX 6

TOLERANCES OF VELESUNIO ANGASI TO ANOXIA

Mussels from the floodplain billabongs of the Magela Creek are seasonally exposed at the Wet-Dry interchange (April-June) to low concentrations of dissolved oxygen and even anoxia, often for prolonged periods. A number of detailed laboratory and field experiments were conducted over the study period to test the tolerance of Velesunio angasi to these low concentrations of dissolved oxygen. A brief summary of one laboratory study only is reported here; the experiments demonstrate the tolerances of various age classes of V. angasi to anoxia.

Experiments were conducted during the Wet-Dry interchange of 1982 (April-May). Three age classes of mussels were tested: young-of-year mussels recruited at the very recently finished 1981/1982 Wet season; 1-year old mussels; and >1-year old mussels (i.e. all other age groups). All 1-year old and older mussels were collected from Nankeen, representing a floodplain billabong. Unfortunately, recruitment of mussels during the 1981/1982 Wet season was poor in the floodplain billabongs (see Fig. 6.4) and young-of-year mussels therefore were collected from Mudginberri, a channel billabong.

Mussels were placed in stoppered reagent bottles holding approximately 11 litres (range, 10.72-11.12 l) of clean and aerated billabong water. Five bottles were used for each of the 3 age classes of mussels tested. Each bottle held 20 (1-year old and >1-year old) or 25 (young-of-year) mussels. Mussels from each age class were distributed amongst the 5 bottles such that in each bottle mussels of the entire size range were represented. Experiments were initiated when aerators were removed from the bottles and stoppers were replaced. Continuous aeration, however, was maintained in one bottle from each age group as a control, for the duration of the studies. Dissolved oxygen (DO) concentrations were measured in each bottle at the beginning of each experiment and at daily intervals subsequently, using a Hach Model 16046 portable dissolved oxygen meter. The meter was calibrated prior to the daily measurements.

After stoppering the bottles, aerobic respiration of mussels brought DO concentrations to anoxia (defined as <0.5 mg/l) after 144, 30 and 24 hours for young-of-year, 1-year old and >1-year old groups respectively. After DO concentrations had reached anoxia, levels were maintained at this concentration (as described below) for the duration of the experiment. Water in each bottle was changed every 24 hours from commencement of the experiments for young-of-year mussels, and every 48 hours for the other two age groups. At each change of water, mussels were removed from the bottles and inspected. Dead animals were discarded while live ones were returned to bottles containing clean water of the same DO concentration that prevailed prior to inspection. DO concentrations were regulated in this way by bubbling nitrogen gas through the new water in each bottle. The entire procedure from removal of mussels to replacement in re-stoppered bottles of clean water was always completed in less than 5 minutes. If dead mussels in the 1-year old and >1-year old groups were observed at daily inspection prior to the routine 48 hour water renewal, they were removed immediately to prevent fouling of the water. (Dead mussels

were recognised by excessive and continuous gaping after agitation of the bottles.)

The experiments were maintained, as described above, until all mussels from each age group had died. No mussels from any age group died prior to DO concentrations reaching anoxia. Similarly, no mussels in the control bottles died over the duration of the experiments. A summary of the counts made of mussels that had succumbed to the anoxic conditions at progressive days (young-of-year) or fortnights (1-year old and >1-year old) is given in Table A6.1 below.

Table A6.1 Numbers of mussels recorded dead after each day (young-of-year) or fortnight (1-year old and >1-year old) of exposure to anoxic conditions.

AGE GROUP	DAY OR FORTNIGHT											
	1	2	3	4	5	6	7	8	9	10	11	12
Young-of-year	1	9	16	20	22	18	8	1	2	1	-	-
1-year old	0	2	4	6	8	13	14	8	13	5	0	4
> 1 year	0	11	23	27	25	3	3	3	3	-	-	-

Young-of-year mussels were least tolerant to anoxia. Mortality in this group was observed between 1-10 days after waters had become anoxic. Greatest mortality was observed on the 5th day after waters reached anoxia. In contrast, however, adult mussels (>1-year old) were exceedingly tolerant to anoxia and survived up to several months in anoxic waters. 1-year olds were particularly insensitive to anoxia, and mussels in this age group survived for up to 24 weeks under these conditions; greatest mortality was found 14 weeks after waters became anoxic. Older mussels (i.e. >1-year old) survived for up to 18 weeks in anoxic waters, while greatest mortality was observed only after 8 weeks.

The likelihood and extent of a genetic difference in the tolerances to anoxia between mussel populations from different billabongs remains to be tested. Thus, while young-of-year mussels from Mudginberri are exceedingly intolerant to anoxia in comparison with the other age groups of mussels from Nankeen billabong, it is possible that juveniles from Nankeen could be less sensitive than those from Mudginberri. Nevertheless, while such differences in the tolerances of mussels of the same age class between two such billabongs of opposing aerobic status may be found to be significant, it is highly likely that the tolerances of juveniles and adults from the same billabong would still be significantly different.

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