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Life-history characteristics and sexual strategy of *Mytilopsis sallei* (Bivalvia: Dreissenacea), introduced into Hong Kong

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(With 7 figures in the text)

First recorded from Hong Kong in 1980, *Mytilopsis sallei* now dominates the intertidal pier community within the Government Dockyard, Victoria Harbour. Analysis of monthly samples of *M. sallei* has demonstrated aspects of the reproductive strategy and life-history characteristics correlated with seasonal changes in local water quality.

Mytilopsis sallei is dioecious, has a high fecundity, matures early (at 8–10 mm shell length), grows fast and the majority of the population is probably semelparous. These are characteristic traits of opportunistic *r*-strategists. Comparable characteristics are typical of other introduced bivalves. Maximum life span of *M. sallei* in the Dockyard is probably less than 20 months with, however, most of the population dying before that. Heavy recruitment, particularly during spring-summer, suffocates older individuals. The shells of dead animals similarly last for little more than one year, dissolution and crushing effecting this. A mat of byssal threads serves to bind the mass and anchor it to the substratum.

Mytilopsis sallei exhibits two periods of reproductive activity and settlement per year. These are possibly two elements of a single recruitment divided into minor (autumn-winter) and major (spring-summer) components by either high summer temperatures or low salinities. Summer and winter recruits of *M. sallei*, respectively, mature to produce the summer and winter juveniles of the following year. Over-stepping generations plus survival of a few individuals into their second year thus ensure continued success of *M. sallei*, and account for its spread and dominance in its introduced range. Such a bimodal pattern appears typical of many Hong Kong intertidal, estuarine and freshwater bivalves.

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Introduction

Now one of the largest container ports in the world, Victoria Harbour, Hong Kong, has been the focus of a number of significant marine introductions (Morton, 1987*a*). Of these, perhaps the

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most important is the dreissenid bivalve *Mytilopsis sallei* (Recluz, 1849). The Dreissenacea have a natural Atlantic range where they occur in fresh waters and coastal lagoons and estuaries. The most significant dreissenid is *Dreissena polymorpha* Pallas introduced throughout the freshwater systems of Europe from the Caspian Sea (Morton, 1979). *Mytilopsis sallei* first came to scientific attention when it was recorded from the Naval Dockyard at Visakhapatnam, Andhra Pradesh, India, and into which it had been introduced in ≈1967 (Ganapati, Lakshmana Rao & Varghese, 1971) (Fig. 1). *Mytilopsis sallei* has an Atlantic range encompassing Central America, shores of the Gulf of Mexico and parts of the Caribbean. It attaches to stones and algal mats in Mexico and occurs in coastal lagoons in Belize and Venezuela (Escarbassiere & Almeida, 1976).

Morton (1981) has described the anatomy of the *Mytilopsis sallei* and suggests that it entered the Pacific via the Panama canal following its opening in 1915 and was then first recorded from Fiji (as *M. allyneana*) by Hertlein & Hanna (1949). Thereafter, the species remained unreported upon until its introduction into India. T. Habe (pers. comm.) suggests that the species was introduced into Shimizu Harbour, Japan, in 1974 and Kaoshung Harbour, Taiwan, in 1977. Chang (1985) records *M. sallei* from an oyster bed at Taperng Bay, near Tungkang Port, in Taiwan, in 1977. Ishibashi & Kosaka (1980) record it from Kiyomizu Harbour, Japan, in 1979. In April 1980, the species was collected alive from Hong Kong waters (Tolo Harbour) attached to floating wreckage (Morton, 1980) (Fig. 2a). This author speculated that the species was more widely distributed in the South China Sea than hitherto realized and could have been brought to Hong Kong attached to Vietnamese refugee boats. With such vessels normally being taken into Victoria Harbour, it was assumed that the species would colonize this place eventually. This occurred and Huang & Morton (1983) recorded it in 1982 from docked vessels at Tsing Yi Island, Victoria Harbour (Fig. 2b). The population was viable and these authors concluded that further spread would be inevitable. Lee (1985, 1986, 1988) researched the ecology and population dynamics of the mytilid *Perna viridis* in Victoria Harbour without detecting *Mytilopsis* and the species has yet to be recorded from the central harbour area. In 1987, however, the Marine Department of the Hong Kong Government brought to my attention *Mytilopsis sallei* colonizing densely a Hong Kong Government Dockyard pier on the Kowloon peninsula (Fig. 2b). Since it is to this dockyard that many refugee boats are brought, at least initially, the discovery of *M. sallei* here was not surprising. It was, however, clear that the species was occurring in large numbers, and superficially at least seemed to dominate the mid and lower littoral, as at Visakhapatnam (Ganapati *et al.*, 1958, 1971).

This study was initiated in 1987 to determine the biological attributes which allow this species to dominate an intertidal community in its introduced range. This has involved a programme of regular sampling to study population dynamics, the expression of sexuality and the cycle of gametogenesis. In addition, water analysis has been undertaken to correlate biological cycles with environmental ones.

Materials and methods

Each month from October 1987 to September 1988 inclusive, visits were made to the mooring pier at the Government Dockyard, Hong Kong. On each visit, a 20 cm × 20 cm area of the pier piles was scraped clean of *M. sallei.* On return to the laboratory, the obtained sample was washed and divided into living animals and empty shells. The living animals were weighed to the nearest 0·1 g and individuals counted and measured along their greatest length to the nearest 1 mm. The sample of empty valves was weighed to the nearest 0·1 g. From this sample was then removed all the intact valves and these were individually counted and measured along their greatest length to the nearest 1 mm. This has allowed construction of monthly length frequency

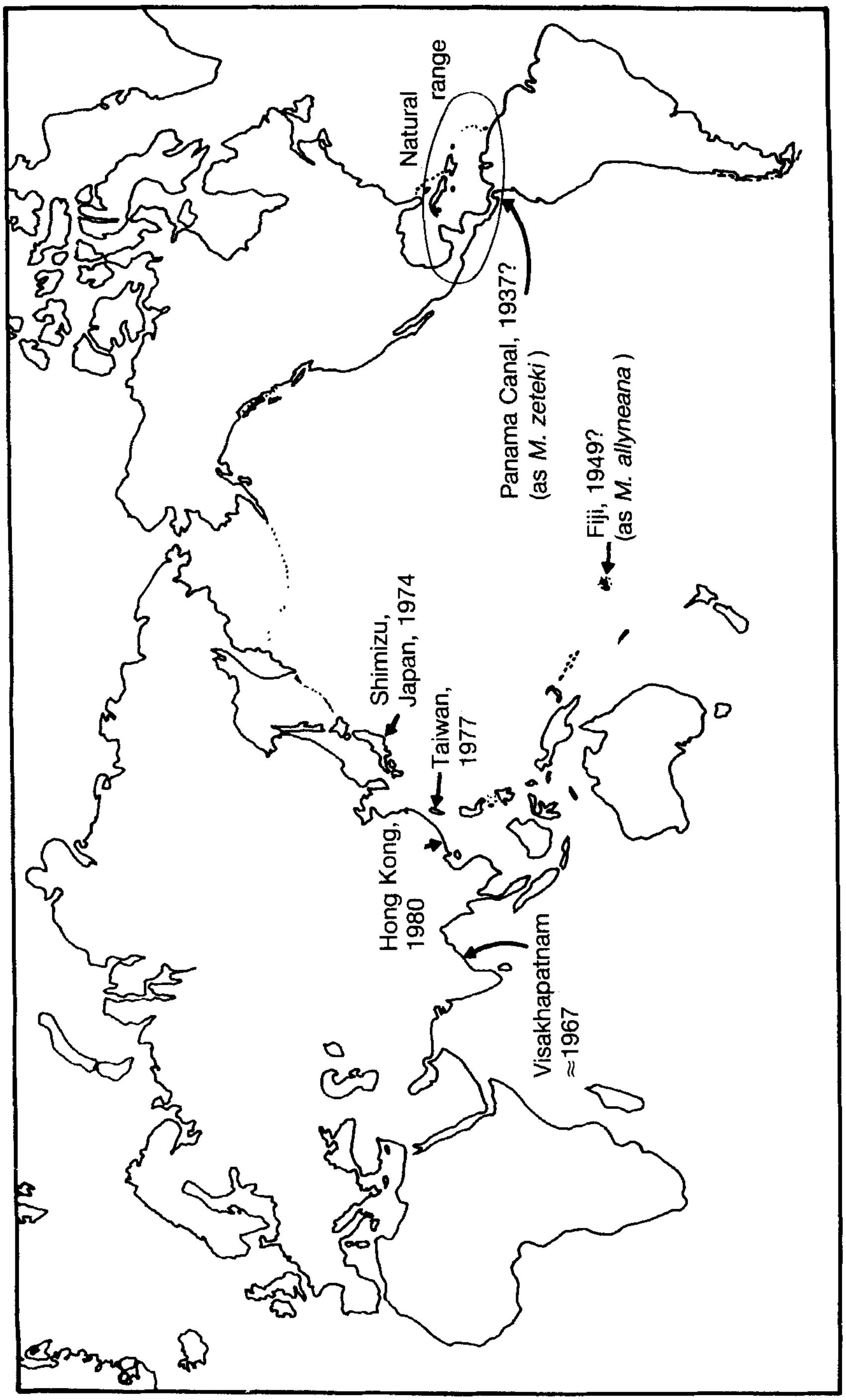

FIG. 1. *Mytilopsis sallei*. Its natural range in the Gulf of Mexico and Caribbean is identified together with locations in the Indo-Pacific from which it has been recorded.

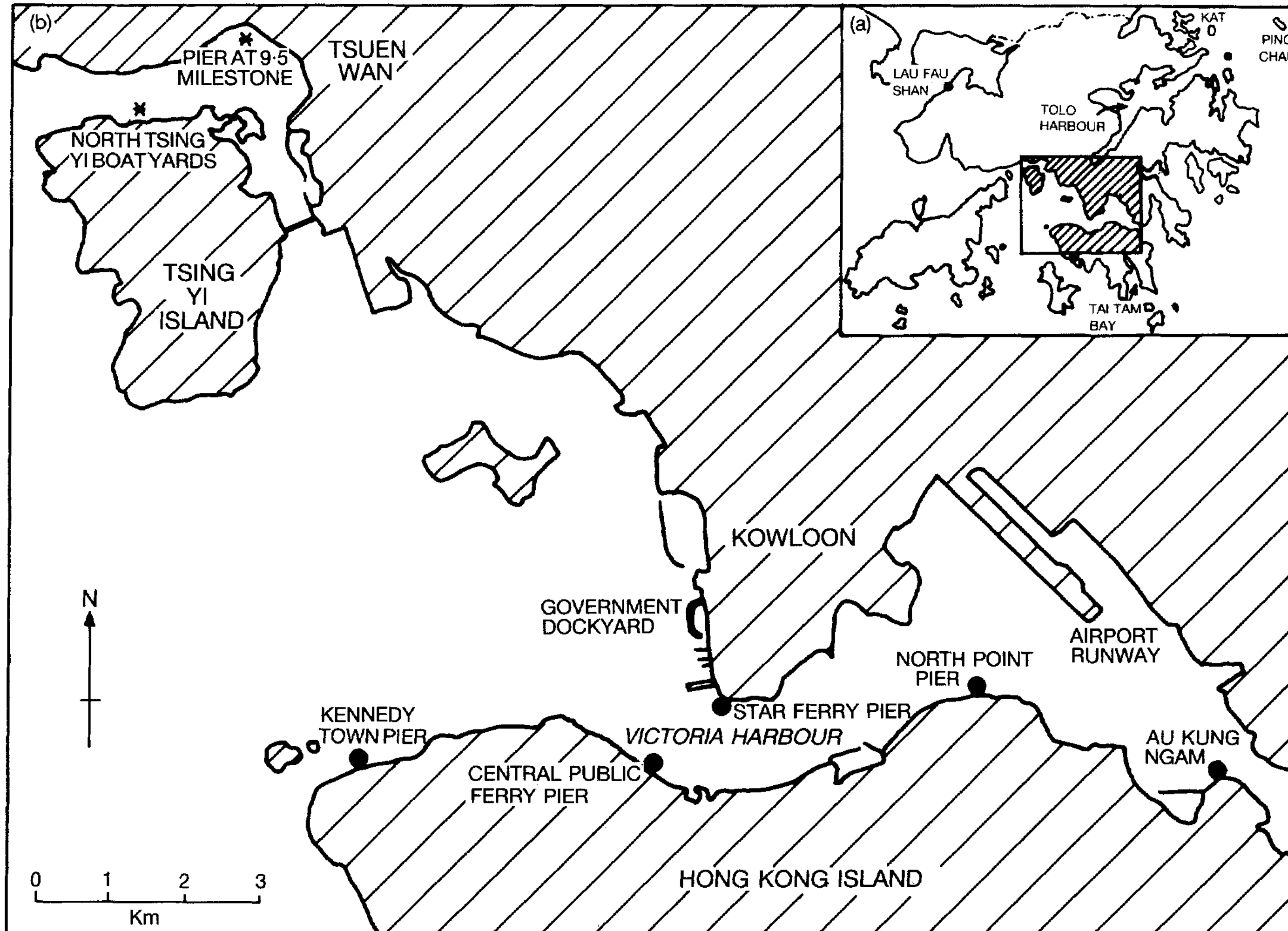

FIG. 2. (a) A map of Hong Kong identifying Tolo Harbour from where *Mytilopsis sallei* was first recorded in 1980. (b) Victoria Harbour, showing Tsuen Wan and the North Tsing Yi Boatyards from where *M. sallei* was recorded subsequently in 1982*. Black circles (●) represent sites from where *M. sallei* has still not been recorded. The Government Dockyard where *M. sallei* dominates the lower intertidal is identified.

histograms for the living and dead components of the population and comparison of the living and dead components of the *M. sallei* masses.

Wherever possible, 5 individuals of each 2-mm length size class comprising each sample were fixed in 10% formalin and subsequently, following routine histological procedures, sectioned transversely at 6 μm through the visceral mass. Alternate slides were stained in either Masson's trichrome or Ehrlich's haematoxylin and eosin and examined to determine sex and state of gametogenesis. The latter was determined by reference to an index of 5 developmental stages used previously for a wide range of bivalves from Hong Kong (Morton, 1982*a*, b, 1985, 1988; Dudgeon & Morton, 1983). Condition 1 is primordial; 2, developing; 3, maturing; 4, mature and 5, spent. This was undertaken for each sex.

On each visit, sea surface temperature was recorded and 3 samples of water obtained in sealed, air-tight, dark glass bottles. On return to the laboratory, the first bottle was used to determine dissolved oxygen levels. The second was placed in a dark chamber to determine BOD_5. The third was used to determine salinity, pH and levels of phosphate nitrate/nitrogen. The latter were analysed using a La Motte Water Analysis pack (La Motte Chemicals Ltd.).

In July and August 1988, 2 pier piles were studied to determine the vertical distribution, not only of *M. sallei*, but also of co-occurring species.

Results

Hydrology of the Government Dockyard

Into Victoria Harbour discharges, untreated, the human and industrial effluents from the cities of Kowloon and Victoria via 19 major seawall and submarine sewer outfalls and > 70 storm drains. The harbour is thus generally regarded as polluted (Reed, 1988) and, in some enclosed situations, a deteriorating trend is clearly evident (Lam, Lui & Kong, 1988). Pollution events, however, have to be considered in the light of Hong Kong's complex hydrology (Morton & Wu, 1975; Morton, 1982*c*, 1989). Victoria Harbour is in Hong Kong's central transition zone between an estuarine environment to the west and an oceanic one to the east. Hong Kong has also a distinctly seasonal climate and this too is reflected hydrologically.

Figure 3 illustrates aspects of water quality in the Government Dockyard. From October 1987 (autumn), sea temperature fell to around 18 °C, where it remained until April. In May, temperature rose to reach a maximum in June of 30 °C. Thereafter, summer temperatures remained stable at between 25–28 °C. This seasonal effect is clearly reflected in dissolved oxygen levels so that as temperature fell from autumn (October) to winter (December), DO levels rose, remained stable between 2·4–3·8 mg.l^{-1} over the winter and then fell again to 1·3 mg.l^{-1} as temperatures rose in spring (May). As temperatures stabilized in the summer, so did DO levels between 2·3–2·9 mg.l^{-1}. BOD_5 levels generally followed those of DO and ranged between 0 in October 1987 and 2·6 in December 1987. Values greater than 2 were also recorded in March, June and September 1988. Most surface available oxygen in the Government Dockyard is therefore under demand. pH fluctuated, without any clear trend, between 7·5–8·0 throughout the year. A further seasonal effect is related to salinity. This remained high at between 30–32 ‰ from October to May. With the arrival of summer, however, rain dilutes the surface water so that in June and August salinities of 28 ‰ and 25 ‰ were recorded, respectively. This rain water effect is not only localized in the form of direct precipitation, but also reflects enhanced input of surface diluted water into the transition zone from western estuarine waters, generally lowering surface salinity. Salinity returned to 30 ‰ in September 1988.

Phosphate levels were generally high over the period October–April, ranging between 0·15–0·76

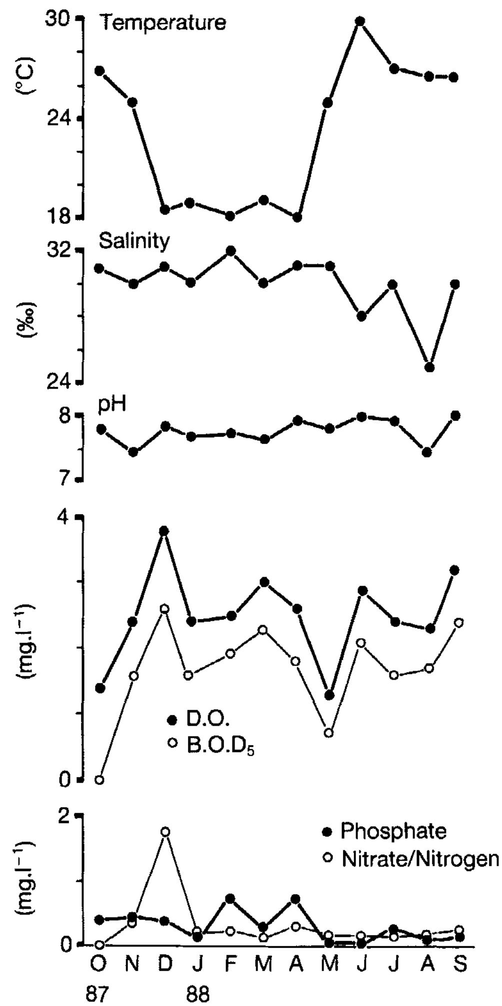

FIG. 3. Surface hydrographic parameters measured at the pier in the Government Dockyard over the period October 1987 to September 1988.

mg.l^{-1}, and low during the summer from May–September, ranging from 0·05–0·15 mg.l^{-1}. Nitrate/nitrogen was maintained at relatively constant levels year round (range: 0–0·38 mg.l^{-1}, except for December 1987 when an all time high of 1·76 mg.l^{-1} was recorded). Nutrient levels thus generally agree with those figures obtained by other authors, e.g. Lam *et al.* (1988) for Victoria Harbour. In this enclosed inlet, however, nutrient loadings are generally higher reflecting, as at other similar sites, enhanced eutrophication through low flushing rates. Enhanced eutrophication could also account for the low levels of available dissolved oxygen.

Vertical distribution

Lee (1985, 1988) has investigated the piers within Victoria Harbour and found that the lower eulittoral and sublittoral fringe is dominated by the mytilid *Perna viridis*. This species is ubiquitous in Hong Kong on such structures.

In the Government Dockyard, however, a different situation occurs (Fig. 4). Here, the upper intertidal is sparsely colonized by two littorines, *Littoraria articulata* (Philippi, 1846) and *Nodilittorina millegrana* (Philippi, 1848). Such littorines occupy crevices in the concrete and occupy the few empty shells of a high-zoned barnacle *Balanus amphitrite* Darwin, 1854. This species is common throughout 'harbour' waters in Hong Kong (Foster, 1982), dominating the eulittoral. Here, a few individuals are zoned high, but over the lower extent of their distribution they are covered by *Mytilopsis sallei* which forms a monospecific belt from this point down to the sub-littoral fringe. Densities as high as >2000 living animals per 20 × 20 cm have been recorded. Unlike general harbour pier piles therefore, those at the Government Dockyard are dominated by *M. sallei*, to the virtual exclusion of all other species, save for nestling polychaetes.

*Population dynamics of **M. sallei***

Numbers and weights of living animals and empty valves per 20 × 20 cm sample of *Mytilopsis sallei* from the Government Dockyard during October 1987 to September 1988 varied considerably (Table I). High numbers of > 1,000 living animals were recorded between December 1987 and May 1988, with a peak in January of 2079, though a maximum weight was recorded in March 1988 at 228·6 g. Numbers of generally < 500 were recorded between June and November. Low weights were also recorded over the same period, with a minimum of 38·0 g obtained in June. Numbers of empty valves were maximal between May and August with generally > 1,000 shells recorded. Similarly, shell weights were highest in June and July, but otherwise weights were fairly uniform. These data have been compared as a series of plots (Fig. 5).

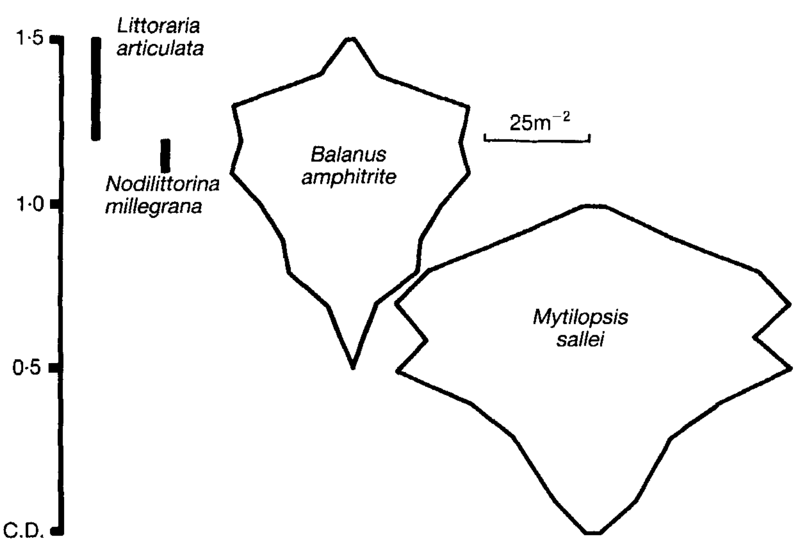

FIG. 4. Vertical zonation of the four major species occupying the pier piles at the Government Dockyard, Victoria Harbour, Hong Kong.

TABLE I

Numbers and weights of living animals and intact empty valves of ***Mytilopsis sallei*** *occupying a 20 × 20 cm quadrat from the Government Dockyard, Victoria Harbour, over the period October 1987 to September 1988*

Month	Living animals Nos.	Living animals Wt. (g)	Empty (intact) valves Nos.	Empty (intact) valves Wt. (g)
October 1987	422	91·6	287	68·6
November	726	89·8	586	126·9
December	1774	117·7	476	94·6
January 1988	2079	110·7	307	66·8
February	1438	213·7	463	83·9
March	1145	228·6	662	84·4
April	1168	147·7	130	22·1
May	1377	107·8	945	83·7
June	413	38·0	1891	173·9
July	311	40·2	1512	130·6
August	334	51·2	1065	99·6
September	421	46·4	752	85·0

The relationship between total empty vs. total living shell weights (Fig. 5a) shows a single peak in April 1988 in which the weight of living animals was 6·68 times that of empty valves. This represents recruitment into the population from those individuals settling in spring-summer (1988a).

The average numbers of living animals relative to empty valves is shown in Fig. 5b, this time with two peaks representing periods of lesser and more intense recruitment in January 1988 (1987b) and April 1988 (1988a), respectively.

The average weight of an empty pair of valves is shown in Fig. 5c with high values over winter representing adult mortality and low weights in March and from May to August representing mortality of newly settled juveniles from the autumn-winter (1987b) and spring-summer (1988a) periods of settlement, respectively. The latter period of juvenile mortality seems more significant than the former, although settlement of the 1988a recruits would mask the mortality of the 1987b recruits. The average weights of living animals (Fig. 5d) show falls in January and May representing peak settlement of juveniles from the 1987b and 1988a recruitments, respectively.

Morton (1981) measured a sample of *Mytilopsis sallei* from Visakhapatnam, India and suggested that the population was dominated by animals less than one year old, settling out in two peaks each year. The above study seems to confirm that observation. Further confirmation has been obtained from the length frequency histograms for *M. sallei* occurring at the Government Dockyard (Fig. 6). The first (October 1987) sample contained two peaks comprising adults settled in 1986 and a smaller peak of juveniles which settled in early 1987—the 1987a recruitment. Starting

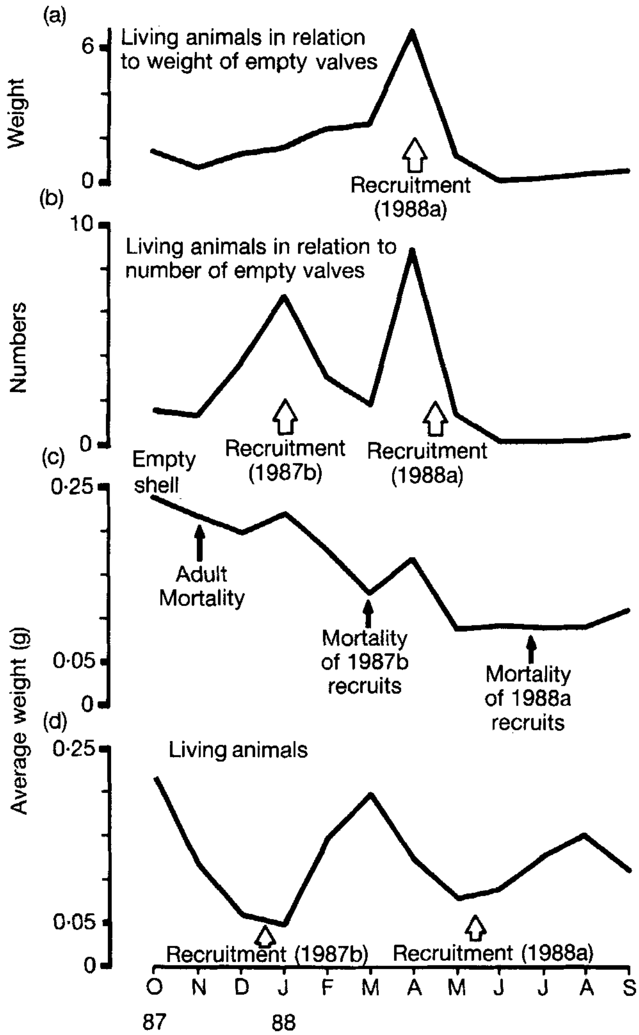

FIG. 5. *Mytilopsis sallei.* The relationships between numbers and weights of living animals versus intact empty valves obtained from 20 x 20 cm samples from the Government Dockyard, Victoria Harbour, over the period October 1987 to September 1988. (a) Total weight of living animals in relation to total weight of empty valves. (b) Total numbers of living animals in relation to total numbers of empty valves. (c) Average weight of an intact empty shell. (d) Average weight of an intact living animal.

in November, a second recruitment of yet smaller individuals was recorded, and designated 1987b. The recruitment of this generation continued at very high levels from December 1987 to March 1988, swamping the earlier (1987a) recruits and eventually also making adults of 1986 a minor component in the population structure. The recruited 1987b animals grew rapidly from November 1987 to May 1988 and by June 1988 the 1986 adults had all died leaving the population dominated by 1987 recruits exclusively. In July 1988, settlement of juveniles again occurred, the 1988a recruitment, and this continued until September 1988 when the study ended.

Thus, in the Government Dockyard, recruitment occurs in two phases, from around May–August (spring-summer) (the 'a' component) and from November–February (autumn-winter) (the 'b' component). As shown in Fig. 5a & b, the spring-summer recruitment is the most important. Both sets of recruits, however, quickly come to dominate the population picture. Mortality of the previous year's recruits is virtually complete by early summer (June).

Analysis of the empty valve samples confirms this picture (Fig. 7). In October 1987, the empty shells were dominated by adults recruited in 1986. Progressive mortality of 1987 recruits as new recruitment continued meant that slowly the latter came to dominate the empty valve picture. By June 1988, as with the living animal samples, the 1986 recruits were no longer present in the sample. Their shells had presumably disintegrated under the pressure of successive waves of settlement. Thereafter, the empty valve picture was dominated by 1987 recruits until, in August, first recruits of the 1988a settlement began dying too.

By May 1988, the 1986 adults were no longer identifiable. Little or no growth of the 1987 (a & b) recruits took place from June–August, presumably because, as will be seen, active gametogenesis and spawning at this time produced the first recruitment (1988a) of the 1988 season.

Mytilopsis sallei thus completes its life cycle in a maximum of 22 months, assuming survivors of the first spring–summer recruitment exercise live to maximal age. The second (autumn–winter) recruitment of the year is important, however, because through rapid growth it swamps the first recruitment, such that few if any will live to this age. Autumn–winter recruits could live for a maximum of 20 months but again this is unlikely since they too will, in turn, be swamped by the spring–summer recruits of the succeeding year. An average maximum life span for this species is thus probably less than 18 months. In essence, therefore, the population is turning itself over approximately every year, with just a few older animals entering their second year to ensure species survival in the event of wholesale mortality of one year class.

Reproduction

Individuals of identifiable sex (Stage 1: primordial) were first recorded at a shell length of 4 mm (Table II). Mature individuals (Stage 4) were first recorded at a shell length of 8 mm. Between 10–12 mm, a full range of sexual developmental stages was recorded and by 14 mm, the first spent individuals (Stage 5). *Mytilopsis sallei* thus attains sexual maturity within one year and recruits from the first spring–summer and second autumn–winter periods of settlement probably contribute, with adults from the previous years settlement, to the total reproductive output of the assemblage to produce first and second settlements of the succeeding year.

Individuals of *M. sallei* are dioecious. The monthly determined sex ratio ranged from a male dominance of 64·1% in May 1988 to a female dominance of 57·1% in April 1988. Males predominated for nine months of the year, giving an average male:female sex ratio of 55·1:44·9. This did not, however, vary significantly from 1 : 1. Similarly, there was no significant change in the sex ratio with increases in shell length (Table II), although males consistently dominated the sex ratio up to a shell length of 16 mm, i.e. the numerically dominant young of the year. Older individuals had a more equal sex ratio.

Changes in mean gonad condition (Table II) reflect the population picture demonstrated by the length frequency histograms (Figs 6 & 7). From October to December 1987, maturing (Stage 3) and mature (Stage 4) individuals dominated the population above 6 mm in shell length. By February 1988, the majority were spent (Stage 5). In March and April, the gonads continued to mature (Stage 3), but by May, they were generally spent again. Thus, there are two phases of

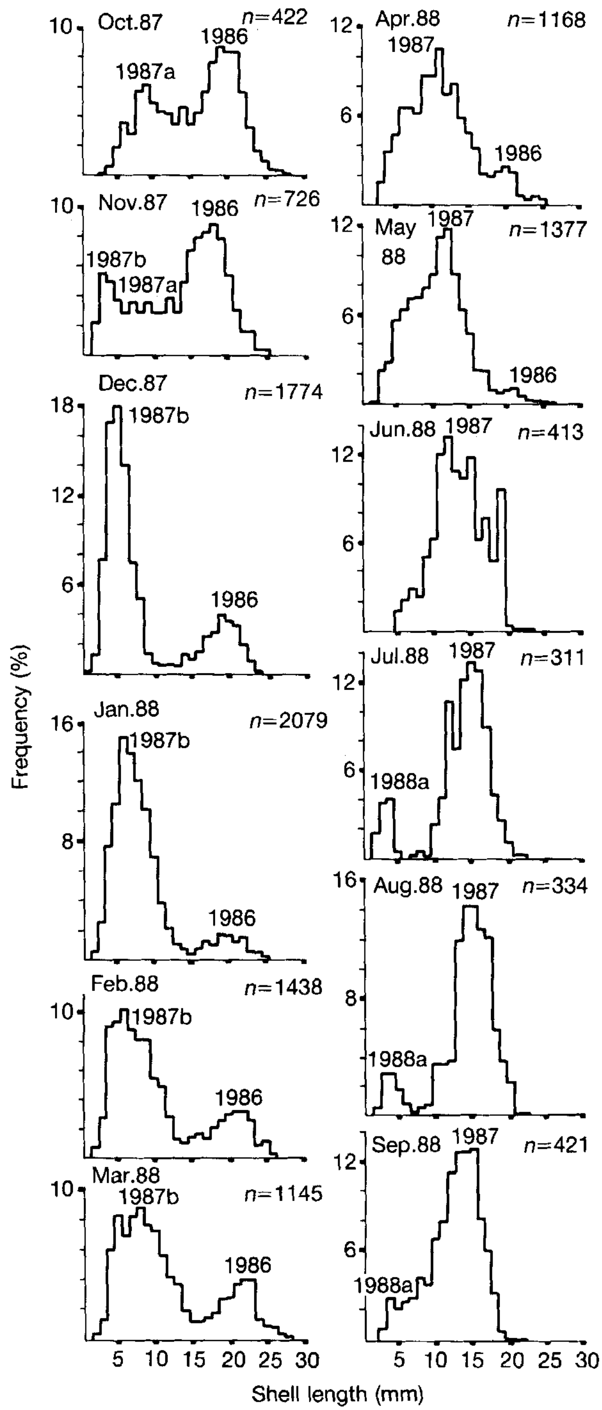

FIG. 6. *Mytilopsis sallei*. Length frequency histograms of the population structure of living animals at the Government Dockyard, Victoria Harbour, over the period October 1987 to September 1988. (n = Nos. 20 × 20 cm sample).

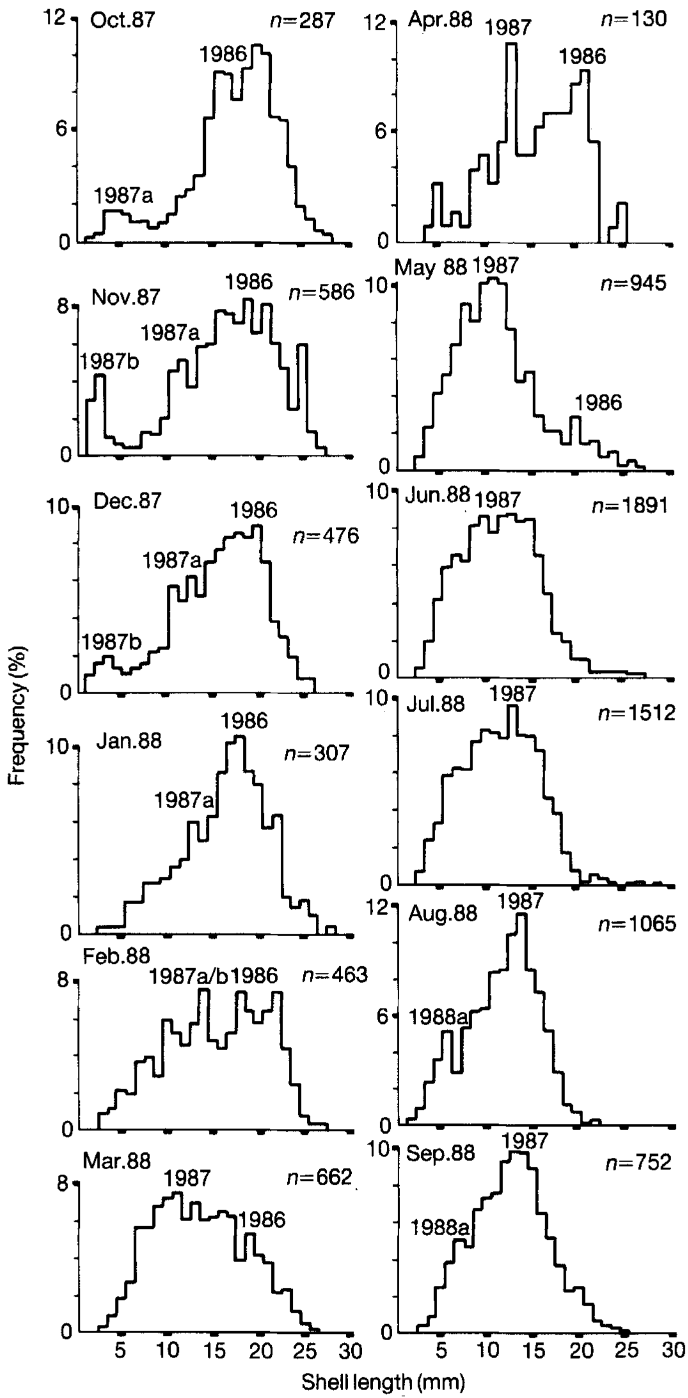

FIG. 7. *Mytilopsis sallei.* Length frequency histograms of the population structure of intact empty shell valves at the Government Dockyard, Victoria Harbour, over the period October 1987 to September 1988. (n = Nos. 20 × 20 cm sample).

TABLE II

The sex and stage of sexual development (1–5) of five individuals of ***Mytilopsis sallei*** *of each 2-mm size class obtained from the Government Dockyard, Victoria Harbour over the period October 1987 to September 1988. The monthly incidence of males and females and mean gonad condition for each sex is shown on the right. At the bottom, the sex ratio of each 2-mm size class is shown*

Δ = Immature ○ = ♂ ◇ = ♀ (in the table, (n) = ♂ of stage n; <n> = ♀ of stage n)

Month	Shell length (mm) 2	4	6	8	10	12	14	16	18	20	22	24	26	28	Incidence (%) ♂	♀	Mean gonad condition ♂	♀
Oct. 1987		Δ(2)(2) (2)(1)	Δ(2)(2) Δ(2)	(3)<3><3> <3><3>	<3><3><3> <3><3>	(3)<3>(3) <4>(3)	(4)<3>(3) <3><3>	(4)(4)<4> (3)<3>	(4)<3><3> (4)<3>	(3)<4>(3) (3)(3)	(3)<3>(3) (3)	(4)<4><4> (4)<5>	<3><3>(4) (5)(5)	(5)(3)(3) <5>	33 55·0	27 45·0	3–4	3–4
Nov.	ΔΔΔ ΔΔ	Δ<1>Δ ΔΔ	Δ<3>Δ (1)Δ	Δ<1>(3) ΔΔ	(3)(2)(1) <2>(2)	(3)<3>(4) <3>(3)	<3>(4)(4) (4)(4)	(5)(4)<3> (4)(5)	<4><4><3> <4>(4)	(5)<4>(4) (4)(4)	<2><4><4> <4>(2)	(4)<4>(4) <3><4>			25 55·6	20 44·7	4	4
Dec.	ΔΔΔ ΔΔ	ΔΔΔ ΔΔ	(2)ΔΔ <1>Δ	<1>ΔΔ Δ(1)	<2>(1)(2) Δ(2)	(2)(3)<2> (4)Δ	<1>(4)(4) (3)(3)	(3)<3><3> (3)(4)	<2>(4)<4> <3><3>	(4)<3>(4) (4)(4)	<4>(4)(4) <3><5>	<4><4><2> (4)(4)			24 57·1	18 42·9	4	4
Jan. 1988	ΔΔΔ ΔΔ	ΔΔΔ ΔΔ	ΔΔΔ Δ(2)	ΔΔΔ <1>Δ	<1><1>(2) Δ<2>	<3>(2)(3) <2><3>	<2>(3)<2> (3)<2>	<3>(4)(3) (4)(4)	<5>(5)(4) <3><3>	(5)(4)(4) (4)(5)	<2><3><5> (5)<3>	(4)(4)<4>	(4)(4)(4) <5><4>		23 52·3	21 47·7	4–5	4–5
Feb.				ΔΔΔ ΔΔ	(2)(3)(2) (3)<4>	(2)(2)(3) (3)(3)	(4)<5>(5) (5)(5)	<5>(5)<5> <5><5>	(5)(5)<4> (5)<4>	(4)<4><5> (5)(5)	(5)<5>(5) <5><4>	<5><5>(4) (4)<4>	(5)(5)<5> (4)(4)		28 62·2	17 37·8	5	5
Mar.	ΔΔΔ Δ	Δ<1>Δ ΔΔ	(2)ΔΔ Δ(1)	Δ(2)<1> ΔΔ	(3)Δ(2) (2)Δ	<2><1>(3) (4)(3)	<3>(3)(4) (4)<2>	<1><3>(4) <3>(4)	(4)(4)<3> (4)<4>	(4)<4>(4) <3><5>	<4>(4)(4) <3>	<4><4>(4) <3><4>	(4)<4><3> <4><4>	(4)(4)<3> <4>(4)	26 50·0	26 50·0	3–4	3–4
Apr.	ΔΔΔ ΔΔ	ΔΔΔ ΔΔ	ΔΔΔ Δ(1)	(2)ΔΔ <2>(1)	<2>(1)(1) (1)(2)	<1><2>(2) (3)<2>	(4)(2)<3> <3>(3)	<3><4><4> <4><4>	<4><3><2> <3>(4)	<4>(4)<3> <2><4>	<3><2><4> (2)<3>	(4)(4)<4> <4>			18 42·9	24 57·1	3–4	3–4
May	ΔΔΔ	ΔΔΔ	ΔΔΔ ΔΔ	(2)(2)Δ ΔΔ	<2>(3)<2> (3)Δ	Δ(2)(2) (3)<3>	<3>(4)<5> <4>(4)	(5)(5)(5) (5)<5>	<3>(5)<3> <5>(5)	(5)<5>(5) <3>(5)	(5)<5>(5) <5>(5)	<5><4>(5) (5)(5)			25 64·1	14 35·9	5	5
Jun.			(3)(2)Δ ΔΔ	(3)(2)(3) <2>(3)	<2><3><3> Δ(2)	<3>(4)(3) (4)<4>	<3><3>(5) (5)<3>	(3)<4><3> <3>(4)	(4)(4)<5> (4)(4)	<3>(4)					19 57·6	14 42·4	3–4	3–4
Jul.	ΔΔΔ ΔΔ	ΔΔΔ ΔΔ		ΔΔ(4) Δ(3)	<3>(4)(4) (4)(4)	<4><3><4> (4)<3>	(4)<4><4> (4)<3>	<3><4>(4) (4)(4)	(4)(4)<3> <3>(4)	(4)(4)(4) (4)<3>	(5)<4>				20 58·8	14 41·2	3–4	3–4
Aug.	ΔΔ	ΔΔ	Δ(2)Δ ΔΔ	ΔΔΔ Δ(2)	ΔΔΔ (2)Δ	(2)(2)(2/3) (2/3)(2/3)	(3)(3)Δ (3)Δ	<2>(3)<2> (4)<2>		<3>(4)<3> <3><3>	<3><3><3> <3>				14 56·0	11 44·0	2–3	2–3
Sep.		(1)ΔΔ ΔΔ	(2)(2)(2) (1)<2>	<2><2>(3)	<3>(4)(3) (3)(3)	<3><3><4> (3)(3)	<3>(3)<3> <3><4>	(4)<4>(3) <3>(4)	<4><4><4> <4>	(4)<4>(4) <4>	(4)				19 50·0	19 50·0	3–4	3–4
I ♂ ♀	34 – –	38 5 2	31 16 2	30 16 12	10 31 19	2 35 23	2 33 25	– 32 27	– 22 32	– 34 22	– 17 28	– 16 21	– 11 9	– 6 3	55·1	44·9		
% I ♂ ♀	100 – –	84·5 11·1 4·4	63·3 32·6 4·1	51·7 27·6 20·7	16·7 51·7 31·7	3·3 58·3 38·3	3·3 55·0 41·7	– 54·2 45·8	– 40·7 59·2	– 60·7 39·3	– 37·8 62·2	– 43·2 56·8	– 55·0 45·0	– 66·7 33·3				

gametogenesis each year to bring the gonads to maturity, first in spring–summer (the 'a' settlement) and second in autumn–winter (the 'b' settlement). The general absence of early gametogenic stages (1 and 2) between these two periods suggests that, in both the winter and the summer, spawning does not deplete the gonads but, rather, that gametogenesis continues to permit individual contribution to both peaks of reproductive activity.

The reproductive picture can be explained thus. Summer recruits from the spring–summer (April) spawning grow rapidly in late summer and after one year will be greater than 10 mm in shell length and thus mature. They will contribute to the reproductive output of the population in the following year. That is, summer recruits contribute to the production of the summer recruits of the following year. Similarly, with the winter recruits. Only a few individuals will enter their second year of life, the settlement pressure being such that after a maxium period of < 2 years, virtually all adults will have died. The larger spring–summer recruitment results from input from maturing individuals of the previous spring recruitment added to by those few individuals, at the base of the population, surviving from the previous year.

The population picture of *M. sallei* in the Dockyard is therefore dominated by overstepping generations of spring and winter recruits producing progeny one year later. This ensures reproductive continuity should one or other recruitment fail, but this is additionally secured by a few individuals surviving into their second year. *Mytilopsis sallei* is thus semelparous, with a few individuals iteroparous.

Discussion

There has, since the 1970s been a number of significant marine introductions into Hong Kong (Morton, 1987*a*), mostly focused on Victoria Harbour, the territory's *raison d'etre*. Two bivalves are included in this list: *Mytilus galloprovincialis* Linnaeus (Mytilidae) and *Mytilopsis sallei* (Recluz) (Dreissenidae). The former species is cultured extensively in Europe and was introduced into Japan either in 1928 (Arakawa, 1980) or between 1930–1935 (Wilkins, Fujino & Gosling, 1983). A blue mussel, called *M. edulis*, is recorded from the mainland coast of China where it is widely cultivated on strings in coastal waters (Anon., 1982). In Hong Kong, the species is widely distributed but occurs in low intertidal densities of between 1–5 m^{-2} (Lee & Morton, 1985). Nowhere has it achieved dominance. Conversely, *M. sallei*, introduced into Hong Kong at around the same time (1980), has become dominant, as demonstrated here, in the Government Dockyard within Victoria Harbour. The history of its colonization of Hong Kong appears to be via populations attached to the hulls of non-flagged vessels. First discovered on floating wreckage, it was later recorded from Hong Kong's central harbour and now dominates the intertidal of an area where refugee boats are first impounded. Since the species is not widely dominant in Victoria Harbour, transmission in ballast water as larvae (Carlton, 1987) is considered less likely, although this was probably the method of passage through the Panama Canal and its subsequent transoceanic dispersal.

In the Government Dockyard, *M. sallei* recalls, almost exactly, the colonization of the Indian Naval Dockyards at Visakhapatnam (Ganapati *et al.*, 1971). The base of the population comprises a mass of empty valves, bound together by byssal threads, while the living surface comprises young of the year individuals that settle upon their parents, eventually suffocating them. The opportunistic nature of *M. sallei* is confirmed by its rapid growth, early maturity, high fecundity and semelparity. Such characteristics classify *M. sallei* as an *r*-strategist (Pianka, 1970; Morton, 1987*b*), a tactic identified for a number of highly successful bivalve invasionists particularly of fresh waters, e.g. *Corbicula fluminea* (Morton, 1977*b*), introduced into North America (McMahon, 1983), and *Limnoperna fortunei* introduced into Hong Kong's potable water supply system from China (Morton, 1977*a*). The marine mussel, *Musculista senhausia*, has similar traits (Morton, 1973) and has been introduced recently into New Zealand and Australia (Slack-Smith & Brearly, 1987; Willan, 1987).

Mytilopsis sallei matures at a shell length of approximately 8–10 mm, in its first year of life. Two periods of settlement occur each year, one in spring–summer, the other in autumn–winter. Two recruitment periods have been described for a number of local bivalves: fresh water, estuarine and marine. Examples include representatives of the Mytilidae, e.g. *Limnoperna fortunei* in fresh waters, *Brachidontes variabilis* in the mangrove environment and *Anomalocardia squamosa* on more open sand shores (Morton, 1977*a*, 1978, 1988). Although single, summer breeders, e.g. *Polymesoda* (*Geloina*) *erosa*, are also known (Morton, 1985), a picture is emerging of a majority with two reproductive phases that may represent a single breeding season divided into two by the summer rainfall which locally and characteristically reduces salinities in the surface waters of the sea throughout Hong Kong, albeit less noticeably in the oceanic east. In this locality, Lee (1986) has shown that *Perna viridis* (Mytilidae) is mature year round, whereas in Victoria Harbour, where surface salinities are reduced more markedly, the breeding season is abbreviated to the summer months (Lee, 1985, 1988). Such a salinity-regulated phenomenon does not obviously explain the early and late summer breeding regimes of freshwater species but since, by consensus, such species are relatively recent immigrants into fresh waters (McMahon, 1983; Morton, 1987*b*), this may be a phylogenetically preserved trait. Conversely, mid-summer rains may limit either fertilization or spawning to early and late drier periods. Alternatively, mid-summer rains may flush out the habitat creating the impression of a bimodal pattern of recruitment.

No hermaphrodites have been recorded for *Mytilopsis sallei*. This is unusual as the great majority of otherwise dioecious species usually possess a few such individuals, e.g. *Corbicula fluminalis*, *Anodonta woodiana*, *Perna viridis* (Morton, 1982*a*; Dudgeon & Morton, 1983; Lee, 1988). The sex ratio of *M. sallei* appears slightly biased towards males (55% vs. 45%) but this is not statistically significant. Such a situation appears typical of many shallow-water marine bivalves. Thus, Pelseneer (1926) records a 54% male bias for *Mytilus edulis*, Griffiths (1977) a 57% male bias for *Choromytilus meridionalis* and Lee (1988) a 56% male bias for *Perna viridis*. For these and other marine bivalves, however, e.g. *Modiolus philippinarum* (Walter & Dela Cruz, 1980), *Geukensia demissa* (Brousseau, 1982), *Mytilus edulis* (Brousseau, 1983; Sprung, 1983) and *Perna viridis* (Walter, 1982), a 1 : 1 sex ratio has been obtained. This seems in sharp contrast to the female bias recorded for a number of fresh and brackish water bivalves by Morton (1987*b*).

Wherever *Mytilopsis sallei* has been introduced it has come to dominate the habitat. This is best documented for Visakhapatnam Harbour, India (for a review see Morton, 1981). This is in part due to its wide thermal and salinity tolerances, but also because of its ability to withstand pollution stresses. Chang (1985) records *M. sallei* as colonizing estuarine oyster beds in Taiwan. Lee (pers. comm.) similarly records it as occurring in brackish water shrimp ponds at Mai Po in Hong Kong's northwestern quadrant where temperatures may range from 10 to 35 °C and salinities from 0 to 27 ‰. Visakhapatnam Harbour and Victoria Harbour are polluted (Ganapati & Raman, 1973; Lam *et al.*, 1988). *Mytilopsis sallei* is tolerant of this too.

A combination of opportunistic life history and reproductive traits and wide environmental tolerances allow *M. sallei* to be transported easily but, also, in its introduced range, to colonize rapidly the new environment and eventually to dominate it.

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