INVITED ARTICLE FROM THE 2023 TEXAS ACADEMY OF SCIENCE TEXAS DISTINGUISHED SCIENTIST

INVASIVE FRESH WATER MOLLUSCS IN TEXAS

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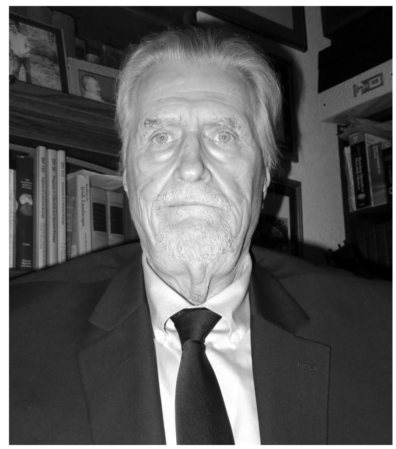

Robert F. McMahon is a Professor Emeritus in the Department of Biology at the University of Texas at Arlington where he also served as Associate Dean of Science and Dean of the Honors College. Since joining the Department in 1972, Dr. McMahon has studied the population dynamics and physiological ecology of invasive marine and freshwater molluscs, including the freshwater golden clam, *Corbicula fluminea*, the zebra mussel, *Dreissena polymorpha*, the giant apple snail *Pomacea maculata* and the marine brown mussel, *Perna perna*. His studies of these invasive species included their growth rates, physiological adaptations, environmental limits, and methods for control. He has served as a member of national and regional invasive species panels including the National Invasive Species Advisory Committee, the Western Regional Panel on Aquatic Invasive Species and presently serves on the Gulf and South Atlantic Regional Panel on Aquatic Invasive Species. For his research contributions to the biology and control of invasive species, he received the National Invasive Species Council's Invasive Species Lifetime Achievement Award in 2015.

Dr. McMahon has a worldwide reputation for his research on the biology and control of invasive molluscs. He has published over 100 articles, technical reports and book chapters on aquatic invasive molluscs and continues to conduct research with colleagues on the biology and control of invasive zebra mussels in Texas. He was awarded a Fulbright Research Fellowship to Trinity College, Dublin Ireland in 1979-80, a Certificate of Achievement by The Western Regional Panel on Aquatic Invasive Species in 2016, the Award for Distinguished Record of Research from the University of Texas at Arlington in 1990, and was named the Texas Academy of Science Texas Distinguished Scientist in 2023.

It was the greatest of honors to be designated the 2023 Texas Distinguished Scientist by the Texas Academy of Science. I consider it to be the capstone of my long career as university professor and research scientist. I want to express my deep appreciation for this outstanding honor and the academy's understanding of the importance of basic research for prevention and control of environmentally damaging invasive species. I have been incredibly fortunate to collaborate with many research colleagues and graduate students in my invasive species research. Particularly important were my 11 Doctoral and 19 Master's students, whose research collaborations and contributions were essential to receiving this honor.

Education.–My interest in aquatic biology extends back into my childhood in upstate New York. I remember being fascinated by the animal world around me including insects, but especially freshwater organisms. I would collect crayfish, frogs, fish and snails from local streams and ponds near our home in Syracuse, NY, and keep them in an aquarium along with tropical fish and would spend hours observing their behavior. My father, who was a physician and majored in zoology in college, provided me with books on animal life which gave me access to the wonders of animal life throughout the world. Thus, I entered college as a zoology major with the intention of applying to medical school after graduation to follow in his footsteps. But, by my junior year I so enjoyed my zoological studies that I began to consider university teaching and zoological research as a career. Thus, in my senior year, I applied to and was accepted in the Zoology Ph.D. program at Syracuse University. My first semester there I took a course in Invertebrate Zoology taught by W.D. Russell-Hunter, an outstanding malacologist. After the first few lectures in his class, I was completely hooked and asked him to be my Ph.D. advisor. My Ph.D. dissertation described the comparative population dynamics and environmental physiology of a small freshwater limpet pulmonate snail, *Laevapex fuscus,* at three different local sites in Central New York. My research demonstrated that populations of this species in different habitats had independently evolved such that a population from a highly productive water body could not survive when held in a low productivity water body while specimens transferred from the low productivity habit to the high productivity habit grew faster and attained much larger sizes than the native high productivity individuals. This result suggested that these snails had independently evolved nutrition strategies in their low and high productivity habitats (McMahon 1973).

During my last year in graduate school in 1972, I applied to colleges and universities for an academic position in which I could teach and conduct research. After many applications, I was invited to interview for a position as an aquatic biologist in the Department of Biology at the University of Texas at Arlington (UTA). I had never traveled outside of the eastern U.S., so I was excited at the possibility of a university position in North-Central Texas and was delighted to be invited to join the department as an assistant professor teaching courses in Introductory Biology and Invertebrate Zoology.

Initial Research on Texas Aquatic Molluscs.–During my first year at UTA, I spent time becoming familiar with area lakes, rivers and streams. I initiated a comparative population study of the life history traits of the limpet pulmonate snail, *Laevapex fuscus*, in three lakes and the closely related pulmonate limpet, *Hebetancyclus excentricus,* in three streams. The Texas *L. fuscus* populations had two or three reproductive periods a year compared to a single period in New York populations that I had studied while those of *H. excentricus* had two reproductive periods per year. The multiple reproductive periods of these two Texas freshwater pulmonate species appeared likely due to the extended periods of time that water temperatures remained above their lower limits for reproduction and growth compared to populations in colder northern U.S. waters that supported only one reproductive period (McMahon 1975a).

Soon after coming to Texas I also initiated a year-long study of the impact of elevated water temperatures on the thermal tolerance of two isolated populations of the common freshwater pulmonate, *Physa acuta* (previously *Physa virgata*), in Lake Arlington (McMahon 1975b). One population was isolated on riprap rocks on the lake's main dam where it experienced normal seasonal water temperatures compared to a second population isolated on riprap in a power station's thermal effluent canal emptying into the lake. Both populations had three reproductive events per year producing three separate generations. As expected, snails isolated in the thermal effluent had comparatively higher thermal tolerance limits compared to those in cooler water on the dam indicative of a capacity for thermal acclimation. Interestingly, when the power plant was shut down during that summer for maintenance and repair from April through August, the thermal tolerance of the effluent population remained considerably elevated compared to that on the dam even through water temperatures were essentially similar at both sites (McMahon 1976). Because the power station had been operating for 18 years, this result suggested the snails isolated in the power station's thermal effluent had evolved an increased thermal tolerance in response to exposure to elevated effluent temperatures within 54 generations. This result indicated that many aquatic invertebrate species may be capable of rapid thermal evolution in response to future climatic temperature elevation.

Research on Corbicula fluminea.–While conducting this snail research on Lake Arlington, the manager of the power station phoned to ask if I could identify some bivalves that had been carried with lake water into a steam condenser box to become lodged in its piping causing the power generator to be shut down (McMahon 1977). I did not immediately recognize the species of clam. After two weeks of searching through identification books, I discovered that it was a freshwater clam with the scientific name of *Corbicula fluminea* (common name Asian or golden clam). The native range of *C. fluminea* extended from Africa through Southern Asia to Western Australia (McMahon 1983). It had first been reported in North America as empty shells in Namaino, Vancouver Island, British Columbia in 1924. The first living populations were later found near the mouth of Columbia River in Washington/Oregon. Thereafter, they spread through California, Arizona and New Mexico into Southern Texas by 1969, extending north through eastern Texas where they were first recorded in 1972 (McMahon 1982). A second North American introduction occurred in 1957 in Paducah, Kentucky where they fouled the raw water systems of a power station on the Kentucky River. This introduction was almost certainly a result of human transport of the clams from the western United States. The clams spread rapidly down the Ohio River into the Mississippi River reaching southern Louisiana by 1962. It then spread across the southern US into Florida waterways by 1963, from which it extended north through eastern U.S. states being found in as far north as Pennsylvania by 1972 (McMahon 1982, 1983).

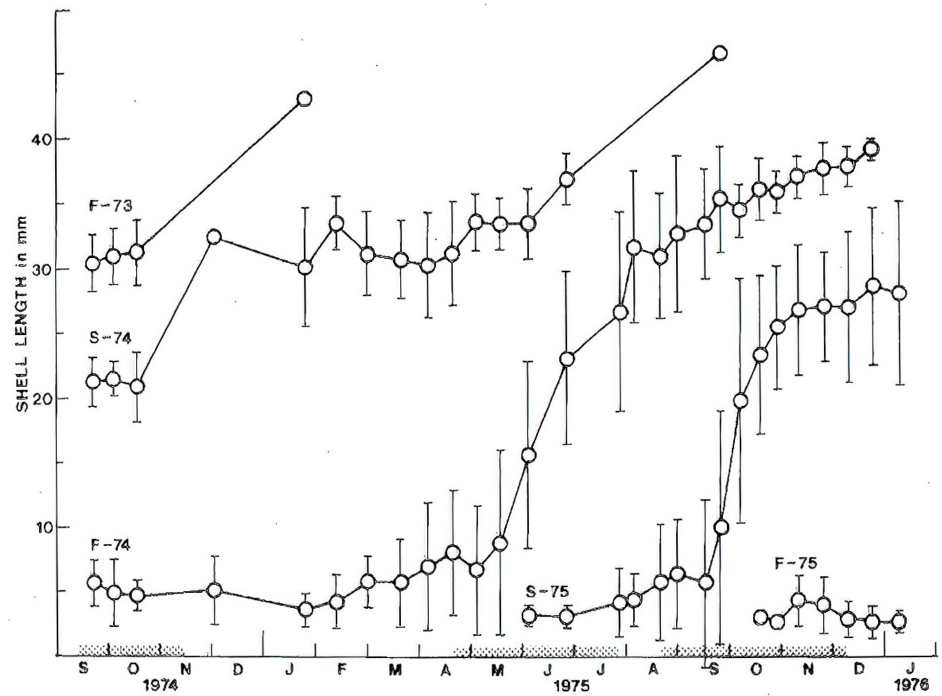

Figure 1. Mean generation shell lengths (SL) versus time of collection for *Corbicula fluminea* from Lake Arlington Texas. Open circles indicate mean SL and vertical bars, standard deviation. Means without SLs are samples of less than 9 individuals. Spawning periods are represented by crosshatched bars on the horizontal axis. S- or F- indicate spring and fall generations (i.e., F-74). (Reproduced with permission from Aldridge & McMahon, *Journal of Molluscan Studies*, 1978, 44:49-70.)

I realized that there were almost no reported studies of the biology and ecology of *C. fluminea* either in its native range or in North America where it's range was rapidly expanding and causing extensive and costly fouling of raw water using nuclear and non-nuclear power stations and other water using facilities including water supply systems and industrial facilities. This led me to initiate research on its basic population dynamics in Lake Arlington. My first graduate student, David W. Aldridge, and I sampled clams with a Peterson Grab from 21 September 1974 through 9 January 1976 at mostly twice monthly intervals. The shell lengths of each clam sample were measured which allowed recognition of separate clam generations and growth rates (Figure 1). In addition, we measured clam densities, the number of newly spawned juveniles, and the percentage of clams incubating developing larvae on their gills. We also determined the total tissue organic carbon content of clams over a size range of individuals in each sample allowing us to determine their productivity and energy flow through the population (Aldridge & McMahon 1978). This research provided the first description of the population dynamics of *C. fluminea* not only in the United States but throughout its world wide range. It also provided a basis for the development of control methodologies for it in both natural aquatic habitats and it's fouling of raw water using systems.

After this initial study of the population dynamics of the *C. fluminea*, my colleagues and I published a series of articles on its biology and fouling control. These studies included its invasive characteristics (McMahon 1999), tolerance of aerial exposure (McMahon 1979a), response to increasing temperature and hypoxia (McMahon 1979b), its general biology (McMahon 1983), capacity for aerial respiration when emersed (McMahon & Williams 1984), oxygen consumption, nitrogen excretion rates and tissue carbon nitrogen ratios (Williams & McMahon 1985), growth, life cycle, upper thermal limits and downstream colonization rates (Williams & McMahon 1986), capacity for downstream dispersal when in poor physiological condition (Williams & McMahon 1989), temperature and humidity impacts on aerial exposure tolerance (Byrne, et al. 1989, 1990), chemical control of fouling in raw water systems (McMahon & Lutey 1988), impact of seasonal tissue loss on down-steam dispersal (Williams & McMahon 1989), variation in size demography (Payne et al. 1989), tolerance of emersion, acid-base balance during emersion and the effects of subsequent re-immersion on hemolymph osmolality, ion composition, ion flux, acid base balance, and ammonia dynamics (Byrne et al. 1988, 1989, 1991a, 1991b), foot feeding behavior (Reid et al. 1992), and tolerance to hypoxia (Matthews & McMahon 1999).

Interestingly, not long after my laboratory completed its studies of the population biology and physiological ecology of Asian clams in Texas, the densities of the clams in the lakes and rivers where we collected them for our research projects began to decline. Declines in *Corbicula* density not only occurred in North Central Texas but were reported in other areas of Texas and throughout in the United States. While *C. fluminea* still occurs in Texas and other U.S. water bodies, its densities remain much lower than reported after initial invasions. Only newly infested water bodies appear to support dense clam populations. Invasive species populations that attain high densities after invasion followed by long–term density declines are said to display “boom-bust” population dynamics (Strayer & Malcom 2006).

Research on Perna perna.–The bivalve genus, *Perna*, includes three species: *P. viridis, P. canaliculus* and *P. perna* . The native range of *P. viridus* extends through the Indo-Pacific to the southwestern Pacific Ocean and from southern Japan to Papua, New Guinea. An invasive species, it was introduced to the Caribbean Islands in 1990 probably through ocean ship transport of adults or larvae and has also been established on Venezuelan shores. It was first recorded in the United States in 1999, initially establishing itself in Tampa Bay. From there, it spread along both the western and eastern coasts of Florida, now extending as far north as coastal South Carolina and westward along the Florida Panhandle. The distribution of *P. canaliculus*, the New Zealand green-lipped mussel, is restricted to its native New Zealand shores. Like *P. viridus*, *P. perna* is highly invasive. In 1990, *P. perna* was first discovered in the United States on jetty rocks in Aransas Pass, Port Aransas, Texas, by David W. Hicks. After its initial discovery, it began to spread rapidly on rocky jetties and other hard surfaced shore structures along the Texas Gulf Coast (Figure 2). At that time, David had just completed an undergraduate degree in Marine Science and entered a Master’s Program at Texas A&M University Corpus Christi where he detailed the spread of *P. perna* for his Masters Degree (Hicks & Tunnell 1993, Hicks & Tunnell 1995).

After completing his Masters Degree, David joined my laboratory as a doctoral student to continue his research on *P. perna*. Little was known of its physiological tolerances so we developed a research program to investigate them, providing important information on its potential for further range expansion in the United States and development of strategies for prevention/control of its biofouling of water using facilities. The results of his dissertation research (Hicks

Figure 2. *Perna perna* fouling of a rocky shore in Port Mansfield, on the Texas Gulf Coast 1995. (Provided by Dr. David W. Hicks).

1999) were published in four research articles. The first detailed the salinity tolerance of *P. perna* from the Texas Gulf Shore (Hicks et al. 2000) indicating that it could tolerate salinities ranging from 15-50 ppt (i.e., parts per thousand). Since sea water typically has a salinity of 35 ppt, this result indicated that the mussel could foul rocky shores, watercraft and man-made structures along the Texas Gulf Coast, but also areas of lower salinity behind Texas coastal barrier islands. The second article described the upper and lower thermal tolerance limits and freeze resistance of Texas *P. perna* in order to estimate its ability to expand its invasion of United States coastal waters (Hicks & McMahon 2002a). The study revealed that it had long-term lower and upper thermal limits ranging from 7.5-30°C and a lower aerial freeze resistance of -2.5°C which would restrict it to subtidal and low intertidal habits. Interestingly, *P. perna* was first found on Texas shores in 1990 when mean near-shore water temperatures remained below its 30°C upper thermal limit and it vanished from Texas shores in 1997 when summer water temperatures rose above its 30°C upper limit. David also examined the respiratory responses of Texas *P. perna* to temperature and hypoxia. This research revealed that the mussel's respiratory rate was suppressed as temperatures declined below 10°C or rose above 30°C, which corresponded to his previous determination of its upper and lower thermal tolerance limits (Hicks & McMahon 2002b). His dissertation research also involved a study of the effects of temperature on the mussel's long-term tolerance of hypoxia (Hicks & McMahon 2005). This study indicated that mussels could tolerate oxygen concentrations of 20% and 30% of full air saturation at temperatures ≥15°C and 20°C, respectfully, with >50% mortality occurring at water temperatures >25°C. His research also indicated that mussel size had an impact on mussel survivorship with tolerance to hypoxia declining with increased mussel size. The hypoxia tolerance of *P. perna* proved similar to that of other native estuarine bivalve species suggesting that could withstand the hypoxia levels encountered in gulf coast estuarine habits.

Research on Pomacea maculata.*–Pomacea maculata,* the island apple snail, is a freshwater snail that has an endemic distribution in central South America where it inhabits ponds, lakes and slow flowing rivers. It is among the largest of all freshwater snails and is an extensive consumer of aquatic vegetation, including young rice shoots (Ramakrishnan 2007). A popular aquarium species, it was first found in the United States at several sites in the Oklawaha River drainage of central Florida where it was thought to have been introduced by aquarium release. Originally identified as *P. insularum*, it was later found to be the closely related *P. maculata.* While *P.maculata* populations were still limited to Florida, it was found presumably as the result of a second introduction in the Angelina River near Sam Rayburn Reservoir in southeastern Texas in 2000. By 2002, it was reported in rice fields in Galveston, Brazoria, and Fort Bend Counties raising concerns over its potential impacts on rice production (Howells and Smith 2002). Thereafter, it spread rapidly westward along the Texas Gulf Coast and as far north as Bud Lake in San Antonio Texas by 2022.

Very little was known of the environmental physiology of *P. maculata* which was required to estimate the limits of its distribution in the United States and for the development environmentally acceptable control methods. Thus, my graduate student, Veena Ramakrishnan, and I embarked on a study of its salinity, pH, desiccation and temperature tolerances (Ramakrishnan 2007). An 86.7% mortality was recorded when specimens of *P. maculata* were exposed to a salinity of 10.2% and 100% mortality occurred within seven days at 13.6% levels that were similar to that reported for other freshwater snail species. Since cultivated rice had similar salinity tolerances, Texas rice fields would be susceptible to *P. maculata* invasion and damage (Ramakrishnan 2007). Our pH tolerance experiment indicated that 100% adult *P. maculata* mortality occurred at pH 2.0, 2.5, and 3.0 within 13, 6 and 4 days respectively, while mortality was not detected at pH 4-7 over a 28 day exposure period. This result revealed that *P. maculata's* tolerance of low pH was similar to that reported for other freshwater gastropods. The pH in rice fields ranges from 2.7-10.3 (Kim 1996) indicating that they could be invaded by *P. maculata* which tolerated pH >4. The desiccation study revealed that size, temperature and relative humidity all had significant impacts on *P. maculata* survival times over a 308 day emersion period. Larger individuals had greater emersion tolerance than smaller individuals. Survival times increased at lower temperatures and higher relative humidity. Survival times were associated with water loss rates being higher in smaller individuals. The results indicated the *P. maculata* could survive in dry rice fields until they were annually flooded allowing them to graze on newly developing rice shoots.

Research on Dreissena polymorpha.–*Dreissena polymorpha* is a small freshwater Eurasian bivalve that produces proteinaceous byssal threads allowing attachment to hard surfaces and the shells of others individuals to form dense populations on rocks and other submerged hard-surfaced material. Its ability to byssally attach to hard surfaces makes it a notorious fouler of piping and other structures in raw water using facilities such as power stations, water treatment plants and industrial plants. Its veliger larvae can settle and attach on the internal walls of water piping where it can grow to a thick layer of adult mussels that impedes water flow, causing shutdowns and expensive mussel removal and repair costs. Zebra mussels were first discovered in the United States in Lake Saint Clair which lies between Lake Huron and

Lake Erie on June 1, 1988 (Benson 2014). After its initial discovery, zebra mussels spread through the lower and upper Great Lakes and were transported other U.S. water bodies attached to hulls of trailered boats or as veliger larvae in bilge water (Benson 2014). Zebra mussels have since spread into water bodies in the Eastern and Mid-Western United States and as far south as Louisiana and Texas.

I initiated studies of this new aquatic invader soon after it became established in the Great Lakes. Initial studies involved testing of the efficacy of newly developed molluscicides and carbon dioxide for control of their fouling in raw water using facilities (McMahon et al. 1989, 1990, 1995). My laboratory's molluscide research lead to the development of two new cannabinoid compounds for zebra mussel macrofouling control that inhibited their byssal attachment but did kill them or harm other aquatic species (Angarano et al. 2007, 2009).

In addition to development of zebra mussel molluscicides, my laboratory initiated studies of the physiological resistances of zebra mussels including their upper thermal limits (McMahon et al. 1993), freeze resistance when emersed (Clarke et al. 1993), desiccation resistance (Ussary & McMahon 1994), starvation (Chase & McMahon 1994), negative impacts of zebra mussel fouling on shells of native unionid mussels (Byrne et al. 1995), effects of temperature on byssal thread production (Clarke & McMahon 1996a), impact of hypoxia and low frequency agitation on byssal attachment thread production (Clarke & McMahon 1996b), and impact of temperature and hypoxia on mussel survival (Johnson & McMahon 1998, Matthews & McMahon 1999, Alexander & McMahon 2004).

Zebra mussels were first found in Texas in Lake Texoma on its border with Oklahoma in 2009 and have since spread south to become established in 33 Texas water bodies in the Red, Trinity, Brazos, Colorado, Guadalupe, San Antonio, and Rio Grande river basins (TPWD 2024). After their arrival, my laboratory began a study of the mussel's population dynamics in Texas Lakes Texoma, Ray Roberts and Belton soon after they became infested (Arteburn & McMahon 2022). The research revealed that zebra mussels in Texas water bodies grew faster and had one year life spans compared to the slower growth rates and 2-5 year life spans reported for populations in more norther regions of the United States. Our study also confirmed that Texas mussels had distinct spring and fall reproductive periods as a result of high summer water temperatures inhibiting spawning compared to a single annual spawning period in cooler more northern North American and European water bodies. The bimodal spawning, one year life spans and rapid growth rates of zebra mussels in Texas water bodies were subsequently confirmed by two other studies (Locklin et al. 2020, 2024). I am continuing my studies of zebra mussels in Texas reservoirs and have recently co-published an article on the development of a rapid and relatively inexpensive means for zebra mussel water body invasion risk assessment (McGarrity & McMahon 2024). Like *C. fluminea*, Texas zebra mussels in some early infested Texas water bodies appear to be undergoing long-term population density declines, suggestive of boom-bust population dynamics (Arterburn & McMahon 2022, Locklin et al. 2024.)

Final thoughts.–I consider myself very fortunate to have had a long and rewarding career as teacher and research biologist at the University of Texas at Arlington. My studies of the biology, life history, population dynamics and physiological ecology of invasive freshwater molluscs were successful only because of the extensive collaboration of many colleagues and graduate students which has been truly exceptional. Certainly, the research described above could not have been conducted without their support and enthusiasm for the study of invasive aquatic species. I consider receiving the Texas Academy of Science Distinguished Scientist Award a wonderful acknowledgement of my long career as a research biologist and I will always be grateful for its recognition of my research contributions.

Literature Cited

Aldridge, D. W. & R. F. McMahon. 1978. Growth, fecundity, and bioenergetics in a natural population of the Asiatic freshwater clam, *Corbicula manilensis* Philippi, from North Central Texas. J. Mol. Stud. 44: 49-70.

Alexander, J. E. & R. F. McMahon. 2004. Respiratory response to temperature and hypoxia in the zebra mussel *Dreissena polymorpha*. Comp. Biochem. Physiol., Part A. 137: 425-434.

Angarano, M., R. F. McMahon, D. L. Hawkins & J. A. Schetz. 2007. Exploration of structure-antifouling relationships of capsaicin-like compounds that inhibit zebra mussel (*Dreissena polymorpha*) macrofouling. Biofouling 23: 295-305.

Angarano, M., R. F. McMahon & J. A. Schetz. 2009. Cannabinoids inhibit zebra mussel (*Dreissena polymorpha*) byssal attachment: a potentially green antifouling technology. Biofouling, 25: 127-138.

Arterburn H. M. & R. F. McMahon. 2022. Population and reproductive dynamics of zebra mussels (*Dreissena polymorpha*) in warm low-latitude North American waters. Biol. Bull. 242(3): 207-221.

Benson, A. J. 2014. Chronological history of zebra and quagga mussels (Dreissenidae) in North America. Pp. 9-31, *in* Quagga and Zebra Mussels, Biology, Impacts and Control (T. F. Nalepa & D. W. Schloesser, eds). CRC Press, Boca Raton, FL, 9:xx+1-775.

Byrne, R. A., R. F. McMahon & T. H. Dietz. 1988. Temperature and humidity effects on aerial exposure tolerance in the freshwater bivalve, *Corbicula fluminea*. Biol. Bull. 175: 253-260.

Byrne, R. A., R. F. McMahon & T. H. Dietz. 1989. The effects of aerial exposure and subsequent reimmersion on hemolymph osmolality, ion composition and ion flux in the freshwater bivalve, *Corbicula fluminea*. Physiol. Zool. 62: 1187-1202.

Byrne, R. A., R. F. McMahon & T. H. Dietz. 1990. Behavioral and metabolic responses to emersion and subsequent reimmersion in the freshwater bivalve, *Corbicula fluminea*. Biol. Bull. 178: 251-259.

Byrne, R. A., B. N. Shipman, N. J. Smatresk, T. H. Dietz & R. F. McMahon. 1991a. Acid-base balance during prolonged emergence in the freshwater bivalve, *Corbicula fluminea*. Physiol. Zool. 64(3): 748-766.

Byrne, R. A., T. H. Dietz & R. F. McMahon. 1991b. Ammonia dynamics during and after prolonged emersion in the freshwater clam *Corbicula fluminea* (Müller). Can. J. Zool. 69: 676-680.

Byrne, R. A., M. L. Burleson, N. J. Smatresk & R. F. McMahon. 1995. Respiratory and acid-base consequences of zebra mussel infestation on valves of unionids. Can. J. Zool. 73: 1489-1494.

Chase, R. & R. F. McMahon. 1994. Effects of starvation at different temperatures on dry tissue and dry shell weights in the zebra mussel, *Dreissena polymorpha* (Pallas). Pp. 501-514, *in* Proceedings: Fourth International Zebra Mussel Conference '94. Wisconsin Sea Grant Institute, Madison, WI.

Clarke, M., R. F. McMahon, A. C. Miller & B. S. Payne. 1993. Tissue freezing points and time for complete mortality on exposure to freezing air temperatures in the zebra mussel (*Dreissena polymorpha*) with special reference to dewatering during freezing conditions as a mitigation strategy. Pp. 4-121, *in* Proceedings: Third International Zebra Mussel Conference 1993 (J. L.Tsou & Y. G. Mussalli, eds.). EPRI TR-102077, Electric Power Research Institute, Palo Alto, CA.

Clarke, M. & R. F. McMahon. 1996a. The effects of temperature on byssal thread production in the freshwater mussel, *Dreissena polymorpha*. Amer. Malacol. Bull. 13: 105-110.

Clarke, M. & R. F. McMahon. 1996b. The effects of hypoxia and low-frequency agitation on byssogenesis in the freshwater mussel *Dreissena polymorpha* (Pallas). Biol. Bull. (Woods Hole, Mass.) 191:413-420.

Hicks, D. W. & J. W. Tunnel. 1993. Invasion of the south Texas coast by the edible brown mussel. *Perna perna* (Linnaeus 1758). The Veliger 36(1): 92-94.

Hicks, D. W. & J. W. Tunnel. 1995. Ecological notes and patterns of dispersal in the recently introduced mussel, *Perna perna* (Linnaeus, 1758) in the Gulf of Mexico. Am. Malacol. Bull. 11(2): 203-206.

Hicks, D. W. 1999. The Environmental Physiology of the Nonindigenous Marine Mussel, *Perna perna* (Linnaeus 1758) in the Western Gulf of Mexico. Ph.D. Dissertation, The University of Texas at Arlington.

Hicks, D. W., D. L. Hawkins & R. F. McMahon. 2000. Salinity tolerance of brown mussel *Perna perna* (L.) from the Gulf of Mexico: An extension of life table analysis to estimate median survival time in the presence of regressor variables. J. Shellfish Res. 19(1): 203-212.

Hicks, D. W. & R. F. McMahon. 2002a. Temperature acclimation of upper and lower thermal limits and freeze resistance in the nonindigenous brown mussel, *Perna perna* (L.), from the Gulf of Mexico. Mar. Biol. 140: 1167-1179.

Hicks, D. W. & R. F. McMahon. 2002b. Respiratory responses to temperature and hypoxia in the nonindigenous brown mussel, *Perna perna* (Bivalvia: Mytilidae), from the Gulf of Mexico. J. Exp. Mar. Biol. Ecol. 277:61-78.

Hicks D. W. & R. F. McMahon. 2005. Effects of temperature on chronic hypoxia tolerance in the nonindigenous brown mussel, *Perna perna* (Bivalvia: Mytilidae) from the Texas Gulf of Mexico. J. Moll. Stud. 71: 401-408.

Howells, R. G. & J. W. Smith. 2002. Status of the apple snail *Pomacea canaliculata* in the United States. Pp. 86-96, *in* Proceedings of the Special Working Group on the Golden Apple Snail (*Pomacea* spp) (T. Wada, Y. Yusa, R. C. Joshi & A. I. Stijn, eds). Seventh International Congress on Medical and Applied Malacology. Los Baños, Laguna, SEAMEO, Philippines.

Johnson, P. D. & McMahon R. F. 1998. Effects of temperature and chronic hypoxia on survivorship of the zebra mussel *Dreissena polymorpha* and Asian clam *Corbicula fluminea*. Can. J. Fish. Aquat. Sci. 55: 1564-1572.

Kim, I. 1996. Occurance of the planktonic crustaceans in relation to pH in the rice fields of eastern Korea. Korean J. Limnology 29: 233-240.

Locklin, J. L., D. N. Corbitt & R. F. McMahon. 2020. Settlement, density, survival and shell growth of zebra mussels, *Dreissena polymorpha*, in a recently invaded low latitude, warm Texas reservoir. Aquat. Invasions 15(3): 408-434.

Locklin, J. L., J. S. Moore & R. F McMahon. 2024. Comparative population dynamics of zebra mussel (*Dreissena polymorpha*) populations in two similar closely adjacent warm-water Texas reservoirs. Aquat. Invasions 19(3): 309-328.

Matthews, M. A. & R. F. McMahon. 1999. Effects of temperature and temperature acclimation on survival of zebra mussels (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*) under extreme hypoxia. J. Moll. Stud. 65: 317-325.

McGarrity, M. E. & R. F. McMahon. 2024. A simplistic water body-specific risk assessment for zebra mussel (*Dreissena polymorpha*) establishment based on physiochemical characteristics. Manag. Biol. Invasions. 15(1): 91-108.

McMahon, R. F. 1973. Growth, reproduction and bioenergetic variation in three natural populations of a freshwater limpet, *Laevapex fuscus* (C.B. Adams). Proc. Malacol. Soc. London 41: 331-351.

McMahon, R. F. 1975a. Growth, reproduction and life cycle in six Texas populations of two species of freshwater limpets. Am. Midl. Nat. 95: 174-185.

McMahon, R. F. 1975b. Effects of artificially raised water temperatures on the growth, reproduction and life-cycle of *Physa virgata* (Gould). Ecology 56: 1167-1175.

McMahon, R. F. 1976. Effluent-induced interpopulation variation in the thermal tolerance of *Physa virgata* (Gould). Comp. Biochem. Physiol. 55A: 23-28.

McMahon, R. F. 1977. Shell size-frequency distributions of *Corbicula manilensis* Philippi from a clam-fouled steam condenser. Nautilus 91: 54-59.

McMahon, R. F. 1979a. Tolerance of aerial exposure in the Asiatic freshwater clam, *Corbicula fluminea* (Müller). Pages 227-241 in J.C. Britton (ed.), "Proceedings, First International Corbicula Symposium." Texas Christian University Research Foundation, Fort Worth.

McMahon, R. F. 1979b. Response to temperature and hypoxia in the oxygen consumption of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Müller). Comp. Biochem. Physiol. 63A: 383-388.

McMahon, R. F. 1982. The occurrence and spread of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Müller), in North America: 1924-1982. The Nautilus: 134-141.

McMahon, R. F. 1983. Ecology of an invasive pest bivalve, *Corbicula*. Pp. 505-561, *in* The Mollusca, Volume 6 (W. D. Russel-Hunter, ed). Academic Press, Inc., Orlando, FL.

McMahon, R. F. & C . J. Williams. 1984. A unique respiratory adaptation to emersion in the introduced Asian freshwater clam, *Corbicula fluminea* (Müller) (Lamellibranchia: Corbiculacea). Physiol. Zool. 57: 274-279.

McMahon, R. F. & C .J. Williams. 1986. Growth, life cycle, upper thermal limit and downstream colonization rates in a natural population of the freshwater bivalve mollusc, *Corbicula fluminea* (Müller), receiving thermal effluents. Amer. Malacol. Bull. Special Edition No. 2: 231-239.

McMahon, R. F. & R. W. Lutey. 1988. Field and laboratory studies of the efficacy of Poly [oxyethylene (dimethyliminio) ethylene (dimethyliminio) ethylene dichloride] as a biocide against the Asian clam, *Corbicula fluminea*. Pp. 61-72 *in* Service Water System Reliability Improvement. Electric Power Research Institute, Palo Alto, California.

McMahon, R. F., B. N. Shipman & J. A. Ollech. 1989. Effects of two molluscicides on the freshwater macrofouling bivalves, *Corbicula fluminea* and *Dreissena polymorpha*. Pp. 55-83 *in* EPRI Service Water System Reliability Seminar, Addendum. Electric Power Research Institue, Palo Alto, California.

McMahon, R. F., B. N. Shipman & E. D. Erck. 1990. Effects of two molluscicides on the freshwater macrofouling bivalve, *Dreissena polymorpha*, the zebra mussel. Proc.Am. Power Conf. 52:1006-101.

McMahon, R. F., T. A. Ussery, A. C. Miller & B. S. Payne. 1993. Thermal tolerance in zebra mussels (*Dreissena polymorpha*) relative to rate of temperature increase and acclimation temperature. Pages 4-97 - 4-118 *in*: J. L.Tsou and Y. G. Mussalli (eds.) "Proceedings: Third International Zebra Mussel Conference 1993." EPRI TR-102077, Electric Power Research Institute, Palo Alto, CA.

McMahon, R. F., M. A. Mathews, L. R. Shaffer & P. D. Johnson. 1995. Effects of elevated carbon dioxide levels on survivorship in zebra mussels (*Dreissena polymorpha*) and Asian clams (*Corbicula fluminea*). Pages 319-336 *in*: Proceedings: Fifth Zebra Mussel and other Aquatic Nuisance Organisms Conference. Ontario Hydro, Toronto, Ontario.

McMahon, R. F. 1999. Invasive characteristics of the freshwater bivalve, *Corbicula fluminea*. Pages 315-343 in R. Claudi and J. Leach (eds.), "Non-indigenous Freshwater Organisms in North America; Their Biology and Impact." Ann Arbor Press, Inc., Chelsea, Michigan.

Payne, B. S., A. C. Miller & R. F. McMahon. 1989. Variation in size demography of lotic populations of *Corbicula fluminea* (Müller). Nautilus 103: 78-82.

Reid, R. G. B., R. F. McMahon, D. O. Foighil & R. Finnigan. 1992. Anterior inhalant currents and pedal feeding in bivalves. Veliger 35: 93-104.

Ramakrishnan V. 2007. Salinity, pH, temperature and hypoxia tolerance in the invasive freshwater apple snail, *Pomacea insularum*. Ph.D. Dissertation, The University of Texas at Arlington, 245 pp.

Strayer, D. L. & H. M. Malcom. 2006. Long-term demography of a zebra mussel (*Dreissena polymorpha*) population. Freshw. Biol. 51, 117-130.

Ussary, T. A. & R. F. McMahon. 1994. Comparative study of the desiccation resistance of zebra mussels (*Dreissena polymorpha)* and quagga mussels (*Dreissena bugensis*). Pages 351-369 *in*: Proceedings: Forth International Zebra Mussel Conference '94." Wisconsin Sea Grant Institute, Madison, WI.

TPWD (Texas Parks and Wildlife Department). 2024. The Invasive Mussel Threat. https://tpwd.texas.gov/huntwild/wild/species/exotic/zebramusselmap.phtml. (Accessed: October 30, 2024).

Williams, C. J. & R. F. McMahon. 1985. Oxygen consumption rates, nitrogen excretion rates, and tissue organic carbon:nitrogen ratios in the introduced Asian freshwater bivalve, *Corbicula fluminea* (Müller) (Lamellibranchia: Corbiculacea). Amer. Malacol. Bull. 3: 267-268.

Williams, C. J. & R. F. McMahon. 1986. Power station entrainment of *Corbicula fluminea* (Müller) in relation to population dynamics, reproductive cycle, and biotic and abiotic variables. Amer. Malacol. Bull. Special Edition No. 2: 99-111.

Williams C. J. & R. F. McMahon. 1989. Annual variation in tissue condition of the Asian freshwater bivalve, *Corbicula fluminea*, in terms of dry weight, ash weight, carbon and nitrogen biomass and its relationship to downstream dispersal. Can. J. Zool. 67: 82-90.