

The Invasive Caribbean *Mytilopsis sallei* (Bivalvia: Dreissenidae): a Short Review

Koh Siang Tan^{1,*} and Teresa Tay¹

¹St. John's Island National Marine Laboratory, Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore, 119227

*Corresponding author: tmstanks@nus.edu.sg

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ABSTRACT The mussel-like bivalve species from the Caribbean, *Mytilopsis sallei*, is now well established in the vicinities of several ports in South and Southeast Asia. Although it may not be as notorious as its relative the zebra mussel *Dreissena polymorpha*, this brackish-water bivalve has the ability to colonise and displace native species in intertidal and subtidal habitats. It is also another testament to how well a tropical species can travel beyond its natural biogeographical boundaries. Here we briefly review its taxonomy, morphology, growth and reproduction, habitat and distribution, as well as its impact on natural habitats after invasion, based on published literature.

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1. INTRODUCTION

Amongst the few known tropical marine invertebrate species from the Caribbean that have recently established in Southeast Asia, the mussel-like dreissenid bivalve *Mytilopsis sallei* (Récluz, 1849) is arguably the most successful alien species. Its freshwater relative, the Asian zebra mussel *Dreissena polymorpha* (Pallas, 1771), can perhaps claim greater notoriety due to the scale of economic damage sustained in the rivers and inland lakes of North America. However, *M. sallei*, or the black-striped mussel as it is sometimes known, has been observed in at least ten countries between Israel and Australia (and beyond) over the last 30 years, a feat of adaptability by any standard for a benthic estuarine macroinvertebrate. Its localized distribution within each country may have spared them the infamy surrounding other members of the family Dreissenidae. Perhaps the inherent nature of tropical marine communities to resist establishment of alien species in their midst has something to do with current observations. Nonetheless, its ability to colonize, invade and persist in tropical estuarine and marine environments is clear. Here we briefly review their taxonomy, larval and adult morphology, invasiveness, geographical distribution, environmental impact and management strategies.

2. TAXONOMY

The highly variable shell morphology of *Mytilopsis* species has led to confusion and their identities are not resolved (see Morton 1981; Huber 2010; Fernandes et al. 2018). A re-examination of relevant type material from both sides of the Atlantic and eastern Pacific, coupled with the analysis of suitable genetic material is probably necessary to distinguish them. There are at least seven tropical species of *Mytilopsis* recognized in the literature, but they are poorly defined in morphological terms. Two species, namely *M. sallei* and *M. domingensis* (Récluz, 1849), were first described from Guatemala (see also

Hinkley 1920) and Dominican Republic in the Bay of Mexico, respectively. Another two species, *M. trautwineana* (Tryon, 1866) and *M. adamsi* Morrison, 1946, were first observed from the eastern Pacific (Colombia and Panama, respectively). From West Africa, two species (*M. africana* van Beneden, 1835 and *M. ornata* Morelet, 1885; described from Senegal and Gabon, respectively) are generally recognized (Oliver et al. 1998; but see Daget 1998 and Huber 2010). A new species of *Mytilopsis*, *M. lopesi*, was recently described from tropical Brazil (Alvarenga and Ricci 1989). Here we loosely regard *M. domingensis* and *M. adamsi* as synonyms of *M. sallei*, in view of their morphological similarities (see also Salgado-Barragán and Toledano-Granados 2006), although Marelli & Gray (1985) regarded *M. sallei* and *M. adamsi* as distinct species. Similarly, *M. allyneana* and *M. zeteki*, described from Fiji and Panama respectively (Hertlein and Hanna 1949), are here considered synonyms of *M. sallei*. Nuttall (1990a) further suggested that *M. domingensis* and *M. africana* are synonyms of *M. sallei*, but he distinguished *M. trautwineana* based on its exceptionally large septum and rounded umbones. *Mytilopsis leucophaeata* (Conrad, 1831), the type species of the genus, has a subtropical to temperate distribution in the Gulf of Mexico and occurs natively along the Atlantic coastline of North America (Marelli and Gray 1983; see also review by Kennedy 2011), but has been introduced to Northern Europe (Oliver et al. 1998; Rajagopal et al. 2002; Oliver 2015; Brzana et al. 2017) and also recently observed in the Black and Caspian Seas (Heiler et al. 2010; Zhulidov et al. 2015) as well as Brazil (Souza et al. 2005; Farrapeira et al. 2010; Fernandes et al. 2018). It is also superficially similar to *M. sallei* (see Pathy and Mackie 1993) but they are generally recognized as separate species based on their dissimilar (but slightly overlapping) native geographical distribution.

Three genera, *Congeria*, *Dreissena* and *Mytilopsis*, are broadly recognized in the family Dreissenidae. *Congeria* contains several fossil species (Morton 1970; Nuttall 1990a,



Figure 1. *Mytilopsis sallei*. Left valves of 12 individuals selected randomly from within a 10 cm x 10 cm quadrat placed over an intertidal colony attached to the surface of a tidal monsoon drain at Potong Pasir in Singapore. Shell lengths ranged between 23 to 28 mm. There is considerable variation in shell outline and shape between individuals.

b) and one extant species, *C. kusceri*, is found attached byssally in underground streams in Eastern Europe (Morton et al. 1998). Members of the genus *Dreissena* are also confined to freshwater environments (Zhulidov et al. 2010) including *D. polymorpha* (zebra mussel) and *D. bugensis* (quagga mussel), whilst *Mytilopsis* species prefer estuarine habitats, although they are able to tolerate freshwater conditions. Species belonging to the genus *Mytilopsis* are distinguished from those in the genus *Dreissena* in that *Mytilopsis* species possess an apophysis or hinge lobe internally, whilst members of *Dreissena* do not. This distinction is also supported by molecular data (Stepien et al. 2001; Therriault et al. 2004). The morphological distinction between *Mytilopsis* and *Congeria* is less clear as they both possess an apophysis (Morton et al. 1998), but based on molecular data, *Mytilopsis* is the sister genus to *Congeria* and this clade in turn forms the sister taxon to *Dreissena* (Stepien et al. 2001).

3. MORPHOLOGY

The shell and anatomy of adult *M. sallei* have been described in detail (Escarbassiere and Almeida 1976; Morton 1981). The heteromyarian, mytiliform valves, which are widest at the posterior and narrowest at the anterior, are unequal in size, with the left valve slightly smaller than the right. The terminal umbones are usually directed ventrally (Figure 1). A byssal notch is well defined anteriorly on the ventral edges of the pair of valves. Externally, the valves in adults are often covered by a thin, radially lamellate pale brown periostracum that is prominent towards the posterior region of the shell, but usually appear worn in the mid-region and anteriormost end of the bivalve to expose the shell surface below. Under the periostracum, some in-

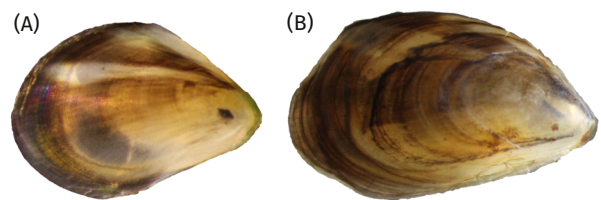


Figure 2. *Mytilopsis sallei*. Right valves of two juveniles reared in the aquarium. (A) shell length = 2.1 mm; (B) shell length = 3.5 mm.

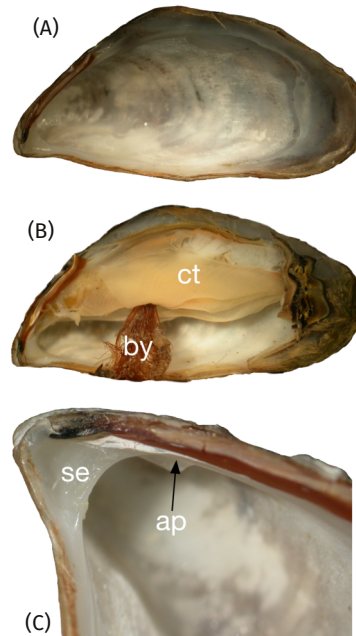


Figure 3. *Mytilopsis sallei*. (A) View of inside surface of shell; (B) view of animal after removal of left valve and part of mantle, showing the left outer ctenidium (ct) and byssus (by), with the foot withdrawn (not visible); (C) detail of anterior region of the shell, showing the septum (se) and apophysis (ap) just under the ligament. Shell length is about 25 mm.

dividuals may have pigmented, light to dark grey concentric markings that have given rise to the name 'black-striped mussel', but the shell is mostly dirty white. In contrast, juvenile shells are often dark brown with more apparent dark concentric markings (Figure 2). Internally, the shell is also white or bluish white (Figure 3A), and no nacre is present. The internal ligament is located anteriorly, and at the anterior end of each valve, a septum (hinge plate) and an apophysis (hinge lobe) can be seen (Figure 3C). The septum receives the anterior adductor muscles, while the apophysis anchors the anterior byssal retractor muscles. The muscle scars outlining these muscle insertions are much smaller than those of the posterior adductor and posterior byssal retractor muscles, which are located dorsally along the pallial line.

The animal within is light orange to pale yellow in coloration (Figure 3B), possessing separate inhalant and exhalant siphons formed from the fusion of the inner folds of the mantle margins that are pigmented light brown. Mantle fusion also occurs between the two siphons, as well as between the inhalant siphon and the small pedal gape. *M. sallei* possesses eulamellibranchiate ctenidia comprising two subequal demibranchs and very small labial palps (Morton 1981). The fine byssus threads (Udhayakumar and Karande 1989) are pigmented long, flattened strips up to 150 μ m wide.

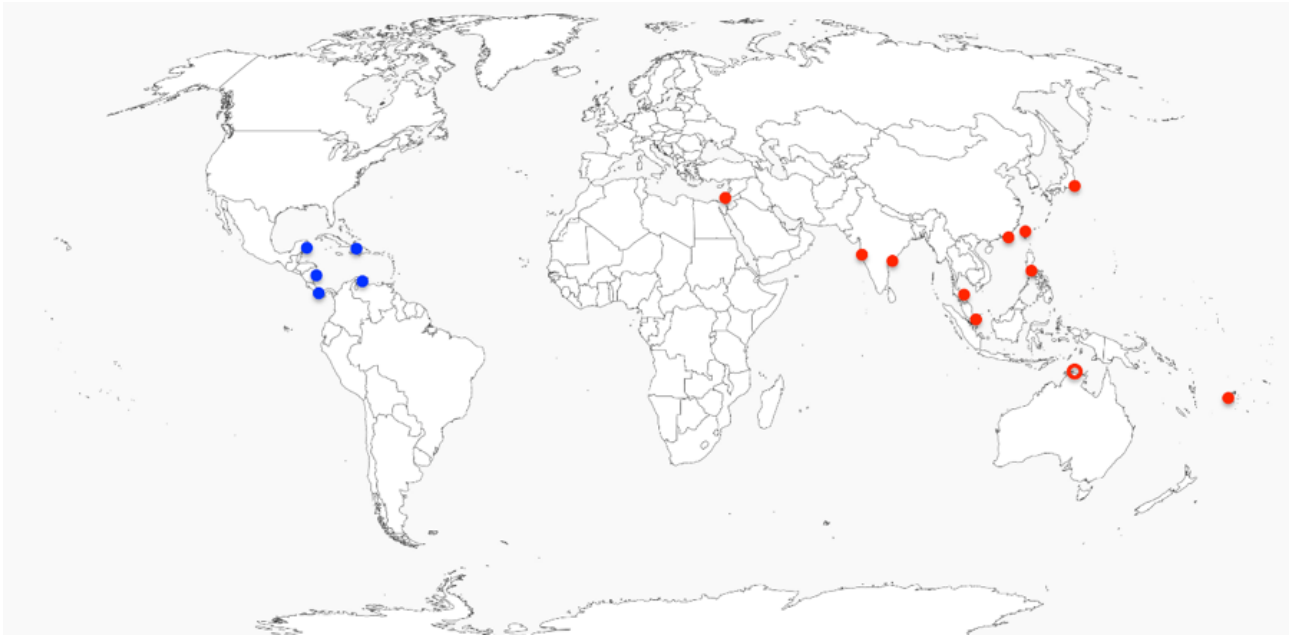


Figure 4. Geographical distribution of *Mytilopsis sallei*, based on published literature. Blue and red circles represent native and introduced populations respectively. Open red circle indicates introduced populations that were eradicated since they were first reported upon.

4. GROWTH AND REPRODUCTION

The larval shells are equivalve and inequilateral, and the hinge lacks a provinculum (He et al. 2016). After fertilization, the D-larva stage occurred within 20 hrs and plantigrade larvae (shell length about 300 μm) in 8–10 days (He et al. 2016), although Kalyanasundaram (1975) reported that larvae settled within four days in the laboratory. Based on size–frequency distribution of samples in Visakhapatnam, India, Morton (1981) suggested that individuals attained shell lengths between 6 and 10 mm within one month of settlement, and subsequently required another three months to reach 20 mm during the summer months. In a separate study, Kalyanasundaram (1975) reported that many individuals reached a size of 30 mm in six months. In Hong Kong, Morton (1989) observed that *M. sallei* completed its life cycle in a maximum of 22 months, with an average of less than 18 months. It is reproductively mature by about 8 mm, suggesting that it can reach sexual maturity within one month of settlement (Morton 1989). Karande and Menon (1975) detected hermaphroditic individuals in samples from Bombay harbour and suggested that *M. sallei* is protandric, but this was not seen in Hong Kong populations (Morton 1989). Mussels from Bombay harbour were found to go through a resting phase from winter to the start of the monsoon season, and sex reversal of males to females usually occurred after this resting phase (Nagabhushanam and Sarojini 1997). In their native range, ripe individuals can be found year-round, but there are two periods of intense spawning activity, apparently coinciding with a rapid drop in salinity (Puyana 1995). In summary, *M. sallei* is characterized by rapid growth, early maturity and high reproductive capacity (Morton 1981, 1989).

5. HABITAT AND DISTRIBUTION

The native distribution of *M. sallei* is centered in the Caribbean islands and Bay of Mexico (Figure 4; Marelli and Berrend 1978; Marelli and Gray 1983; Nuttall 1990a; Vilarity and Polania 2002). They may have been carried on hulls of ships to West Africa and beyond since the 16th century. It

is generally believed that they were also introduced to the Eastern Pacific via the Panama Canal (Jones and Rützler 1975; Morton 1980; Nuttall 1990a, b) to Fiji (Hertlein and Hanna 1949), Japan (Habe 1980; Furuse and Hasegawa 1984; Kimura and Horii 2004), Taiwan (Chang 1985), Hong Kong (Morton 1980; Huang and Morton 1983), China (Wang et al. 1999; Lin and Yang 2006), the Philippines (Cagauan 2008; Ocampo et al. 2014), Thailand (Wangkulangkul and Lheknim 2008), Singapore (Sachidhanandam and Chou 1996; Chan 1997; Tan and Morton 2006), Malaysia (Tan and Morton 2006), India (Ganapati et al. 1971; Karande and Menon 1975), Egypt (Hoffman et al. 2006), and Israel (Galil and Bogi 2009) (Figure 4). However, Marelli and Gray (1985) opined that *M. adamsi*, described from the Pearl Islands off Panama, is a native Eastern Pacific species distinct from *M. sallei*, and they maintained that *M. adamsi* (and not *M. sallei*) is the species now widespread in Asia. It remains possible that the native distribution of *Mytilopsis* species encompasses both sides of the American continent (Nuttall 1990a, b), but without genetic evidence this controversy is unlikely to be resolved. Risk of introduction remains high due to their persistent presence in major Asian and Indian ports. High haplotype variability of the mitochondrial COI gene in *M. sallei* from populations in Asia and India (Wong et al. 2011) suggests on-going genetic exchange. Based on their current latitudinal distribution and occurrence, they are able to survive and reproduce over a wide range of temperatures and salinities. In Singapore, *M. sallei* has been observed both intertidally and subtidally on a variety of natural and artificial substrata including wood, concrete, and plastic surfaces (Figure 5).

As a result of the uncertainties in defining *M. sallei*, its invasive history remains speculative. However, it appears likely that the first descriptions of *M. sallei* in the Pacific during the 1940s were initially thought to be new species (*M. adamsi* Morrison 1946; *M. allyneana* Hertlein and Hanna 1949; *M. zeteki* Hertlein and Hanna 1949). Subsequently, in the 1970s, *M. sallei* was reported from India, and populations became established in ports around Northeast and Southeast Asia between Japan and Singapore in 1980s, presumably through shipping (see

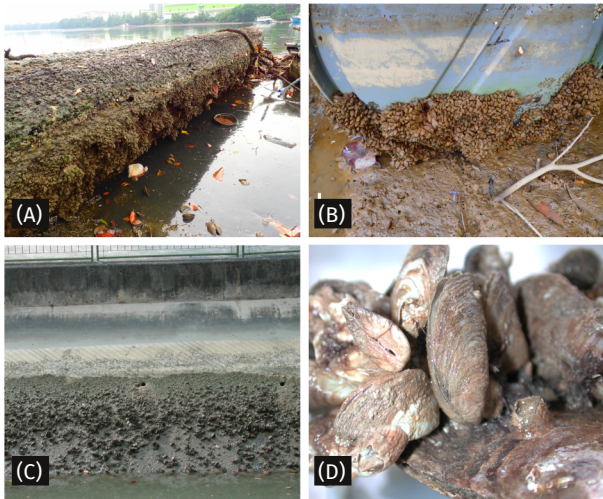


Figure 5. *Mytilopsis sallei* on different substrata in Singapore. (A) dead log; (B) plastic barrel; (C) sloping concrete wall of tidal canal; (D) on the shell surface of another bivalve *Isognomon ehippium*.

Chavanich et al. 2010). Larvae of *M. sallei* were subsequently detected in ballast water in Hong Kong (Chu et al. 1997). Similarly, if it is believed that *M. africana* is synonymous with *M. sallei*, as suggested by Nuttall (1990a), it appears quite possible that they were also transported from the Caribbean across the Atlantic Ocean as marine fouling on vessels plying the slave trade during the 16th and 17th centuries. No major ecological disasters have been reported involving *M. sallei*. An infestation that recently occurred in a marina in Darwin, Australia was eradicated by chemical means (Willan et al. 2000; Bax et al. 2002). In Asia, the populations appear to be stable and persistent, and while localized they may be the dominant organism on intertidal and subtidal hard surfaces of sheltered, estuarine harbours and brackish water aquaculture farms. The most recent record from Southeast Asia is its occurrence in Manila Bay, the Philippines (Ocampo et al. 2014) although Cagauan (2008) refers to this species as already present in the Philippines a decade earlier without further details.

6. IMPACT

Despite the widespread occurrence of *M. sallei* in Asian ports, there have been very limited investigations concerning their impact, management and control. Available studies indicate that adults are able to survive over a wide range of salinities between freshwater and hypersaline conditions up to 50 psu (Karande and Menon, 1975; Raju et al. 1975; Escarbassiere and Almeida, 1976; Rao et al. 1987; Wangkulangkul 2018). In Visakhapatnam, *M. sallei* dominated fouling panels placed in severely polluted waters with fluctuating salinities between 7 and 32 psu (Rao and Balaji 1994). Similarly, *M. sallei* reduced the species diversity index of macrofauna on fouling panels in Xiamen, China (Cai et al. 2014). *Mytilopsis sallei* has also been able to tolerate a range of temperatures from 5–40°C in the laboratory (Rao et al. 1975), although a study by Astudillo et al. (2017) reported that at low temperatures, byssal thread production were significantly reduced. Karande et al. (1993) showed that *M. sallei* has a very high tolerance to tributyltin oxide, with LC_{50} values reaching $13 \mu\text{g L}^{-1}$. LC_{50} values also showed that when exposed to certain heavy metals, copper was found to be the most toxic in *M. sallei*, followed by cadmium, and lastly zinc (Devi 1995). Its congener *M. trautwineana* has been shown to have beneficial effects on

shrimp aquaculture in Colombia when present in low densities by removing particulate matter, but shrimp survival is reduced when the bivalves occur in high densities (Aldridge et al. 2008). Given their occurrence in such high densities, *M. sallei* could conceivably act as a biological filter to remove and consolidate particulate matter and plankton from the water (e.g., Lin and Yang 2006). However, the beneficial or deleterious effects of such filtration to ecosystems remain unclear (see review by Sousa et al. 2009).

M. sallei is a particularly aggressive invasive species due to its rapid reproductive and fast-growing capabilities. Impacts of the mussel have been documented in several studies. In India (Ganapati et al. 1971; Morton 1981; Pati and Rao 2012), Hong Kong (Morton 1989), and Taiwan (Liao et al. 2010; Minchin et al. 2016), *M. sallei* causes severe fouling. It is particularly a major pest in India, where it has successfully colonized Visakhapatnam and Mumbai harbours and is reportedly spreading south (Gaonkar et al. 2010; Swami and Udhahakumar 2010). In Visakhapatnam harbour, *M. sallei* has completely suppressed the original fouling communities, dominating fouling communities almost singularly, and forming large clusters several centimeters thick which has to be removed at regular intervals (Raju et al. 1988; Shetty et al. 1989). The mussels also spread rapidly when accidentally introduced in Darwin, achieving unexpectedly high densities of more than 10 000 individuals/m² within 5–6 months (Hutchings et al. 2002). The mussel has also occupied Haad-Kaew Lagoon, Songkhla Lake in southern Thailand, attaching to fishing and aquaculture equipment in high densities (Wangkulangkul and Lheknim 2008).

Efforts to reduce or eradicate *M. sallei* have not been documented, apart from the drastic measures adopted in a marina in Darwin, Australia using a combination of chlorine and copper sulphate (Willan et al. 2000; Bax et al. 2002) which resulted in their complete removal. Chlorination is routinely employed to control its congener *M. leucophaeata* in Europe (Rajagopal et al. 2002). An experimental study by Karande et al. (1982) found that adult fouling organisms could be very tolerant to chlorine, with a high concentration of chlorine (15–20 ppm) for at least 60 hr needed to kill and remove *M. sallei*. Even a relatively high concentration of chlorine would be required to kill their larvae. However, settlement of larvae can be prevented at lower concentrations, which is a more practical and economic solution. A recent study by He et al. (2017) reported the effects of several inorganic ions and neurotransmitters on the larval settlement and metamorphosis of *M. sallei*, results which may be useful in managing their control. The study found that excess levels of potassium ions, as well as the neurotransmitter dopamine, were able to induce mussel larvae to settle and metamorphose. In contrast, magnesium and ammonia ions at high concentrations had an inhibitory effect on *M. sallei* larval settlement.

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