

Introduction, distribution, spread, and impacts of exotic freshwater gastropods in Texas

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Abstract We examined the patterns of distribution, vectors of introduction, and potential ecological impacts of freshwater exotic species in Texas over the last 45 years. Currently, five species of exotic gastropods are established: channeled-type applesnail (*Pomacea insularum*), red-rim melania (*Melanoides*

tuberculatus), quilted melania (*Tarebia granifera*), giant rams-horn snail (*Marisa cornuarietis*), and Chinese mysterysnail (*Cipangopaludina chinensis*). In contrast to the northern part of the US, where shipping appears to be the most important vector for the introduction of aquatic invasive species, aquarium and ornamental trade dominated among unintentional vectors of introduction of all freshwater exotics in Texas, resulting in different patterns of distribution, spread, and ecological impacts. The rate of spread of exotic gastropods in Texas varied from 39 waterbodies colonized over 18 years for *P. insularum* to only three waterbodies during last 45 years for *C. chinensis*. Four of five exotic gastropods were found in highly vulnerable aquifer-fed springs and rivers, which contain numerous endemic and endangered species. The fifth species, *Pomacea insularum*, is an agricultural pest. Potential negative ecological effects of exotic gastropods include impacts on wetlands and wetland restoration, competitive exclusion of native snails, and the introduction of exotic parasites, trematodes, which could infect fish and waterfowl, including federally protected species. Aquifer springs with stable temperature regimes are refuges for both cold and warm intolerant species.

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Introduction

Most recent reviews of the distributions of freshwater invaders and the vectors that spread invaders consider shipping activities, including ballast water, as the main vector of initial introduction of exotic species and for North America focus on the northern and central regions of the US (e.g., Mills et al., 1993, 1996, 1998; Fofonoff et al., 2003; Drake & Lodge, 2007). Other important vectors, such as the aquarium and ornamental trade, and associated activities, have received much less attention (Padilla & Williams, 2004; Rixon et al., 2005). However, these other vectors play a significant role in the introduction of nuisance species across all of North America (Padilla & Williams, 2004), and could be the dominant vector in areas far from ballast water and in warm climates suitable for many subtropical and tropical plants and animals typically found in aquarium and ornamental trade. For example, while only 6% of all aquatic invaders were introduced into the Great Lakes basin through aquarium and ornamental trade (Mills et al., 1993), in Florida this vector was estimated to be responsible for the introduction of more than 70% of fish (Padilla & Williams, 2004, and references therein). The introduction and spread of exotic species through the aquarium and ornamentals industry and associated activities is likely to result in different geographic patterns of introduction and spread than for shipping. The ecological impacts of the introduction of aquarium and ornamental species may also be different than those for species introduced by shipping activities.

In addition, the set of species introduced through aquarium and ornamental trade is usually quite different than those in the ballast water introductions, and may be more likely to be successfully introduced (Padilla & Williams, 2004). The majority of aquatic organisms introduced through aquarium and ornamental trade are warm water species, and are intolerant of sustained cold winter temperatures. Aquifer-fed, warm waterbodies are not only suitable environments for these invaders, but may also provide refuge, buffering species from the effects of cold winter temperatures. Most of the exotic gastropods and many exotic fishes in Texas are found in aquifer-fed springs and rivers (Howells, 2001a; authors' data). These same aquifers contain numerous endemic species, including federally listed endangered and threatened species

(www.edwardsaquifer.net/species.html). Introduction of invaders into such environments may create a serious threat to local biodiversity.

Gastropods dominate among freshwater invertebrates introduced through the aquarium trade and related activities (Padilla & Williams, 2004), and are the most diverse component of exotic freshwater invertebrates in Texas (Howells, 2001a) as well as in North America in general and in Europe (Karatayev et al., 2008; accepted). We examined the distribution, vectors of introduction, and potential ecological impacts of freshwater exotic gastropods in Texas over the last 45 years, and suggest that they may be indicative of freshwater invertebrates in general introduced through the aquarium trade and related activities.

Materials and methods

To assess the distributions, vectors of introduction, spread, and impacts of introduced gastropods in Texas we used both field studies and historic data from the literature and a database maintained by Texas Parks and Wildlife Department (TPWD). We also looked for other published research through web-based searches including searches of invasive species databases, primary literature in scientific journals, books, reports, and the authors' personal holdings. Published records included Murray (1964, 1971, 1975), Clench & Fuller (1965), Murray and Wopschell (1965), Murray & Haines (1969), Abbot (1973), Dundee (1974), Kotrla (1975), Fullington (1978), Lindholm & Huffman (1979), Jokinen (1982), Neck (1984, 1985, 1986), Horne et al. (1992), Neck & Schultz (1992), McDermott (2000), Howells (2001a, b, c), Howells & Smith (2002), Mitchell et al. (2005), Howells et al. (2006), and Tolley-Jordan & Owen (2007).

To assess the current distribution of exotic gastropods in Texas, we conducted a statewide survey during 2005–2008. We used two different methods of study based on the differences in biology of exotic gastropods. *Pomacea insularum* is a large snail that mostly populates shallow areas in the macrophytes zone and lays large, pink egg masses above the water; the presence of egg masses is known to be a good indicator of snail presence/absence during the reproductive period when we sampled (Martin et al.,

2001). For the *P. insularum* survey, we visited all 12 sites where these snails were previously reported as well as surrounding waterbodies in the same and nearby counties, for a total of 393 sites in 13 counties in the southern Texas. For this survey, streams were surveyed at public road crossings alone to prevent any possible trespassing on private land. In areas where snails were found, coverage was increased to sample every nearby tributary. On each site at least a 20-m section of the stream underneath the bridge, and out of it, was searched for live or dead snails and their egg masses. At each site we recorded the presence/absence of live snails, egg masses, or dead shells. Other exotic gastropods are much smaller than *P. insularum*, do not lay egg masses above the water, and populate deeper waters, and therefore required more efforts to detect their presence/absence. For these gastropods we visited 21 areas and/or waterbodies where these species had been previously reported as well as 20 additional waterbodies in 19 counties. At each site we initially conducted a timed search (1 person/h). If exotic gastropods were found and were abundant, we collected all of the mollusks found in 3–5 quadrats of 50 × 50 cm. For each sample, all gastropods were identified and counted, and voucher specimens were preserved in 90% ethanol.

Results

Several species of freshwater exotic gastropods have been reported from Texas waterbodies, some of which have established populations and some that survived for a short period of time and then disappeared. Species that failed to survive or for which there is no recent confirmation of an established population include: Florida applesnail (*Pomacea paludosa*), spike-top applesnail (*Pomacea bridgesi* (= *P. diffusa*, Rawlings et al., 2007)), marbled apexa (*Stenophysa marmorata*), and tawny apexa (*Stenophysa maugeriae*) (Howells, 2001a; Howells et al., 2006; authors data). Five species of exotic gastropods were found to have established populations in Texas at the time of our survey: channeled-type applesnail (*Pomacea insularum*), red-rim melania (*Melanoides tuberculatus*), quilted melania (*Tarebia granifera*), giant rams-horn snail

(*Marisa cornuarietis*), and Chinese mysterysnail (*Cipangopaludina chinensis*).

Current invaders

Pomacea insularum d'Orbigny

This species is native to South America (reviewed in Cowie & Thiengo, 2003). Although this genus was reported to be in Texas since the 1970s (Fullington, 1978), the first reproducing population, identified as *P. canaliculata*, was found in a tributary of Buffalo Bayou, Harris County, in 1989 (Neck & Schultz, 1992). Although nearly all introductions of applesnails in Texas were initially thought to be *P. canaliculata*, recent genetic analyses have shown that introduced snails in Texas are *P. insularum* (Rawlings et al., 2007). In 2000, TPWD found populations of *P. insularum* in the American Canal, Brazoria, and Galveston counties, and Mustang Bayou, Brazoria County (Howells, 2001b), about 50 km away from first reported population. According to Howells (2001a), in 2001, *P. insularum* was found in Houston, in the Briscoe Canal and Halls Bayou, Brazoria County, and in a pond in Bedford, Tarrant County, app. 390 km north from the first reported population. This last population was an independent introduction that survived a few winters, but vanished by 2005 (D. K. Britton, US Fish & Wildlife Service, Arlington, TX, and R. F. McMahon, The University of Texas at Arlington, pers. comm.; Howells et al., 2006). By 2002, *P. insularum* was reported from 12 locations in Texas (Howells & Smith, 2002).

Before our survey, *P. insularum* was known from six counties in southeastern Texas (centrally located in the Texas rice growing belt) (Howells et al., 2006). Our survey in 2005 and 2006 confirmed the presence of this snail in seven southeast Texas counties (Austin, Galveston, Harris, Chambers, Fort Bend, Waller, and Brazoria) (Fig. 1). Of the 393 sites surveyed, snails were found in 53 (13% from all sites surveyed). *Pomacea insularum* was found in 18 large waterways (Brazos River, American Canal, and Horsepen, Sims, Bessies's, Armand, Buffalo, Mustang, Chocolate, Dickinson, New, and Whites Bayous), 2 reservoirs (Barker and Addicks), and in 19 small creeks, ponds, and ditches (Table 1), a maximum of 80 km from the first reported population.

Fig. 1 Current distribution of exotic gastropods by county (shaded) in Texas: *Pomacea insularum*, *Melanooides tuberculatus*, *Tarebia granifera*, and *Marisa cornuarietis* (which have the same distribution), and *Cipangopaludina chinensis*

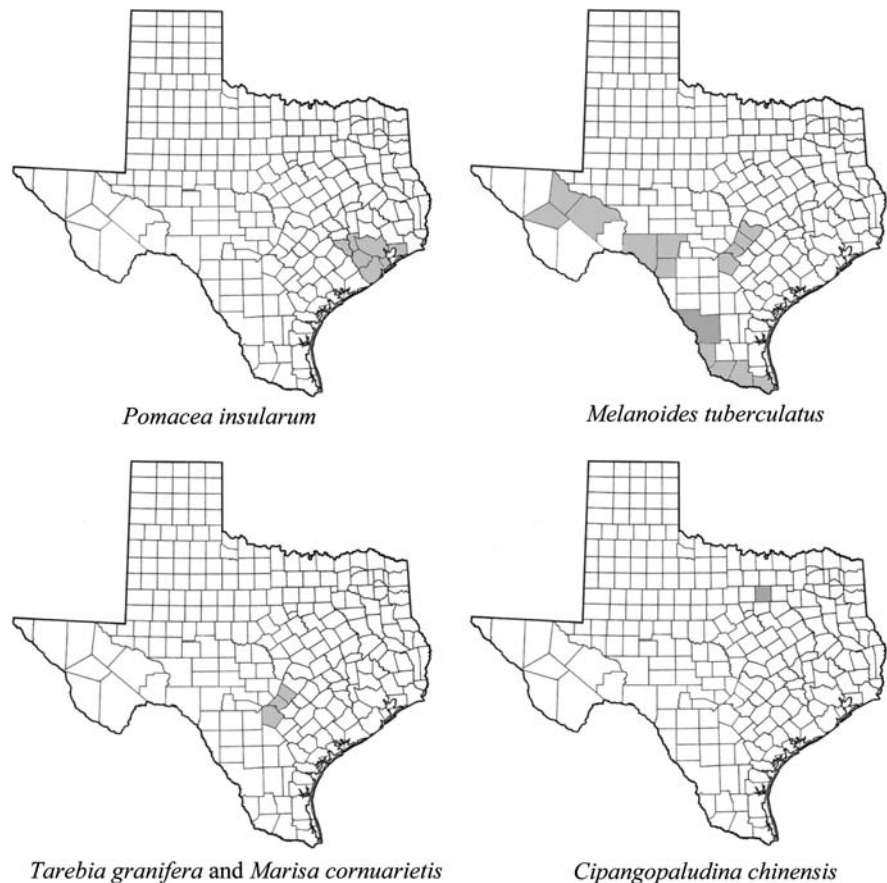


Table 1 Introduction and rate of spread of exotic gastropods in Texas

Species	Date of first observation or report	Numbers of waterbodies colonized (rate of spread)	Waterbody type where found
<i>Pomacea insularum</i>	1989 (Neck & Schultz, 1992)	39 (2.17)	Ditches, canals, streams, rivers, ponds, and reservoirs
<i>Melanooides tuberculatus</i>	1963 (Murray, 1964)	24 (0.53)	Rivers, springs, reservoirs
<i>Tarebia granifera</i>	1963 (Murray, 1964)	3 (0.07)	Springs and spring-fed rivers
<i>Marisa cornuarietis</i>	1981 (Horne et al., 1992)	3 (0.12)	Springs and spring-fed rivers
<i>Cipangopaludina chinensis</i>	1965 (Clench & Fuller, 1965)	3 (0.07)	Spring-fed pond

The rate of spread (in parentheses) is calculated as the number of waterbodies colonized per year

Melanooides tuberculatus (Müller)

Red-rim melania is native to subtropical and tropical areas of northern and eastern Africa and southern Asia (Abbot, 1952; Neck, 1985). In the 1930s, *M. tuberculatus* was introduced to the US by a San Francisco aquarium dealer. The first record of an established population of *M. tuberculatus* was from Lithia Springs, Florida (Abbot, 1952). Soon this

species spread across Southern United States, including California, Florida (Abbot, 1952), Texas (Murray, 1964), Louisiana (Dundee & Paine, 1977), Arizona, and Oregon (Murray, 1971). Currently, the presence of *M. tuberculatus* has been confirmed in 15 states, including the most southern and several western states with geothermal waters (Mitchell et al., 2005). Texas was colonized by *M. tuberculatus* prior to 1963 (Abbot, 1973). Snails were first found in the

headwaters of the San Antonio River, Bexar County, and in Comal Springs in Landa Park, New Braunfels, Comal County (Murray, 1964). Later this species was reported from the Las Moras Creek, Bexar County (Murray, 1971), San Antonio River (Brackenridge Park, San Antonio) (Kotrla, 1975), Balmorhea springs (Balmorhea State Park, Reeves County, Fullington, 1978), and from an old river channel of the Rio Grande, Cameron County (Neck, 1985), a maximum of 580 km from the original site where they were first documented. By the 1970s *M. tuberculatus* became common in almost all springs in south and central Texas (Lindholm & Huffman, 1979).

During 2006–2008, we sampled over 40 waterbodies for *M. tuberculatus*, 16 of which were known to have populations of this species in the past. *Melanoides tuberculatus* was still present in 12 of those 16 waterbodies. Only a few dead shells were found at Sunken Garden Spring (Austin). This spring had been dry for 3 months shortly before our sampling, and the drought probably destroyed the remaining population. Oxbow Pond (LaComa Tract of the Lower Rio Grande Valley) was almost completely dry and overgrown with shrubs and trees. A nearby small creek that still had running water was checked, but no evidence of *M. tuberculatus* was found. No live snails or their shells were found in Balmorhea Reservoir (Reeves County).

We found new populations of *M. tuberculatus* in six waterbodies, including Falcon Reservoir (Zapata and Starr counties). Based on published data and our survey, *M. tuberculatus* is currently present in at least 24 waterbodies in 15 counties in Texas (Table 1, Figs. 1, 2).

Tarebia granifera (Lamarck)

The quilted melania is native to India, Southeast Asia, The Philippines, Japan, and Hawaii (Abbot, 1952). The first record of an established population of *T. granifera* in the US was from Lithia Sulphur Springs, near Tampa, Florida, in December 1947 (Morrison, 1954). According to Abbott (1952), these snails were accidentally introduced by contaminated tubs used by an aquarium dealer in Lithia Springs, Florida, probably from Hawaii. In Texas, these snails were first reported in 1964 from the San Antonio River (including the effluent from the San Antonio

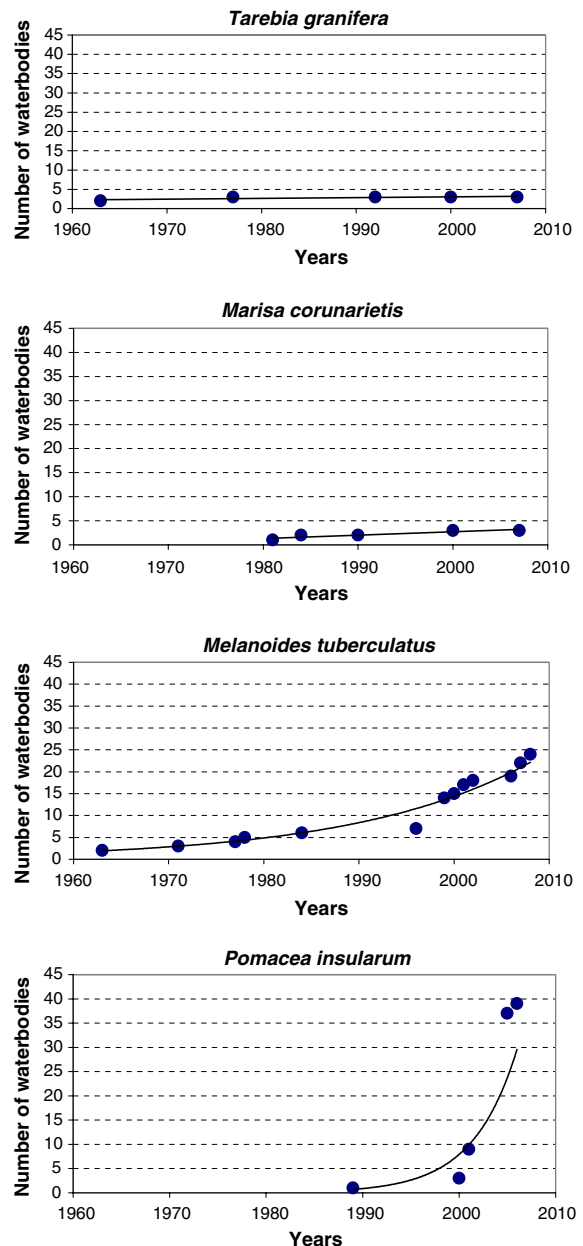


Fig. 2 The cumulative number of Texas waterbodies colonized by the exotic gastropods *Tarebia granifera*, *Marisa cornuarietis*, *Melanoides tuberculatus*, and *Pomacea insularum* since their first record in Texas. The data were fitted with exponential regression

Zoo), Bexar County, and from Comal Springs in Landa Park, New Braunfels, Comal County (Murray, 1964) (Table 1). However, based on the information from local aquarium dealers, Murray and Wopschell (1965) suggested that *T. granifera* was introduced into the San Antonio area as early as 1935. This is

much earlier than the first record of an established population of *T. granifera* in the US by Morrison (1954). If these data (Murray and Wopschell 1965) are correct, the *T. granifera* population in the San Antonio River was established long before the record by Morrison (1954). In 1977–78, *T. granifera* was reported from the upper reaches of San Marcos River (Lindholm & Huffman, 1979). Recent surveys (Howells, 2001a; R. Gibson, US Fish and Wildlife Service, National Fish Hatchery and Technology Center, San Marcos, Texas, pers. comm.) did not reveal any additional populations in Texas. In our current survey, we found *T. granifera* in all three waterbodies where these snails had been previously reported (Comal Springs and San Marcos and San Antonio rivers). All waterbodies are supplied from spring water aquifers and have very stable water temperatures of around $22 \pm 2^\circ\text{C}$, during the year. No new populations of *T. granifera* were found during our study.

Marisa cornuarietis (Lamarck)

Giant rams-horn snail is native to northern South America and Trinidad (Robins, 1971). The first record of an established population of *Marisa cornuarietis* in the US was in Florida in 1957 (Hunt, 1958). In Texas, this species was reported for the first time in 1984 from the headwaters of the San Marcos River in a municipal park in San Marcos (Neck, 1984), but was observed there in 1981 by Horne et al. (1992). In 1983, *Marisa cornuarietis* was found in Comal Springs in Landa Park (Horne et al., 1992), and in 2000 in the headwaters of the San Antonio River (Howells, 2001a), about 70 km away. Therefore, the distribution of this species was similar to that of *T. granifera*, and restricted to spring-fed headwaters of rivers with stable water temperatures. In the fall of 2006 we found *Marisa cornuarietis* at only San Marcos River and Comal Springs. Although we did not find these snails in the San Antonio River, the water level during our sampling was extremely high, preventing thorough examination, and thus the status of this population remains unclear.

Cipangopaludina chinensis (Gray)

The Chinese mysterysnail is native to East Asia (Pace, 1973). Live *C. chinensis* (identified as

Paludina japonica) were first reported in North America by Wood (1892) who found them in Chinese markets in San Francisco in 1892. By the turn of the 20th century, these gastropods were successfully established on the west coast of North America (reviewed in Clench & Fuller, 1965; Jokinen, 1982). The current distribution of *C. chinensis* in North America includes at least 12 states in the US and in Canada south of Montreal (Jokinen, 1982, 1992; Benson, 2007). In Texas, *C. chinensis* has been reported from a pond in Waco, McLennan County (Clench & Fuller, 1965), and from Kidd Springs (spring-fed city park pond) in Dallas, Tarrant County (Fullington, 1978). According to Fullington (1978), well-established colonies were found in both places, approximately 140 km apart. Other localities where *C. chinensis* or their shells were found in Texas included Lake Sweetwater, Nolan County (a single dead shell was found, Howells, 2001a), Backman Lake, Dallas County (abundant dead shells, but no live snails found, Howells, 2001a), and a reservoir in Houston (few dead shells were found, authors' data). Although Howells (2001a) reported that there were no confirmed populations in Texas, in August of 2007 we found numerous *C. chinensis* in Kidd Springs (spring-fed city park pond) in Dallas, Tarrant County, at densities up to 100 m^{-2} . According to the city park personnel, these snails had been in this pond for several decades, and likely since the 1960s. There are also unpublished reports of this species in three additional locations in Tarrant County, but only two of these at Randall Mill Park and in a pond in Fort Worth are known to be still extant (David Brittan, US Fish and Wildlife Service, Arlington, Texas). In 2007 we found numerous dead shells of *C. chinensis* in Backman Lake, but no live snails were present.

Thermal limits

Pomacea insularum

The applesnail, which is of subtropical origin, has the lowest thermal tolerance among all invasive gastropods except for *C. chinensis*, which is a temperate species (Table 2). In December of 2004 we found that *P. insularum* survived for over two days at water temperature as low as 6°C without noticeable mortality in several small ponds in southeastern Texas. Another population of *P. insularum* that had existed

Table 2 Temperature limits for exotic gastropods in Texas

Species	Lower limit (°C)	Upper limit (°C)
<i>Pomacea insularum</i>	100% mortality after 8 days at 2°C and after 25 days at 15°C (Ramakrishnan, 2007)	36.6°C (Ramakrishnan, 2007)
<i>Melanooides tuberculatus</i>	100% mortality after 2 days at 9°C and 30 days at 15°C (Mitchell & Brandt, 2005)	32°C (Mitchell & Brandt, 2005)
<i>Tarebia granifera</i>	100% mortality after 24 h at 6°C (Chaniotis et al., 1980) 10°C chronic limit (Abbot, 1952)	38°C (Chaniotis et al., 1980)
<i>Marisa cornuarietis</i>	100% mortality after 8 h at 8°C (Robins, 1971)	35°C (Robins, 1971)
<i>Cipangopaludina chinensis</i>	0°C (Kipp & Benson, 2008; http://aquatic-hobbyist.com)	30°C (Kipp & Benson, 2008; http://aquatic-hobbyist.com)

Temperature range was calculated as the difference between lower and higher acute temperature limits

for several years in northern Texas (Tarrant County, near Fort Worth) failed to survive, likely due to low winter temperatures (Howells, 2001a; Howells et al., 2006; D. K. Britton and R. F. McMahon, pers. comm.). According to Ramakrishnan (2007), under the laboratory conditions *P. insularum* suffered 100% mortality at 15°C within 25 days. However, snails were able to tolerate much lower temperature for a shorter period of time: at 2°C all snails died only after 8 days of exposure, and at 5°C, snails died after 10 days. These data indicate that the acute thermal limit for *P. insularum* is much lower than the chronic limit, and both of the limits should be taken into consideration in predicting the potential spread of the species. In addition, *P. insularum* can burrow in the sediments of waterbodies or in soil in rice fields and hibernate over the winter. There are no data on the lower temperature limit for the survival of hibernating *P. insularum*. However, it is likely that hibernating snails may survive lower winter temperatures. The upper thermal limit for *P. insularum* is about 36°C (Ramakrishnan, 2007, Table 2).

Similar to *P. insularum*, *M. tuberculatus* has a chronic lower thermal limit of 15°C for one month. However the acute thermal limit of *M. tuberculatus* is lower; this species cannot survive 2 days at 9°C (Mitchell and Brandt, 2003). *Melanooides tuberculatus* is also known to bury in the mud and hibernate throughout the winter (Livshits & Fishelson, 1983), and therefore may survive lower temperatures. The upper temperature limit for *M. tuberculatus* is around 32°C (Table 2), as this gastropod was found in Golden Springs in New Zealand at 30.4°C, but was absent from sites with 32.7°C and higher (Duggan, 2002). In the United Arab Emirates (Ismail and Arif,

1993), *M. tuberculatus* may survive in areas with water temperature at 31°C, and according to laboratory experiments, *M. tuberculatus* can survive temperature below 32.5°C (Mitchell and Brandt, 2005).

Tarebia granifera

Abbott (1952) reported that *T. granifera* died at 10°C; however he did not report the time of exposure. In laboratory experiments, Chaniotis et al. (1980) demonstrated for *T. granifera* 100% mortality after 24 h of exposure at 6°C, 60% mortality at 9°C, and no mortality at 10°C (Table 2). In acute laboratory experiments, *T. granifera* survived for 24 h at 38°C without any mortality (Chaniotis et al., 1980); however, for a long-term population survival, this limit may be lower.

Marisa cornuarietis

Robins (1971) showed that exposure to 8°C for 8 h is fatal to *Marisa cornuarietis*, which indicates that the low acute temperature limit for this species is similar to that for *T. granifera* (Table 2). Although this snail survived for 24 h at 35°C without any mortality in acute laboratory experiments (Robins, 1971), for a long-term population survival this limit may be lower.

Cipangopaludina chinensis

Unlike the other species of exotic gastropods that have invaded Texas, *C. chinensis* is widely distributed across most of the US and Canada north to

Montreal (Jokinen, 1992; Benson, 2007). Based on data from both field and aquarium observations, *C. chinensis* may survive within a temperature range from 0 to 30°C (Kipp & Benson, 2008; <http://aquatic-hobbyist.com>). This species has the lowest low and high temperature limits among all exotic gastropods in Texas (Table 2).

Vectors of introduction and spread

Pomacea insularum

This species was initially introduced to Texas through aquarium and ornamental trade (Howells, 2001a; Howells et al., 2006). It appears that at least in some cases the subsequent spread of *P. insularum* in Texas could be due to repeated independent introductions also associated with the aquarium and ornamental trade. The secondary spread of *P. insularum* could also be by natural migration (downstream as well as upstream) or by catastrophic events like tropical storms and floods. According to Howells and Smith (2002) it is likely that Tropical Storm Allison in June of 2001 and two additional floods helped to distribute *P. insularum* in southern Texas. In addition, channeled-type applesnails are harvested for sale in pet stores (Howells, 2001b), which may contribute to their spread. At least one case of the introduction of applesnails by a landowner into a private pond to control macrophytes was documented in Texas (Howells, 2001b).

Melanoides tuberculatus

Similar to *P. insularum*, the initial introduction and in some cases the subsequent spread of *M. tuberculatus* in Texas was due to repeated independent introductions associated with the aquarium and ornamental trade (Murray, 1971, 1975; Neck, 1984) rather than by secondary spread, and is often the result of “persons dumping the contents of unwanted aquariums in available streams” (Murray, 1975). In addition, *M. tuberculatus* was apparently spread by the transport of scientific equipment that was not adequately disinfected (R. Gibson, US Fish and Wildlife Service, National Fish Hatchery and Technology Center, San Marcos, Texas, pers. comm.). This last mechanism might be a vector for the introduction of *M. tuberculatus* into remote springs,

while aquarium dumping appears to be the dominant vector more in densely populated areas.

Tarebia granifera and *Marisa cornuarietis*

These species were introduced and likely spread to all three localities from which they were reported (Comal Springs, San Marcos and San Antonio rivers) by the aquarium industry (Hunt, 1958; Murray, 1971; Neck, 1984; Howells, 2001a). Natural secondary spread for *Marisa cornuarietis* in lotic systems has been reported by rafting downstream on floating macrophytes (Robins, 1971). In addition, *Marisa cornuarietis* can migrate upstream against moderate current (Ferguson & Palmer, 1958).

Cipangopaludina chinensis

The main vector of introduction for *C. chinensis* in Texas was probably aquarium and ornamental trade (Fullington, 1978; Howells, 2001a). All localities where these gastropods were recorded in Texas likely were repeated independent introductions associated with the aquarium and ornamental trade.

Discussion

Introduction and spread

A total of 9 species of gastropods have been reported to be introduced into freshwaters of Texas. Of these, only five species currently have active populations: *P. insularum*, *M. tuberculatus*, *T. granifera*, *Marisa cornuarietis*, and *C. chinensis*. All of these species were most likely introduced through activities associated with the aquarium and ornamental trade (Murray, 1971, 1975; Fullington, 1978; Neck, 1984; Howells, 2001a; Howells et al., 2006). These exotic gastropods represent over 50% of the non-native freshwater invertebrates introduced to Texas. Other exotics likely to have been introduced into Texas waters from the aquarium and ornamental trade include *Daphnia lumholtzi*, which was likely introduced through the release of exotic fish and plants imported by the aquarium trade (Havel & Hebert, 1993), and an exotic oligochaete, *Branchiura sowerbyi*, which is currently widespread in Texas (authors unpublished data) and was probably introduced to the

US with other aquarium species (Mills et al., 1993). The exotic clam *Corbicula fluminea* is the most widely distributed aquatic invertebrate invader in Texas (Karatayev et al., 2005). Although the aquarium and ornamental trade is not believed to be the major source of introduction for this species, it is found in pet stores and is available from mail order aquarium pet dealers (Karatayev et al., 2005).

Aquarium and ornamental trade and associated activities are the dominant vectors of introduction for all freshwater invertebrates and the second most important vector for freshwater fish in Texas, after deliberate stocking by federal and state agencies (Table 3). None of the introduced freshwater invertebrates and fish in Texas was introduced through ballast water, contrasting with the northern part of US, and especially Great Lakes basin, where over 75% of all freshwater introductions since 1970 are thought to have arrived with ballast waters (Mills et al., 1993). Aquarium release is also the largest vector of fish introduction in Florida and the second largest source (after stocking) in the US (Padilla & Williams, 2004 and references therein). Even though the aquarium industry is one of the five major sources for introduction of all aquatic invaders (Ruiz et al., 1997), it has received relatively little attention from scientists and policy makers (Padilla & Williams, 2004). Our data indicate the importance of this vector and the need for special attention from the scientific community as well as policy makers and managers. Measures are needed both in terms of regulation and

public education to reduce the negative consequences of future introductions and the spread of exotic species.

The rate of spread of exotic gastropods in Texas varied several orders of magnitude and varied from a typical exponential expansion to virtually no spread through time (Fig. 2). Species also varied greatly in terms of the number of waterbodies invaded, from at least 39 waterbodies invaded over the past 18 years by *P. insularum* (2.17 waterbodies per year) to three waterbodies invaded by *C. chinensis* over 45 years (0.07 per year) (Table 1). *Pomacea insularum* inhabits the largest range of waterbodies including ditches, canals, streams, rivers, ponds, and reservoirs. In contrast, thus far *C. chinensis*, *T. granifera*, and *Marisa cornuarietis* have not spread beyond where they were initially detected, and are likely limited to thermally stable warm springs. Although *M. tuberculatus* was initially found in thermally stable springs and a spring-fed river, it has spread into several streams, rivers, and reservoirs with more variable temperature regimes.

We suggest that it is a higher tolerance to low winter temperatures that has allowed *P. insularum* to colonize more waterbodies than *M. tuberculatus*, *T. granifera*, and *Marisa cornuarietis*. *Melanoides tuberculatus* is less tolerant to acute exposure to the cold temperature than *P. insularum*, but more tolerant than *T. granifera* and *Marisa cornuarietis* (Table 2). This higher tolerance to low winter temperature has allowed *M. tuberculatus* to spread beyond thermally stable springs and colonize at least 24 waterbodies, while *T. granifera* and *Marisa cornuarietis* are still restricted to three thermally stable springs and spring-fed rivers (Table 1). In contrast, the spread of *C. chinensis*, and especially the establishment of long-term persistent populations outside thermally stable spring-fed waterbodies in Texas, is likely to be limited by high summer temperatures rather than cold winters. Therefore, thermally stable aquifer-fed waterbodies are a perfect environment for both warm water exotic gastropods that cannot tolerate low winter temperatures (e.g., *T. granifera*, *Marisa cornuarietis*) and cold water exotics (*C. chinensis*) that cannot tolerate high summer temperature. These aquifer-fed springs and rivers contain numerous endemic and endangered species, making them especially vulnerable to impacts of disturbance, including invaders.

Table 3 Pathways for the introduction of freshwater fish and invertebrates in Texas (modified from Howells, 2001a)

Invader	Pathway	Number	Percent of total
Fishes	Stocked	10	47.6
	Aquarium and ornamental trade	7	33.3
	Bait	2	9.5
	Eggs on transplanted marsh plants	1	4.8
	Unknown	1	4.8
	Total	21	
Invertebrates	Aquarium and ornamental trade	5	71.4
	Unknown	2	28.6
	Total	7	

Impacts on aquifer-fed ecosystems

Of the 5 species of introduced gastropods, only one, *P. insularum*, is a potential agricultural pest (Howells et al., 2006). This species can also impact wetlands and play a role in impacting wetland restoration efforts because of feeding preferences for certain wetland species (Burlakova et al., 2008). All other exotic gastropods in Texas are found in Edwards Aquifer-fed spring and rivers. This aquifer contains over 40 highly adapted aquatic, subterranean species, including seven federally listed endangered species: Texas blind salamander (*Typhlomolge rathbuni*), fountain darter (*Etheostoma fonticola*), San Marcos gambusia (*Gambusia georgei*), Texas wild rice (*Zizantia texana*), Comal Springs riffle beetle (*Heterelmis comalensis*), Comal Springs dryop beetle (*Stygoparnus comalensis*), peck's cave amphipod (*Stygobromus pecki*), and one threatened species, San Marcos salamander (*Eurycea nana*) (www.edwardsaquifer.net/species.html). This large number of endemics greatly raises the potential negative effects of the introduction of exotic gastropods on the native biodiversity.

Impacts on macrophytes

Marisa cornuarietis is a voracious herbivore that may substantially reduce the density of aquatic vegetation (Hunt, 1958; Horne et al., 1992). This species was even investigated as a potential agent for macrophyte control (reviewed in Robins, 1971; Cowie, 2001). Horne et al. (1992) reported that many plants in Landa Lake (part of the Comal Springs, New Braunfels) were completely grazed by *Marisa cornuarietis*. Grazing was so effective that park employees discontinued mowing macrophytes in the lake, which was previously necessary to allow swimming and recreational activities. Neck (1984) also suggested that *Marisa cornuarietis* could have a negative effect on the endangered wild rice (*Zizania texana*) that is endemic in the San Marcos River. However, initially high densities of *Marisa cornuarietis* in Comal Springs were followed by a population crash in 1990 (Horne et al., 1992). In 2001–2002 the population density of *Marisa cornuarietis* in Comal Springs and Landa Lake was $<1 \text{ m}^{-2}$ (Tolley-Jordan & Owen, 2007). During our survey, the density of *Marisa cornuarietis* in Comal Springs

and Landa Lake was also very low (only 2 individuals found). *Marisa cornuarietis* was somewhat more abundant in the San Marcos River, but densities did not exceed 1 m^{-2} . Populations of all three exotic gastropods found in aquifer-fed springs in Texas may be characterized by “boom and bust” dynamics (R. Gibson (US Fish and Wildlife Service, National Fish Hatchery and Technology Center, San Marcos, Texas, pers. comm.). If so, we may expect that in the future populations of *Marisa cornuarietis* may cause significant damage to aquatic macrophytes.

Impact on native mollusks

It is well documented that both *M. tuberculatus* and *T. granifera* can outcompete and even eradicate populations of native snails. In the Caribbean region they eliminated native populations of *Biomphalaria glabrata* and *B. straminea* (Jobin, 1970; Jacobson, 1975; Butler et al., 1980; Prentice, 1983; Pointer et al., 1994). In the same region *Marisa cornuarietis* consumed the egg sacks and immature stages of both species of *Biomphalaria*, greatly impacting their populations (Chernin et al., 1956; Ferguson & Palmer, 1958; Radke et al., 1961). Eradication can be so dramatic that these exotic snails were used as biological control agents for *Biomphalaria*, and thus their parasites, to control the spread of shistosomes in the Caribbean islands (reviewed in Pointer, 1999). The introduction of *T. granifera* in Cuba caused the extirpation of the endemic snail *Pachychilus violaceus*. Two other endemic thiarids (*Hemisinus brevis* and *H. cubani-anus*) are still present, but in danger of extinction (reviewed in Pointer, 1999). Murray (1971) suggested that *M. tuberculatus* might pose a serious threat in waterbodies in the Western United States that support communities of highly endemic native snail, including Comal Springs—a type locality for *Elimia comalensis*, and habitat for 4 other native species of gastropods that are currently found in extremely low densities (Tolley-Jordan & Owen, 2007). Neck (1984) also suggested that *Marisa cornuarietis* impacts *E. comalensis* in the San Marcos River. *Melanoides tuberculatus* and *T. granifera* also co-occur with *E. comalensis* in the Comal River, but apparently differ in their habitat use, with *E. comalensis* preferring higher flows in lotic habitats (Tolley-Jordan & Owen, 2007).

We found that in some localities, very low densities of *M. tuberculatus* were associated with

high (over 4,000 m⁻²) densities of *E. comalensis* (e.g., Barton Springs in Austin, Travis Co). In others (e.g., Comal Springs, New Braunfels, Comal County), we found high densities of both the endemic *E. comalensis* and *M. tuberculatus*. Although in the San Marcos River and Comal Springs *E. comalensis* has coexisted for at least 30 years with *T. granifera*, *M. tuberculatus*, and *Marisa cornuarietis* and still maintains relatively high population densities, other native snails in these locales were found at much lower densities than exotics. Pointer (1999) found that on Martinique Island the invasion of thiarids greatly reduced populations of *B. glabrata* and *B. straminea*, but not native ampullariids and neritids. Therefore, the impacts of exotic snails are likely to be species specific on native species. Because quantitative studies of native snails in aquifer-fed waterbodies of Texas were never conducted before the introduction of exotic snails, it is impossible to evaluate the invasion effect on local species. Tolley-Jordan & Owen (2007) suggest that declines in spring flows due to water withdrawal and drought may favor exotic mollusks, which are more likely than natives to prefer lentic habitats and silt substrates.

Hosts for exotic parasites

In their native range in China both *Melanoides tuberculatus* and *T. granifera* serve as intermediate hosts for human parasites: the Chinese liver fluke (*Clonorchis sinensis*) and the oriental lung fluke (*Paragonimus westemani*) (Abbott, 1952; Morrison, 1954; Murray, 1964). These trematodes have not yet been found in North American *M. tuberculatus* (Mitchell et al., 2005). However, in Texas both *M. tuberculatus* and *T. granifera* are intermediate hosts for the exotic trematode *Philophthalmus gralli*, which infects waterfowl (Murray & Haines, 1969; Nollen & Murray, 1978), and *Centrocestus formosanus*, which infects fish and piscivorous birds, including federally protected species (Mitchell et al., 2000, 2005). While *P. gralli* is not considered a serious threat to animal health (Tolley-Jordan & Owen, 2007), *C. formosanus*, the gill trematode, is known to cause serious economic losses to the tropical fish industry and is harmful to wild fish (reviewed in Mitchell et al., 2005).

In 1996, the majority of the fish inspected from Comal Springs were infected with cysts of

C. formosanus, including the endangered fountain darter. All of 209 darters from Comal Springs inspected in 1997–1998 were infected with this gill trematode, including 48 fish with more than 50 cysts per gill arch (Mitchell et al., 2005). Infection rates in the San Marcos River are much lower with only 2.8% of 145 inspected fountain darters being infected (mean infection intensity 0.25 cysts per gill arch of infected fish). Both the gill trematode and its exotic gastropod hosts continued to spread in North America, causing serious damage to fish (reviewed in Mitchell et al., 2005). In 2001–2002, a third exotic trematode of Asian origin, tentatively identified as *Haplorchis pumilio*, was found in *M. tuberculatus* from Comal Springs (Tolley-Jordan & Owen, 2007). In contrast, none of the native *E. comalensis* was infected (Tolley-Jordan & Owen, 2007).

The spread of exotic parasites and diseases with the introduction of exotic species is a worldwide problem that is commonly overlooked, but may have a devastating effect on invaded ecosystems (Karatajev et al., 2008). The introduction of crayfish plague (caused by the fungus *Aphanomyces astaci*) with the North American crayfish into Europe caused local extirpation and fragmentation of previously uniform European crayfish populations and more than a 10-fold drop in commercial catches of this species (reviewed in Westman, 2002). Introduction of the trematode parasite, *Apophallus muehlingi*, with the exotic gastropod *Lithoglyphus naticoides* into the River Volga Delta resulted in epizootics among young cyprinid fishes, which experienced up to 80% mortality due to parasite infections (Biserova, 1990). This trematode is also pathogenic to their final vertebrate hosts, which are birds and mammals, including humans (Biserova, 2005).

Conclusion

Five species of exotic gastropods have been established in Texas since 1960s, namely, *P. insularum*, *M. tuberculatus*, *T. granifera*, *Marisa cornuarietis*, and *C. chinensis*. All of these exotic gastropods were introduced through activities associated with the aquarium and ornamental trade. The rate of spread of exotic gastropods in Texas has been rapid for some (*P. insularum*) and very slow for others (*C. chinensis*). Three of the five species of exotic gastropods in

Texas appear to be limited to thermally stable springs and spring-fed rivers and ponds, which contain numerous endemic and endangered species, and thus pose serious environmental threats to these fragile habitats and the species they contain. This apparent habitat limitation is also supported by studies of thermal limits in these species. Negative ecological impacts of these exotics are likely to include competitive exclusion of natives, and the introduction of parasites that can imperil fish and birds, including federally protected species. These results highlight the importance of aquarium and ornamental trade and associated activities as an important source of freshwater invaders, and the need of both regulation and public education to reduce the negative consequences of future introductions and the spread of exotic species.

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