

TWO INVASIVE MUSSELS IN THE GENUS *PERNA* IN THE GULF OF MEXICO

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Introduction

The bivalve genus, *Perna* (Bivalvia: Mytilacea), includes three extant species; *P. perna* (the brown mussel), *P. viridis* (the green mussel), and *P. canaliculus* (the green-lipped mussel) (Siddall 1980). The subtropical, marine, intertidal mussel, *Perna perna*, invaded Texas, Gulf of Mexico shores in 1990 and now ranges from Veracruz, Mexico, to Freeport, Texas (Hicks and Tunnell 1993, 1995). Records for *P. perna* include India, Sri Lanka, Madagascar, the Red Sea, the east coast of Africa from central Mozambique to False Bay, South Africa, and the African west coast from Luderiz Bay north into the Mediterranean where it extends from Gibraltar to the Gulf of Tunis (Berry 1978). It also occurs in South America on the Atlantic coasts of Brazil, Uruguay, Venezuela, and in the West Indies (Berry 1978). Some authors recognize two other species; *P. picta* from the Mediterranean and northern Africa and *P. indica* from southern India. These latter species have been synonymized with *P. perna* (Siddall 1980, Vakily 1989). In 1999, *P. perna*'s tropical, estuarine congener, *Perna viridis*, was discovered in Tampa Bay, Florida and currently ranges from Venice to St. Petersburg, Florida (Ingrao pers. obs.). Prior to invasion of the Gulf of Mexico, *P. viridis* was first discovered outside of its endemic Indo-Pacific range at Point Lisas, Trinidad in 1990 (Agard *et al.* 1992), Venezuela's Gulf of Paria coast in 1992, where it is sympatric with *P. perna* (Segnini de Bravo *et al.* 1998), and Kingston Harbour, Jamaica in 1998 (D. Buddo and T. Bowes, per. comm.). The endemic, Indo-Pacific distribution of *P. viridis* ranges from the Persian Gulf to the southwestern Pacific Ocean and from southern Japan to Papua, New Guinea (Cheung 1993). International shipping is the likely vector for introduction of both species into the Gulf of Mexico, either as adults byssally attached to ship hulls or larvae in ballast seawater. Mitochondrial DNA sequence analyses have indicated that nonindigenous Gulf of Mexico *P. perna* populations exhibited a clear genetic affinity with populations from Venezuela (Holland 1997).

This paper summarizes the present status of introduced *P. perna* and *P. viridis* in the Gulf of Mexico and compares aspects of their biology, ecology, and physiology likely to influence their capacity to colonize the estuarine and coastal waters of North America. The biology of the third *Perna* species, *P. canaliculus*, which is geographically confined to New Zealand, will not be discussed in this paper.

Morphology

Perna species can be distinguished from indigenous North American mytilaceans by their lack of an anterior adductor muscle (Siddall 1980). However, *P. perna* and *P. viridis* cannot be differentiated on shell characteristics, which are highly variable and similar in both species. The shells of both species have smooth exterior surfaces interrupted by concentric growth lines, straight ventral margins, and one to two hinge teeth. The periostracum of *P. perna* varies from red-maroon, to dark brown, to black, often with marginal areas of yellow and green (Siddall 1980, Rios 1985, Berry 1978). Infrequently, the periostracum may be entirely emerald green, especially in juvenile specimens (i.e., < 25 mm) (Berry 1978, Hicks per. obs.). The periostracum of juvenile *P. viridis* is typically green to blue-green while, in adults, the older, more central portions of the shell tend to be various shades of brown (Siddall 1980). Occasionally, the shells of both juveniles and adults are entirely brown making them indistinguishable from *P. perna* (Ingrao per. obs.). The shell of *P. perna* reaches a length of 170 mm long (90 mm average) whereas that of *P. viridis* can exceed 300 mm (Vakily 1989).

P. perna and *P. viridis* can only be reliably differentiated on soft-part anatomical and cytogenetic characters. The most reliable anatomical character is presence of enlarged sensory papillae along the mantle margins of *P. perna* (Siddall 1980). Chromosome counts allow more objective identification. *P. viridis* (including Florida populations, Hicks per. obs.) is characterized by having 15 pairs of homologous chromosomes (Ahmed 1974) and *P. perna* (including Texas populations, Holland *et al.* 1999), 14 pairs of homologous chromosomes (Ahmed 1974).

Life History Traits

Spawning periods in *Perna* are highly variable (for reviews see Vakily 1989, and Hicks *et al.* in press). In *Perna* species inhabiting seasonal, subtropical environments, spawning is restricted to warmer months (Shafee 1989, Hicks *et al.* in press) while those in more temperature-stable tropical habitats tend to spawn sporadically throughout the year (Veléz 1971). The temporally restricted spring/summer spawning periods of temperate *Mytilus* species (e.g., *Mytilus edulis*) appear to allow reproductive synchronization with spring/summer phytoplankton blooms that support planktotrophic larval development (Seed 1976). In contrast, tropical/subtropical *Perna* may be stimulated to spawn during unpredictable phytoplankton blooms or periods of elevated temperatures (for a review see Griffiths and Griffiths 1987) leading to their characteristic asynchronous reproductive patterns. Both *P. perna* and *P. viridis* become sexually mature at 15-30 mm shell length (i.e., 2-3 months of age) (Siddall 1980, Vakily 1989). Sexes are separate. The testes are white while gravid ovaries are orange/red (Vakily 1989). Fertilization is external. The fertilized egg develops into a veliger larvae within 16 h (Sivalingam 1977) which remains in the plankton for 15-20 days prior to settlement (Appukuttan *et al.* 1984). *P. perna* pediveligers may delay settlement for several weeks if suitable substratum is not encountered (Lasiak and Bernard 1995). Settlement-competent pediveligers utilize byssal threads to attach to a variety of both natural (e.g., rocks, mangrove prop roots, compact mud and sand) and made-made substrata (e.g., rock jetties, piers, buoys, petroleum platforms) (Vakily 1989, Hicks and Tunnell 1995, Segnini de Bravo *et al.* 1998). Both species have a two to three year life span that varies among populations (Berry 1978, Lee 1986, Abada-Boudjema and Dauvin 1995, Hicks *et al.* in press).

Growth and Productivity

High growth rates and short life spans allow *Perna* species to sustain higher annual production rates than temperate *Mytilus* species. Among *Perna* species, shell growth rates are influenced by environmental factors such as temperature, food availability, settling density, tidal emersion, currents, and pollution (Vakily 1989, Cheung 1993, Hicks *et al.* in press). At one year's age, the shell lengths in indigenous, wild populations of *P. perna* are reported to range from 25-79 mm (Marques *et al.* 1991, Tomalin 1995). First year shell-lengths in Texas *P. perna* populations fell within this range at 42 to 53 mm, suggesting that environmental conditions in the Gulf of Mexico are suitable for this species (Hicks *et al.* in press). First year growth rates for *P. viridis* are markedly higher than those of *P. perna* at 93-119 mm for Indian populations (Narasimhan 1980, Rajagopal *et al.* 1998) and 96.5 mm for Madras populations (Shafee 1979), with the highest recorded growth rate (119 mm y⁻¹) among individuals infesting the raw water intake screens of a coastal power station (Rajagopal *et al.* 1998).

Annual productivity rates (standing crop flesh plus shell organic production) reported for endemic populations of *P. perna* range from 1.31 to 7.61 kg m⁻² y⁻¹ (Berry 1978, Shafee 1992). Values for two Texas *P. perna* populations were 1.86 and 2.44 kg m⁻² y⁻¹ (Hicks *et al.* in press). The only estimate of annual productivity for *P. viridis* is for a slow-growing (49.7 mm shell length in the first year), pollution-stressed population in Hong Kong at 1.19 kg m⁻² y⁻¹ (Cheung 1993). However, as the shell growth rates of most *P. viridis* populations are greater than those of *P. perna*, it is likely that the annual productivity in natural populations is at least equal to or greater than that of the latter species.

In terms of organic energy allocation, both species allot a major portion of nonrespired assimilation to organic shell production. In Texas *P. perna* populations, 42-54% of standing crop production was allocated to organic shell production (Hicks *et al.* in press) which is similar to that recorded for other *P. perna* populations at 32.9% to 47.1% (Berry 1978, Shafee 1992). A *Perna viridis* population allocated 55.5% of assimilation to organic shell production (Cheung 1993).

Capacity and Resistance Adaptations

Temperature: While factors such as extremes in salinity, or availability of suitable substratum may limit the abundance of marine intertidal invertebrates on a microgeographic scale, it is temperature tolerance that generally dictates their macrogeographic distributions. With few exceptions, members of the genus *Perna* inhabit waters with relatively stable temperature regimes (Vakily 1989). Annual ambient temperature ranges for *P. perna* populations include 10°-27°C in Africa (Abada-Boudjema and Dauvin 1995, Jackson 1976), 21°-32°C in India (i.e., those species previously designated as *P. indica*, Appukuttan *et al.* 1980, Rajagopal *et al.* 1997) and 18°-29°C in South America (Jacobi 1987, Veléz 1971). Ambient temperature ranges recorded in *P. viridis* populations are higher than those of *P. perna* at 12°-32°C in Hong Kong (Lee 1986, 1988, Cheung 1993), 25-32°C in India (Vakily 1989), 24°-32°C in the Philippines (Walter 1982), and 28-33°C in Thailand (Vakily 1989).

Tolerated temperature ranges often limit the natural distributions of marine bivalves. However, methodological variation in temperature tolerance determinations often reduces their utility in assessing the influence of temperature on species' distribution patterns and in predicting the

eventual distribution of newly invading species. Incipient lethal temperature limits (i.e., the temperature beyond which an organism can no longer survive for an indefinite period of time) are the best predictors of a species' natural, environmental thermal limits. Incipient lethal temperature limits are determined by 'chronic' testing in which specimens are held at constant temperatures for periods long enough to result in significant mortality. This approach allows the absolute upper or lower lethal temperatures to be determined as those falling just outside the range in which significant mortality occurs. However, the majority of laboratory-determined thermal limits for bivalves are "acute" lethal temperatures, assayed by exposing individuals to temperatures increasing (decreasing) at a specific rate until heat coma or death occurs (Henderson 1929). Acute testing allows direct relative comparisons of thermal tolerance among species, however, its dependence on exposure to short periods of thermal stress, results in overestimates of the actual incipient temperature range which ultimately limits a species' geographical distribution.

Based on acute testing, *P. viridis* has higher upper thermal limit than *P. perna* (Segnini de Bravo *et al.* 1998). Acute lethal limits for *P. perna* were 38.3°, 39.6°, and 40.5°C when exposed to temperatures increasing at 0.2°, 0.5° and 0.8°C min⁻¹, respectively, while those for *P. viridis* were higher with respective values of 40.8°, 41.8°, and 43.1°C (Segnini de Bravo *et al.* 1998). These values were similar to those of 44°C and 46°C recorded for Indian specimens of *P. perna* and *P. viridis*, respectively (Rajagopal *et al.* 1995a, 1995b) and for Texas specimens of *P. perna* at 44°C (Hicks 1999) and 37.4°-42.6°C for Venezuelan specimens (Chung and Acuña 1981) on exposure to temperatures increasing at 0.1° and 0.2-0.8°C min⁻¹, respectively. When exposed to temperatures increasing at a lower rate of 1°C day⁻¹, the acute upper thermal limits of Venezuelan specimens of *P. perna* and *P. viridis* declined to 34.5° and 37.5°C, respectively (Segnini de Bravo *et al.* 1998).

When subjected to true chronic testing, the incipient upper thermal limit for Texas specimens of *P. perna* was 30°C (Hicks 1999) and for Malaysian specimens of *P. viridis*, 35°C (Sivalingam 1977), values considerably lower than those recorded by acute testing of the thermal limits of these two species even when they were exposed to a rate of temperature increase of only 1°C day⁻¹ (*P. perna* = 34.5°, *P. viridis* = 37.5°C, Segnini de Bravo *et al.* 1998). The incipient upper limit for normal embryonic development in *P. perna* is 25°C while that of the veliger larva is equal to that recorded for adult specimens at 30°C (Romero and Moreira 1980, Hicks 1999). No comparative data are available for developmental stages in *P. viridis*.

When exposed to temperatures decreasing at a rate of 1°C d⁻¹, the acute lower limits of Venezuelan specimens of *P. perna* and *P. viridis* were 3° and 6°C, respectively (Segnini de Bravo *et al.* 1998). In contrast, when chronically exposed to low temperatures, the incipient lower limit of Texas specimens of *P. perna* was 7.5°C (Hicks 1999) and Malaysian specimens of *P. viridis*, 10°C (Sivalingam 1977). These chronic estimates are higher than those estimated by acute methodology at 3° and 6°C, respectively, even on exposure to a rather low rate of temperature decrease of 1°C day⁻¹ (Segnini de Bravo *et al.* 1998).

Thus, the acute and incipient upper and lower thermal limits of *P. viridis* are approximately 2-3°C higher than those of *P. perna*, reflecting the more tropical nature of the former species. The relatively narrow thermal tolerance limits of *P. perna* at 7.5-30°C appear to limit this species'

distribution to truly subtropical waters. Its incipient upper thermal limit of 30°C prevents colonization of truly tropical and estuarine waters which routinely exceed 30°C during the summer. Similarly, its relatively high lower thermal limit excludes it from more temperate regions where winter water temperatures generally fall below its incipient limit of 7.5°C. Its relatively narrow incipient temperature range may be the basis of its disjunct distributions in subtropical habitats where it is often restricted to shores receiving cool ocean currents, but is excluded from those excessively cooled by coastal upwelling (Berry 1978, Grant *et al.* 1992).

Salinity: Species of *Perna* have broad salinity tolerances (Vakily 1989). *P. viridis* primarily occurs in estuarine habitats ranging 18 to 33 ppt salinity (Shafee 1976, Vakily 1989), whereas, *P. perna* is generally restricted to open-seawater, high-energy, hard-shore habitats where salinity remains near that of full-strength seawater (*i.e.*, 35 ppt) (Berry 1978). While *P. perna* rarely occurs naturally in estuarine habitats, it can thrive when artificially cultured in them (Indrasena and Wanninayake 1994).

Laboratory estimations of salinity tolerance for specimens *P. viridis* are variable. Chronic testing yielded an incipient limit of 24-80 ppt for Malaysian specimens (Sivalingam 1977), while acute testing, involving exposure to salinities increasing or decreasing at a rate of 1 ppt day⁻¹, yielded a tolerated range of 0-64 ppt for Venezuelan specimens (Segnini de Bravo *et al.* 1998). Chronic testing, yielded an incipient low salinity limit of 16 ppt for Indian specimens of *Perna viridis* (Sundaram and Shafee 1989), similar to the incipient value of 24 ppt recorded for Malaysian specimens (Sivalingam 1977). Estimations of incipient salinity limits for *P. perna* include similar ranges of 15-50 ppt and 19-44 ppt for Texas (Hicks *et al.* 2000) and Brazilian (Salomão *et al.* 1980) specimens, respectively. In contrast, acute exposures to salinities increasing or decreasing at a rate of 1 ppt day⁻¹ estimated a broader tolerance range of 8-54 ppt for Venezuelan specimens of this species (Segnini de Bravo *et al.* 1998). While both *P. perna* and *P. viridis* tolerate a wide range of salinities, the greater salinity tolerance range of *P. viridis* reflects preference for estuarine habitats relative to the general restriction of *P. perna* to exposed shores with stable marine salinity regimes.

Eventual Distribution in the Gulf of Mexico

The life history traits of *P. perna* and *P. viridis* and other mytilid species make them highly invasive, leading to their world-wide introductions. These traits include: extensive capacities for larval and adult dispersal, rapid growth, early maturity, elevated fecundity, and high productivity. Such characteristics allow them to dominate communities into which they have been anthropomorphically introduced and rapidly expand their ranges after introduction. Their capacity to develop massive populations leads to radical alterations of community structure including extirpation of indigenous species and alteration of trophic energy flow (Morton 1997). Further, as major macrofoulers of raw water systems (Rajagopal *et al.* 1991, 1995a, 1995b), the presence of *P. perna* and *P. viridis* poses serious economic threats to raw-water using coastal industries and utilities in the Gulf of Mexico. Indeed, the first reports of *P. viridis* in North America were populations infesting the raw-water intake structures of power stations in Tampa Bay, Florida (Ingrao per. obs.).

Perna perna initially colonized exposed rock jetties in the Gulf of Mexico. Their initial colonization of jetty rocks reflected their preference for open-water, hard-shore environments in

their natural habitat. However, this species subsequently invaded Texas, Gulf of Mexico estuaries, including the Lavaca-Tres Palacios estuary, Corpus Christi Ship Channel, lower Laguna Madre, and Brownsville Ship Channel (Davenport 1995, McGrath *et al.* 1998). The hypoxia (Hicks 1999) and salinity tolerances (Hicks *et al.* 2000) of *P. perna* are similar to those of other estuarine bivalves, suggesting that they can tolerate the oxygen and salinity extremes associated with estuarine habitats. As *P. perna* has been successfully cultured in estuaries (Indrasena and Wanninayake 1994), factors other than oxygen concentration and salinity must prevent its permanent estuarine establishment, the most likely of which is a relatively poor thermal tolerance. The summer surface water temperatures of Texas estuaries frequently exceed the 30°C upper incipient thermal limit of *P. perna* (Hicks 1999). Thus, Texas estuarine populations of *P. perna* tend to be highly ephemeral, rarely persisting through summer months (McGrath *et al.* 1998). Further, a general collapse of Gulf of Mexico *P. perna* populations occurred in 1997/1998 when mean summer water temperatures approached or exceeded its incipient upper limit of 30°C. Thus, *P. perna* appears to have invaded Texas coastal habitats when conditions were temporarily conducive to settlement and growth. The present collapse of this species on Gulf shores suggests that their ecological and economic impacts will occur only during periods of low summer surface water temperatures ($\leq 30^\circ\text{C}$).

In contrast, *P. viridis* was first discovered in estuarine habitats on Florida's west coast (*e.g.*, Tampa Bay) where water temperatures range from 11-32°C (Lewis and Estevez 1988). The 35°C incipient upper thermal limit of *P. viridis* (Sivalingam 1977) may have allowed this species to become successfully established in these warm Florida estuarine habitats and will almost certainly allow it to disperse throughout the Gulf of Mexico.

While temperature tolerance limits the broad-scale geographic distribution of *Perna* species, their colonization of microhabitats depends on other environmental variables, particularly availability of suitable hard substrata. While the plantigrade larvae of mytilacean mussels can settle on filamentous substrata, adults require permanent hard surfaces, restricting natural populations to rocky shores or the bases of mangrove trees. However, as evidenced by the introductions of *P. perna* and *P. viridis* into the Gulf of Mexico, the presence of natural hard substrata is not necessary for invasion. The U.S. Gulf of Mexico's seaward and estuarine shores consist almost exclusively of sandy beaches or other unconsolidated material, with hard shores being restricted to widely dispersed man-made structures such as pilings, piers, channel markers, platforms, buoys, jetties and seawalls. Despite a lack of natural hard substrata, both species have developed dense populations on these disjunct man-made structures which are common to practically all U.S. coastal environments.

The planktotrophic larval stages of *P. perna* and *P. viridis* remain free-swimming for 15-20 days, during which they can disperse great distances on ocean currents or be transported between continents in the ballast water of ocean-going ships. Additionally, adult *Perna* populations byssally attach to the hulls of international vessels (Carlton 1987) leading to their transportation and release into areas outside their endemic range. Texas and the southern Gulf of Mexico and Atlantic states are interconnected by the marine/estuarine Intracoastal Waterway (ICWW), extending from Brownsville, Texas to Boston, Massachusetts. Texas alone has more than 1,763 km of estuarine barge channels (McGrath *et al.* 1998). Thus, barge and other commercial shipping plying the ICWW will be the main vector by which these species will extend their

present ranges in the Gulf of Mexico. As *P. viridis* is better adapted to the temperature and salinity regimes of these coastal estuarine waters, their dispersal through the ICWW is likely to be rapid and their colonization of Gulf of Mexico coastal waters extensive. In contrast, the low temperature tolerance of *P. perna* may present a barrier to its further distribution into Gulf of Mexico estuarine habitats unless these habitats remain permanently below 30°C.

Conclusions

The potential for long-term establishment of *P. perna* and *P. viridis* in Gulf of Mexico and North American coastal habitats remains uncertain. Within the ten year period that *P. perna* has occurred on Gulf of Mexico shores, populations have achieved densities, growth and productivity rates rivaling those of endemic populations (Hicks *et al.* in press). However, these populations eventually collapsed when summer water temperatures exceeded their upper incipient limit of 30°C (Hicks 1999) and have not yet recovered. Thus, *P. perna* cannot be considered to be permanently established in the southwestern Gulf of Mexico. Gulf populations of *P. perna* remain at low densities and are likely to recover only during periods when Gulf waters do not exceed 30°C. However, intense thermal selection of these populations has the potential to lead to development of a thermally tolerant physiological race, as likely has occurred in southern India (i.e., those previously cited as *Perna indica*, Rajagopal *et al.* 1995a), allowing eventual re-expansion of this species' range and ecological/economic impacts in the Gulf of Mexico. In contrast, *P. viridis* appears to be physiologically tolerant of the environmental extremes characterizing Gulf of Mexico coastal habitats, suggesting that there are no biotic or abiotic barriers to its future rapid expansion throughout our coastal waterways. Because of the high likelihood of its further dispersal through the ICWW and potential for severe, negative ecological and economic impacts in Gulf coastal environments, it is imperative that a coordinated monitoring program for *P. viridis* be established. The distribution and condition of *P. perna* populations should also be monitored in this program, particularly as this species could be transported into and colonize coastal habitats with more favorable temperature regimes than occur within its present range on the Texas coast. Further, an assessment of the potential for barges and other large vessels to act as vectors for both species within the ICWW should be of highest priority. Lack of monitoring in the early stages of zebra mussel invasion of North American freshwaters lead to their unexpected macrofouling of numerous raw-water facilities with major economic consequences (Claudi and Mackie 1994). The valuable lessons learned from zebra mussel invasion of North American inland waters should not be ignored when evaluating the potential negative impacts that these two new bivalve invaders could have on Gulf of Mexico coastal habitats and industries.

Acknowledgments

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