COMPARATIVE LIFE HISTORY TACTICS AND SEXUAL STRATEGIES OF THE FRESH AND BRACKISH WATER BIVALVE FAUNA OF HONG KONG AND SOUTHERN CHINA

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ABSTRACT

Relatively few bivalve species inhabit the various components of the fresh and brackish water environment of southern China, including Hong Kong. Of these, the Corbiculacea are the most diverse, accounting for 7 of the 11 known species. Three unionids occur in southern China but only one, *Anodonta woodiana*, is found in Hong Kong. The Mytilidae are uniquely represented by the freshwater *Limnoperna fortunei*.

Hong Kong habitats are relatively diverse resulting from proximity to the Pearl River estuary and to the establishment of man-made habitats, i.e. reservoirs and slow flowing agricultural ditches and furrows. Two species groups, both definable as K-selected, respectively colonise large permanent lotic or lentic habitats or small lentic environments with predictable perturbations. Representatives of the former are typically dioecious (there also being a greater proportion of females and a small percentage of hermaphrodites), long lived (> 10 years), with one reproductive season each year which can be correlated with major seasonal climatic and hydrological events. They are all iteroparous and nonbrooding, except for *Anodonta woodiana*. An opposite situation is seen in occupants of small lentic, relatively stable, habitats, in which the effects of seasonal drying are more pronounced and yet still "predictable". These species are typically small, short lived (< one year), simultaneous hermaphrodites, generally semelparous and with brooding and reproductive timing correlated less with major climatic events, than with locally important environmental perturbations, probably permitting great interpopulation variability.

A third category of bivalves, typified locally by *Corbicula fluminea*, and to a lesser extent *Limnoperna fortunei*, lives for two to three years and can be broadly defined as r-selected species. These occupy a wide range of lotic and lentic, and perennial and ephemeral habitats often with unpredictable major perturbations. In the case of *C. fluminea* a variety of sexual expressions are assumed in different habitats and fertilised eggs are ctenidially brooded. This species is polymorphic with regard to shell form and colour and, most important, sexual expression. I believe that high genotypic variability and phenotypic plasticity may characterise this hitherto little-studied category of highly opportunistic and recent bivalve colonists of the freshwater domain, accounting not only for their success but also the plethora of species names attributed them.

For a number of years, I have been researching the fresh and brackish-water bivalve fauna of Hong Kong and southern China. Lack of detailed information regarding the habitat distribution of many mainland species, notably members of the Unionacea, precludes detailed discussion of them, other than to record some of them as southern Chinese species. For those species found in Hong Kong, however, including two species of Pisidiidae not hitherto investigated from continental China, enough basic information on life history tactics and sexual strategies is available to allow some important generalizations to be made.

This study therefore summarises available information on a guild of fresh and brackish water bivalves, some occupying similar, others different, habitats in Hong Kong. It attempts to demonstrate that the bivalve fauna of this subtropical place is divisible into three categories, broadly identified by application of the deterministic K- and r- selection theory to life history tactics (MacArthur and Wilson, 1967; Pianka, 1970).

Each group of bivalves possesses broadly similar reproductive strategies and is encompassed by a suite of life history traits appropriate to the broad characteristics and

American Malacological Bulletin, Vol. 5(1) (1987):91-99

temporal stability of the environment inhabited. Although agreement is with Burky (1983) that current theoretical generalizations may be inappropriate or inadequate when applied to most populations of freshwater bivalves (especially where, as in China, such comparative information is virtually nonexistent), it is hoped that this study will provide a conceptual framework for comparison with studies of better-known faunal assemblages made elsewhere.

CLIMATE, GEOMORPHOLOGY AND HYDROLOGY

The climate of Hong Kong is subtropical, winters cool (a mean minimum of 13.2°C in January) and dry (a mean minimum of 26.9 mm precipitation in January), summers hot (a mean maximum of 31.6°C in July) and wet (a mean maximum of 431.8 mm in June).

Geomorphologically, Hong Kong comprises an eroded mountain chain of metamorphosed sedimentary rocks with granitic and volcanic intrusions. Following the last ice age, sea water levels have risen by some 10 m, so that former river valleys and lowland areas are now drowned. The numerous offshore islands represent former mountain tops. The majority of Hong Kong is, therefore, of steep bedrock covered by a thin layer of top soil. To the northwest, however, Hong Kong abuts the delta and flanks the western mouth of the Pearl River, the largest river of southern China, draining an area of some 228,000 km² and with an annual flow of 308 billion m³. Because of the climate, over 80% of this discharge occurs in summer. This area of Hong Kong comprises flat alluvial plains, with numerous rivers, all tributaries of the Pearl, creating extensive estuarine flats, bordered by mangroves and marshlands. Within the Pearl River delta, therefore, is the potential for wide habitat segregation, but this is not generally true of Hong Kong itself.

Because of the land's steep slopes, surface runoff is rapid, a situation which has been exaggerated by extensive diversion of stream and river waters into catchments to supply potable water for Hong Kong's expanding population of around 6 million.

Streams are therefore "flashy". Many dry up in winter and flood in summer following torrential rains, especially after a typhoon. A biological side benefit of potable water supply has been the construction of large lakes as reservoirs. The first of these, Plover Cove, was completed in 1967. It was created by damming a 14 km² tidal inlet and formed Hong Kong's first "reservoir in the sea". The second, High Island, was completed in 1979 and built by damming an area of sea separating a large island from the mainland. Hitherto, because of geomorphology, Hong Kong had no natural lakes and only small, winter drained, reservoirs. A number of bivalves, i.e. *Anodonta woodiana* (Lea), *Corbicula fluminea* (Müller) and *Limnoperna fortunei* (Dunker), have been introduced into Plover Cove and High Island.

Agricultural practices have also modified the freshwater environment by widescale diversion of lowland streams into flooded vegetable gardens. This has created shallow, semipermanent, artificially managed, nutrient enriched, slow-flowing watercourses. Of late, however, because of extensive development for urban renewal, these habitats are disappearing, reconforming the environment.

The diversity, species composition and relative abundance of Hong Kong's fresh and brackish water bivalve fauna thus results from and is dependent upon the changing influences of climate, geomorphology, and human modification. A greater variety of species occurs in the surrounding lands and waters of China, but how Hong Kong's discrete bivalve fauna is adapted to this dynamic environment, exposes underlying principles.

SYSTEMATICS

Table 1 lists the species of fresh and brackish water bivalves recorded from southern China (Guangdong Province). Excluded from this list are a number of brackish water mangrove-associated bivalves which have clear phylogenetic affinities with marine families. Thus, *Polymesoda (Geloina) erosa* (Solander) (Corbiculidae) is included because it exclusively occurs around fresh water seeps draining through high, upper zone, mangroves. Conversely, the low zoned, mangrove associate, *Gafrarium pectinatum* (Linnaeus) (Veneridae), is excluded. Similarly the wholly and uniquely fresh water mytilid *Limnoperna fortunei* is included, but the brackish water mangrove associate, *Brachidontes variablis* (Krauss) is excluded because of a much wider local distribution on many kinds of shores (Lee and Morton, 1985).

Taxonomic problems have surrounded a number of these species, notably *Anodonta woodiana* (Unionacea), *Polymesoda (Geloina) erosa* (Corbiculacea) and *Corbicula fluminalis* (Müller) and *C. fluminea* (Corbiculacea). In the case of *Anodonta woodiana*, Brandt (1980) first reported *Cristaria (Pletholophus) discoidea* (Lea) and *A. gibba* Clessin from Hong Kong and Dudgeon (1980b) described some aspects of the biology of the former species. It is now known (Dudgeon and Morton, 1983; 1984) that both of these names actually refer to *A. woodiana*. This species is widely distributed in China, has been introduced into Indonesia (Djajasasmita, 1982) and has a variable shell form, so much so that Liu *et al.* (1979) record it as comprising four subspecies. Species of *Polymesoda* are difficult to differentiate, though this has been undertaken by Morton (1984) and only *P. erosa* has been recorded from mainland China, although two other species are reported from mangroves elsewhere in Asia.

Greatest taxonomic problems reside with the Asian species of *Corbicula*. An array of species has been described, but Morton (1979a; 1986a) considers that these can all be ascribed to two, i.e. *Corbicula fluminalis* and the highly variable *C. fluminea*. The latter has been introduced into N. America, Europe and Argentina (Britton and Morton, 1979, 1982, 1986; Morton, 1986a). The problems lie in the fact that *C. fluminea*, at least, is polymorphic with respect to shell form, colour and expression of sexuality (Britton and Morton, 1986; Morton, in prep.). Two distinct colour morphs occur in the American southwest, one straw-coloured, the other dark

Table 1. The fresh and brackish water bivalves recorded from Hong Kong and the southern Chinese Province of Guangdong.

	Southern China	Hong Kong
Mytilacea		
Limnoperna fortunei (Dunker)	+	+
Unionacea		
Union douglasiae (Gray)*	+	—
Lamprotula leai (Gray)*	+	—
Anodonta woodiana (Lea)	+	+
Corbiculacea		
Polymesoda (Geloina) erosa (Solander)	+	+
Batissa (Cyrenobatissa) subsulcata Clessin	+	—
Corbicula fluminalis (Müller)	+	—
Corbicula fluminea (Müller)	+	+
Musculium lacustre (Müller)	+	+
Pisidium clarkeanum G. and H. Nevill	?	+
Pisidium annandalei Prashad	?	+

*Information obtained from Liu *et al.* (1979)

(Fontanier, 1982; Hillis and Patton, 1982; Britton and Morton, 1986). The same is true of Hong Kong, though the discovery of an intermediate morph establishes a high degree of phenotypic plasticity for this species related to variations in hydrology and thus occupation of a heterogeneous environment (Morton, in prep.).

LIFE HISTORY TACTICS AND SEXUAL STRATEGIES

Anodonta woodiana probably did not occur in Hong Kong prior to the development of larger permanent reservoirs. The construction of Plover Cove in 1967, with colonisation by a range of organisms commencing in 1968 (Morton, 1977a, b), has permitted the establishment of a population of *A. woodiana* that survives as glochidial larvae on fish fins, even if the parent population is largely killed off in winter as a result of drawdown. A study of *A. woodiana* by Dudgeon and Morton (1983), showed that individuals probably live (in Hong Kong) to a maximum age of 12 years. In Plover Cove, the species is dioecious with females predominating in a ratio of 3:2. A small number of individuals (0.3%) are hermaphrodites. Males possess mature gonads throughout the year, whereas females come into reproductive condition during the spring. Eggs are produced throughout the summer and are brooded in the outer demibranchs of the ctenidia. In any one year there is a single phase of recruitment in summer, glochidia residing for a mean time of 14.4 days on the host at 15°C but only 6 days at 27°C (Dudgeon and Morton, 1984).

Polymesoda (Geloina) erosa is restricted to mangrove stands in east Asia (Morton, 1984) and shows remarkable physiological adaptations to a high-zoned life in this habitat. These include pedal gape feeding on subterranean waters, aerial respiration and an ability to tolerate extended periods of desiccation (Morton, 1975b; 1976; Depledge, 1985). The species typically inhabits streams or seeps draining through the mangal and is covered by most tides, if for only a short time. Thus, despite habitation of a "difficult" environment, it is tidally "predictable", and the species has evolved a range of behavioural and physiological adaptations suited to it. Sexually, however, *P. erosa* is unspecialized. Each individual is dioecious though, as with *A. woodiana*, a greater percentage of individuals are females (i.e. 51.5%, with 38.5% male and 9.5% immature) (Morton, 1985a). *P. erosa* does not incubate fertilized eggs in the ctenidia. Age analysis is difficult because of considerable acid mangal erosion of the shell, but individuals clearly live longer than one or two years.

Batissa (Cyrenobatissa) subsulcata Clessin is a large corbiculid occurring in the Pearl River system and occasionally found for sale in Hong Kong markets. There are no references to this species in the Chinese literature but Dudgeon (1980a) obtained a small commercial sample and undertook simple analysis of it. The largest specimen was 73 mm long and had 9 growth rings. Construction of a Walford plot (Walford, 1946) showed that a maximum theoretical length of 77 mm was possible. Such individuals might be expected to have 11 growth rings. Nothing is known of the life history or reproductive strategies of this species, but assuming there is either one or two periods of reproductive activity each year then clearly a life span of either 11 or 5.5 years is theoretically possible.

The mangrove associated *Polymesoda erosa* and the riverine *Corbicula fluminalis* are both dioecious, oviparous and breed but once a year. In view of the close taxonomic relationship and obvious anatomical similarities between these three corbiculids, I speculate that *Batissa subsulcata* can be likewise dioecious, nonbrooding, with a single cycle of gametogenesis each year and living for a maximum of approximately 11 years.

A freshwater mytilid has been recorded from wide areas of China. Most Chinese authors, i.e. Tchang *et al.* (1965), Chen (1979) and Liu *et al.* (1979), refer to this as *Limnoperna lacustris* Martens, which Habe (1977) synonymises with *L. fortunei*. Mizuno and Mori (1970) record *L. fortunei* from Thailand while Brandt (1974) records *L. supoti* Brandt from Thailand, and Brandt and Temcharoen (1971) record *L. depressa* Brandt as new from Laos and Cambodia. Morton (1973, 1975a, 1977b, 1982b) refers to *L. fortunei* from Hong Kong. The species is known to occur in the headwaters of the Pearl River around Guangzhou (Canton) (Miller and McClure, 1931). It has been introduced from this region, in potable water supplies, to Hong Kong where it now occurs in Plover Cove Reservoir (Morton, 1975a) and in pipelines both to and from the reservoir. It has not, however, spread into natural watercourses. In southern China therefore the species normally occupies more permanent, predictable, lentic and lotic habitats but not natural streams and temporary watercourses. Throughout its wide range, however, the species, has been attributed with much opportunism

(Morton, 1973; 1975a, 1977b).

Although *Limnoperna fortunei* has been recorded from brackish waters (Miller and McClure, 1931) it has also colonised Plover Cove following the advent of stable conditions therein (Morton, 1977b). The species is dioecious, 65.7% of the population being female. No hermaphrodites were found in a sample of 291 individuals examined by Morton (1982b). Eggs are fertilized externally and settlement occurs twice a year in summer (June-August) and winter (November-December), when air and water temperatures are approaching maxima and minima, respectively. The species is estimated to live for two or three years (Morton, 1977b).

Corbicula fluminalis occurs in the Pearl River estuary, but no information is available on its salinity tolerance. An analysis of population structure in this species by Morton (1982a) has shown that a maximum theoretical length of 64 mm is possible in the Pearl River and that the life span may be up to 10 years. A single growth ring is produced each year. Breeding occurs once a year in winter.

An analysis of 656 individuals over a 20 month period has shown that 49.7% of the population were female, 45.7% male, and 4.5% hermaphrodite. However, a greater percentage of smaller, younger, individuals were female (59.2%) and larger, older, individuals were predominately male (58.5%). Morton (1982a) interpreted this as a trend towards protogyny and as an aspect of an overall strategy, along with the low incidence of hermaphroditism, towards enhancing the options available for reproductive success in a large lotic environment. No evidence of ctenidial brooding of fertilized eggs was found but, strangely, glands which in *Corbicula fluminea* develop in the inner demibranch only when larvae are being brooded, also developed in younger specimens of *C. fluminalis*. The question was posed by Morton (1982a): does *C. fluminalis* have variable sexual strategies over different components of its range?

Evidence for such variability is not available for *Corbicula fluminalis*, but is accumulating for a close relative, *C. fluminea*. This species is widespread in China with an enormous natural distribution plus an introduced distribution in North America, Europe and South America (Morton, 1986a). Many species names describe it, but it has a highly variable shell form, colour and maximum size and can osmoregulate in salinities up to 13% (Morton and Tong, 1985). It is, moreover, characterized by great variability in life history traits and sexual strategies. *C. fluminea* lives for between 3 - 4 years, with two peaks of larval production typically in spring and autumn. Fertilized eggs are brooded in the inner demibranchs to a larval shell length of some 220 μm. Individuals can be dioecious or hermaphroditic (Kraemer, 1979). Reproductive strategy is very variable. Morton (1983) showed that in a lentic habitat (Plover Cove), the population comprised approximately equal proportions of males, females and hermaphrodites. In an agricultural flooded furrow, however, the population comprised approximately equal numbers of females and hermaphrodites only. A variable expression of sexuality in this dimension is relatively easy to understand, but the most recent researchers by Britton and Morton (1986) and Morton (in prep.) on this species in North America and Hong Kong, respectively, have shown it to be highly polymorphic with respect to shell form, colour and sexual expression. Two form extremes are defined as A and B. A form individuals are typically straw-coloured with widely spaced concentric lamellae and are predominately female (i.e. 73% female vs. 25% hermaphrodite). B form individuals have dark shells as the result of progressive enlargement and fusion of umbonal colour flashes seen in all juveniles. Concentric lamellae are narrowly spaced and these morphs are predominately hermaphroditic (75% hermaphrodite vs. 18% female). The two morphs may be sympatric or allopatric, this being determined by inter- and intra-stream variations in water quality, notably with regard to hardness for shell form and potassium (in combination with pH, dissolved oxygen and carbon dioxide) for colour and the expression of sexuality (Morton, in prep.).

Hillis and Patton (1982) consider these morphs to be distinct species on the evidence of fixed homozygous allelic differences at 6 of 26 genetic loci; nevertheless, Morton (in prep.) has identified a morph intermediate in shell colour between A and B, and believes all morphs to be expressions of a single genotypically variable and phenotypically plastic species.

The holarctic species, *Musculium lacustre* (Müller), has been studied elsewhere (Mitropolskji, 1965; Mackie, 1978b; 1979; Mackie and Huggins, 1983). In Hong Kong it occurs in agricultural drainage ditches and has been shown by Morton (1985b) to be a simultaneous hermaphrodite, but with evidence that the testis matures first. Maturity is attained at a shell length of 2 mm, though the majority of individuals are brooding larvae within marsupia of the inner demibranchs at a length of between 4 - 6 mm. The larvae are released at a length of 1.5 mm and, growing rapidly, quickly mature to contribute to a succeeding generation. Thus, although recruitment occurs in two major peaks each year, in spring and autumn, this is not because of iteroparity, but represents life cycle completion by two overlapping generations. The spring recruits give birth to the fall recruits which in turn give birth to the succeeding spring recruits. *M. lacustre* is thus generally semelparous and univoltine. A few of the late-born spring generation can, however, overwinter to contribute to the spring generation of the succeeding year. These animals would thus be iteroparous and bivoltine. This is not so with the fall generation and a life span estimate of between either 6 (autumn generation) or 12 (spring generation) months seems appropriate for this species in Hong Kong.

Pisidium clarkeanum G. and H. Nevill and *P. annandalei* Prashad are sympatric in the flooded furrows of vegetable gardens in Hong Kong's New Territories and have been studied by Morton (1986b). The former species attains a maximum length of 7.0 mm, the latter 4.0 mm. Both are simultaneous hermaphrodites and ovoviviparous. *P. clarkeanum* is sexually mature at a shell length of 2.0 mm and *P. annandalei* at 1.5 mm, though larvae are not brooded in the former until a length of 3.0 mm is attained and in the latter at 2.0 mm. Larvae are released at a length of 1.2 mm in *P. clarkeanum* and 0.8 in *P. annandalei*.

Three generations are produced each year by both

species, but since these represent single recruitments from the preceeding generation, both species are basically semelparous and univoltine. Because of an overall greater longevity, *Pisidium clarkeanum* can, however, following one birth period, produce a second generation to contribute to the succeeding generation and is thus iteroparous and bivoltine. This strategy is unlikely in *P. annandalei* and rarely, if ever, can individuals be iteroparous. Maximal life span estimates for these two species are thus 8 months (*P. clarkeanum*) and 4 months (*P. annandalei*).

Life history traits and sexual strategies of the Hong Kong species of fresh and brackish water bivalves are summarised in Table 2. There seems to be a division of the species into three categories. There are those species occupying large, permanent, water masses, i.e. either lakes or rivers, which can be defined as predictable habitats influenced only by major climatic changes. Here the species are generally large, have an enhanced longevity of >10 years and are characteristically dioecious (though small percentages of all are hermaphroditic) and iteroparous. Unlike the other species characterizing this category, *Anodonta woodiana* is a confirmed brooder, but this can be explained by the highly specialised method of dispersal, uniquely adopted by representatives of the Unionacea, a glochidia larva attaching to fish fins (Dudgeon and Morton, 1984). Generally, with this one exception, these bivalves are non-brooders and can all be defined as K-selected species.

A second category of bivalves includes but two species, i.e. *Limnoperna fortunei* and *Corbicula fluminea*. These bivalves are also iteroparous, with life spans of between 2 - 4 years. A shell length of some 30 - 40 mm is common. In terms of sexual strategies, however, the two are different. *L. fortunei* is dioecious (with no hermaphrodites), and *C. fluminea* has a wide range of sexual expressions, but with larval brooding. These can best be defined as r-selected species adapted to the invasive colonisation of a wide range of aquatic environments. There is strong evidence that both species have entered fresh waters relatively recently. Reduced life spans, ages of maturity and the retention of an invasive planktonic juvenile dispersal stage in the case of *L. fortunei* or of internal fertilization but release of large numbers of shelled larvae in the case of *C. fluminea* facilitate such opportunism.

In contrast to the classical examples of K- and r-selected categories of species defined above, there are three species of pisidiid bivalves found in Hong Kong, i.e. *Musculium lacustre, Pisidium clarkeanum* and *P. annandalei*, which are more difficult to categorise. These species are all

Table 2. The life history tactics and sexual strategies of the fresh and brackish water bivalves of Hong Kong and southern China.

	Species	Sexual expression	Semelparous/ iteroparous	Brooding	Recruitment periods/year	Life span	Authority
K-selected species of large permanent lotic or lentic habitats	*Anodonta woodiana*	Dioecious	Iteroparous	Outer demibranch	Once (Spring)	12 years	Dudgeon and Morton, 1983, 1984
	Corbicula cf. *fluminalis*	Dioecious with a trend towards protogyny	Iteroparous	Not	Once (Winter)	10 years	Morton, 1982a
	Polymesoda (Geloina) erosa	Dioecious	Iteroparous	Not	Once (Summer)	>8 years	Morton, 1985a; Morton (unpublished data)
	Batissa (Cyrenobatissa) subsulcata	Dioecious	Probably iteroparous	?	?	10-11 years	Dudgeon, 1980a; Morton (unpublished data)
r-selected species of lotic and lentic habitats with unpredictable perturbations	*Limnoperna fortunei*	Dioecious	Iteroparous	Not	Twice (Spring & Autumn)	2-3 years	Morton, 1977b, 1982b
	Corbicula fluminea	Dioecious/ hermaphrodite	Iteroparous	Inner demibranch	Twice (Spring & Autumn	3-4 years	Morton, 1977a, 1983
K-selected species of small lentic habitats with predictable perturbations	*Musculium lacustre*	Simultaneous hermaphrodite	Generally semelparous	Inner demibranch	Twice (Spring & Autumn	6-12 months	Morton, 1985b
	Pisidium clarkeanum	Simultaneous hermaphrodite	Generally semelparous	Inner demibranch	Three	4-8 months	Morton, 1986b
	Pisidium annandalei	Simultaneous hermaphrodite	Generally semelparous	Inner demibranch	Three	4 months	Morton, 1986b

short-lived, i.e. less than 1 year, attain a shell length of less than 10 mm, and are generally semelparous, with the possibility (only) of iteroparity. They all brood few larvae in highly specialized ctenidial marsupia and are exclusively hermaphroditic. Two or three overlapping generations are produced each year. The above adaptations suit these species to life in small artificially lotic habitats which in Hong Kong experience predictable perturbations, particularly in terms of seasonal variations of wetting and drying. These species are physiologically and reproductively adapted to such predictable seasonal events, just as the K-selected large lentic and lotic species are adapted to predictable winter reductions in ambient temperature. In such a case therefore, Hong Kong's pisidiid species should also be categorized as K-selected species, albeit with reproductive strategies and life history tactics which are completely different from their relatives inhabiting larger water bodies (Table 3).

DISCUSSION

This study is concerned with defining the different reproductive strategies and life history tactics adopted by various species of fresh and brackish water bivalves from southern China.

The environmental predictability associated with lentic and lotic water bodies of larger scale is clearly reflected in their bivalve inhabitants by enhanced longevity, gonochorism, external fertilization and non-brooding, all K-selected features. Conversely, pisidiid inhabitants of small lentic habitats, either of shorter (seasonal) or long term scale, are characteristically small, short-lived (less than 1 year), typically hermaphroditic, semelparous and brood but a few larvae within highly specialised ctenidial marsupia. These too can be considered as K-selected traits albeit occurring in species occupying what are usually considered to be r-variable habitats.

Between these two groups of species in Hong Kong are two bivalves one of which, at least, gives a different insight into the adaptations that allow species to transgress important ecological boundaries. Much of this discussion will relate to *Corbicula fluminea,* but in some ways *Limnoperna fortunei* is similar, i.e. both can occur in lentic and lotic situations and both live for 2 - 3 years. Less detail is known of *L. fortunei*, however, and which, unlike *C. fluminea*, is dioecious and non-brooding (Morton, 1982b).

Corbicula fluminea occupies a wide range of habitats throughout its natural range (which includes Hong Kong) and in its introduced range in North America. Lakes, rivers, streams, ponds, ditches and drains are equally favoured. A picture is emerging of a species with wide variations in shell form and colour (polymorphism) and, most important, wide variations in sexual expression. *C. fluminea* can be either dioecious or hermaphroditic, and different populations comprise such individuals in different ratios. Schaffer (1974) argued that populations which live in unpredictable environments should be polymorphic for reproductive characteristics, and Giesel (1974) demonstrated that polymorphic populations were more fit (in terms of average rate of increase and total population size after 300 reproductive intervals) than were monomorphic ones. Generally these principles and characteristics of r-selected species have been applied to pisidiid bivalves producing many young and occupying a wide range of unpredictable habitats (Heard, 1977). However, other pisidiids are K-strategists, occupying more stable habitats and producing few offspring, as with the Hong Kong species (Morton, 1985b, 1986b).

For the Pisidiidae, however, important inter-population differences in sexual strategies (but not sexual expression) have been documented and have been reviewed by Burky (1983). In either temporary ponds or perennial habitats, *Musculium securis* (Prime) is respectively iteroparous or semelparous (Mackie, 1978b; McKee and Mackie, 1981). Mackie and Flippance (1983) have shown that in a big pond *Sphaerium rhomboideum* (Say) has one birth peak a year, lives for longer than 14 months, and is iteroparous. In a small, temporary pond, the same species has 3 birth peaks, a faster average summer growth rate, a shorter life span, is either semelparous or iteroparous and suffers less mortality. Holopainen (1979) has shown that littoral populations of *Pisidium*

Table 3. The generalised life history tactics and sexual strategies of fresh and brackish water bivalves occupying habitats characterised by different degrees of predictability in southern China and Hong Kong.

	Habitat range	Habitat type	Longevity (years)	Semelparous /iteroparous	Recruitment periods/ annum	Sexual expression	Extent of parental brooding
1. K-selected species	Narrow	Perennially predictable:	>10	Iteroparous	1	Dioecious (females predominating; a few hermaphrodites	External fertilization (Oviparous)*
2. r-selected species	Wide	Perennial/ ephemeral	Intermediate 2-4	Iteroparous	2	Mixed: Dioecious/ hermaphrodites	Oviparous/ ovoviviparous
3. K-selected species	Narrow	Seasonally predictable:	<1	Semelparous	>2	Hermaphrodites	Ovoviviparous

*the exception is *Anodonta woodiana*

casertanum (Poli) produce one larval litter per year, but that profundal populations of the same species have two litters per year.

Such modifications in the Pisidiidae, however, relate to interpopulation variations in longevity, rates of growth, reproductive timing, larval growth rates and relative rates of adult vs. larval mortality and can be regarded as variations in life history traits permitting colonization of a range of seasonally fluctuating or short lifespan microhabitats. Intraspecific comparisons of pisidiid populations, moreover, point out that if juvenile mortality is more variable than adult mortality then the stochastic bet-hedging theory of Stearns (1976; 1977) may be more applicable than any categorisation into r- and K- (Hornbach *et al.*, 1980b; Way *et al.*, 1980; McLeod *et al.*, 1981). One could argue that the mix of sexual expressions adopted by inhabitants of predictable habitats, e.g. *Corbicula fluminalis* (Morton, 1982a) with a small percentage of hermaphrodites in an otherwise dioecious population is another expression of the mixed tactic theory. Such a strategy would also be typical of *Anodonta woodiana* (Dudgeon and Morton, 1983) and *Margaritifera margaritifera* (Linnaeus) (Smith, 1979).

Of much greater significance resulting from (but perhaps also permitting) colonization of a far wider range of habitats are the polymorphisms in shell form, colour and sexual expression adopted by *Corbicula fluminea*. Species of *Sphaerium, Musculium* and *Pisidium* are readily identifiable, the affinity of species based on morphology being consistent with the general size and shape of the shells of the species studied (Hornbach *et al.*, 1980a), and always simultaneous hermaphrodites (Mackie, 1978a). This is not so with *C. fluminea*. Shell form and colour vary to such an extent that literally hundreds of species names have been ascribed to it (Morton, 1979a); and sexual expression varies between lotic and lentic populations and even within sub-populations inhabiting different branches of the same streams. In such cases, a subtly different hydrology is believed responsible for observed variations in morph ratios.

It is well known that molluscan shell form and colour are genotypically determined and phenotypically plastic. For a review of this subject see Berger (1983). The best example is of *Mytilus galloprovincialis* Lamarck regarded by some as a separate species from *M. edulis*, (e.g. Wilkins *et al.*, 1983), but as a subspecies or ecomorph by others, (e.g. Gosling, 1984). Such "species" are genotypically variable and phenotypically plastic and the term "opportunistic" has often been applied to them. Exhibiting a wide range of form, such species are apparently successful in an equally wide range of habitats. This is particularly true of some freshwater bivalves, notably byssally attached species which move into a wide variety of microhabitats after having been introduced into areas outside their natural range. The Dreissenacea offer the best examples, i.e. *Dreissena polymorpha* Pallas in Europe (Morton, 1979b) and *Mytilopsis sallei* (Recluz) (Morton, 1981) in Asia. Although studies upon these bivalves are few, it is known that each genus contains highly variable species. Zahdin (1965), for example, considers there to be 7 species of *Dreissena* in the U.S.S.R., all determined by subjective character analysis. Nine species of *Mytilopsis* are supposedly extant, but with 66 synonyms. Marelli and Gray (1983) redescribe *M. sallei* (Recluz) and *M. leucophaeta* (Conrad) on shell characters alone, but note the original descriptions can easily apply to specimens of any species of the genus. As noted earlier, new species of *Limnoperna* are being erected (Brandt and Temcharoen, 1971). Where objective analysis has been applied to shell characters, e.g. *Corbicula fluminea* (Britton and Morton, 1986), "species" differentiation has not been possible. The proliferation of species names for *Dreissena*, *Mytilopsis*, *Corbicula* and *Limnoperna* therefore seem to this author to probably reflect no more than high genotypic variability and phenotypically plastic character traits which mark highly opportunistic (r-selected) and recent colonists of the freshwater domain.

Most studies of freshwater bivalves have concerned themselves with the Unionacea and Pisidiidae, which are phylogenetically old residents of freshwater systems and therefore highly specialised both physiologically and reproductively and in terms of life history traits.

This study of a discrete guild of southern Chinese bivalves, however, exposes and draws attention to the importance of another category of opportunistic species in studies of freshwater ecology.

ACKNOWLEDGMENTS

I am most grateful to Prof. R. F. McMahon, The University of Texas at Arlington, for his critical reading and constructive criticism of the first draft of this manuscript.

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