



Impact of Data Availability on Site Assessment and Predictive Behavior of Aquatic Invasive Species

by Judy F. Shearer and Michael J. Grodowitz

PURPOSE: The purpose of this study was to determine the status of available documentation of the physiological ecology of several invasive aquatic species in relation to the ability to predict which sites will be susceptible to invasion.

INTRODUCTION: As of 2001, it was estimated that approximately 50,000 nonindigenous species had been introduced into the United States (Pimentel et al. 2000). Some are beneficial, including food crops (e.g. corn, wheat), livestock (e.g. cattle, sheep), landscape enhancement (e.g. crape myrtles, boxwoods), or biological pest controls (e.g. host-specific biological control insects and pathogens). Others, however, have caused major economic losses and harmful impacts to the environment. Over the past 40 years, introductions have increased because of human population growth and mobility and increased trade among nations (Pimentel et al. 2000).

Fundamental to establishment success for any invasive species is a source of food and a place to live and reproduce (Worner and Gevrey 2006). Additionally, to understand invasiveness, one must be cognizant about the conditions required for invasion, species-specific characteristics, and ecosystem susceptibility (Worner 2002). Successful establishment of a species arriving in a new environment is dependent on a variety of biotic and abiotic factors, including climate and environmental conditions of the habitat being invaded. The biology of an invasive species may be well understood, but knowledge concerning environmental tolerances of invasive species is severely lacking.

Predicting where a nonindigenous species will invade is a major challenge to invasive species researchers. In recent years, niche modeling tools have been used to forecast the spread of invasive species over broad landscapes. Tools such as BIOCLIM, CLIMEX, and GARP (Genetic Algorithm of Rule-Set Production) correlate the distribution of a species to climatic and/or environmental variables (Loo et al. 2007). GIS (Geographic Information Systems) allows spatial models to be mapped and suitable habitat for an invader to be identified. Recently, such models have been used to predict the potential range of the newly introduced New Zealand mudsnail (*Potamophyrus antipodarum*) into North America (Loo et al. 2007). According to the models, most of the United States with the exception of the Southeast (from Texas eastward) has the potential to be invaded. In examining tolerances for the mudsnail, the authors found severe shortcomings of information on key variables, particularly for aquatic species. They pointed out that large-scale data on physical and chemical water variables are in many cases rare and unavailable for intercontinental comparisons. Additionally climate changes may invalidate the predicted range expansion of some species.

One of the few species for which extensive environmental tolerance data have been collected is the zebra mussel (*Dreissena polymorpha*). Due to its damaging impact on the environment, the species has been extensively studied in North America since its arrival into Lake St. Clair, in 1985. Claudi

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and Mackie (1994) point out the importance of using site-specific parameters collected over a 2- to 5-year period to predict whether a site is at risk to invasion. By taking frequent measurements (at least weekly), valuable information concerning the mean monthly variations of the measured parameters can be documented. For zebra mussels, the most important variables were temperature, calcium levels, and pH but knowledge of lesser variables such as alkalinity, nutrient levels (total phosphorous content), turbidity, conductivity, and dissolved oxygen were also of use. By documenting the amplitude of tolerances at a specific site, researchers can now predict whether the probability of invasion is low, medium, or high and site managers can plan accordingly and set up monitoring and prevention programs.

Unfortunately many U.S. Army Corps of Engineers installations that are presently free of nonindigenous aquatic species may be susceptible to invasion depending on site-specific characteristics. Knowing what characteristics make facilities susceptible and filling in environmental tolerance data gaps is essential for developing site assessment models that can be used to predict potential for a species to become an invader. Toward this end, the authors have examined available documentation on several invasive aquatic species. By doing so, data gaps can be identified that must be resolved before predicting which specific sites will be susceptible to invasion.

Chinese mitten crab (*Eriocheir sinensis*)

Current distribution: Established populations in California (Chinese Mitten Crab Working Group (CMCWG) 2003; Hanson and Sytsma 2008; U.S. Geological Survey (USGS) 2008). Reports from the Great Lakes and Chesapeake Bay to the Hudson River in the eastern United States (National Invasive Species Information Center (NISIC) 2008; USGS 2008, CMCWG 2003).

Through careful examination of published accounts, Hanson and Sytsma (2008) found considerable variation in habitat values in native and introduced ranges of Chinese mitten crabs. Invaded estuaries varied in size from 200 to 1328 km (average 602 km), tidal intrusion varied from 100-326 km (average 155 km), maximum salinity intrusion varied from 67 to 107 km (average 85 km), and mean flushing time varied from 23-65 days (average 45 days). Hanson and Sytsma determined that two ecological conditions (estuary size and flushing time) were of primary importance in predicting if a western North American site could sustain significant populations. Estuaries less than the average size (602 km) probably would not support significant mitten crab population. Flushing time was determined to be an important factor because the larval developmental period is spent as a planktonic zoea. Previous research documented that larval development and survival was temperature and salinity dependent. Anger (1991) found survival in salinities that varied from 15 to 32 ppt and temperatures that ranged from 12 to 25 °C. Additional studies determined that salinities between 20 and 25 ppt and temperatures between 15 and 25 °C provided optimum survival parameters (Anger 1991; Kim et al. 1995; Huang et al. 2001). Temperatures below 9 °C resulted in complete mortality in the first larval stage (Anger 1991). Based on the above parameters Hanson and Sytsma (2008) concluded that the majority of the Pacific Northwest and Alaskan estuaries were not at risk for establishment of significant mitten crab populations and that only Puget Sound was highly susceptible to invasion. Although water temperatures in Alaska would most likely prohibit larval development, global warming could elevate Alaskan waters to a high risk level. Unfortunately a similar Hanson and Sytsma (2008) study has not been done for the eastern United States. Although

Chinese mitten crabs have been reported from the region, it is not known if environmental tolerances will be conducive to their establishment and survival.

Data gaps: Compilation of estuary size and flushing time for the Eastern United States.

New Zealand mudsnail (*Potamopyrgus antipodarum*)

Current distribution: Great Lakes and states along and west of the Continental Divide (NISIC 2008; USGS 2008).

Developing site-specific modules for New Zealand mudsnails may be extremely difficult because their invasiveness varies among different clones and with environmental conditions. Clonal lineages may have narrow or broad ecological tolerances. Over their native range, mudsnail clones are very diverse and exhibit plastic variation under different environmental conditions (New Zealand Mudsnail Management and Control Working Group (NZMMCWG) 2007). European introductions have been reported to consist of three clones including one in continental Europe that has broad tolerances (NZMMCWG 2007). The clone designated as Euro A occurs in fresh water in continental Europe, Euro B in estuaries in the Baltic Sea, and Euro C in Great Britain. At present, there are also three different clones of mudsnails in the United States. The clone found in the Great Lakes is the same as Euro A. A second clone now found in at least nine western states spread from an introduction into the Snake River in Idaho and is thought to have come to the United States via Australia, and a third distinct clone has recently been found in the Snake River (NZMMCWG 2007).

In its native country, New Zealand mudsnails occupy a wide range of habitats including lakes, rivers, streams, and springs (NZMMCWG 2007). Within the habitats a wide range of temperature, osmotic concentrations, flow, substrate and disturbance regimes have been documented. In laboratory studies, the upper thermal tolerance limit was found to be 32 °C for snails acclimated to 15 °C (Quinn et al. 1994). Less is known about the lower lethal tolerances but the mudsnail's ability to survive in northern Europe and the intermountain west of North America suggest that it is capable of surviving low temperatures for several months. Cox and Rutherford (2000) report mudsnail temperature tolerances from 0 to 34 °C in New Zealand. Dybdahl and Kane (2005), in looking at snail clonal sublines from three populations, found that in the United States overall fitness peaked at 18 °C and declined at cooler and higher temperatures. Young snails may be particularly vulnerable to temperature fluctuations. Desiccation experiments documented that small young snails (1 to 2.5 mm) do not survive for more than a few hours at temperatures above 21 °C while larger individuals (> 4mm) survive for less than 25 hr at 21 °C (Richards et al. 2000). Because mudsnail reproduction is linked to temperature (Winterbourn 1970; Dybdahl and Kane 2005), those populations subjected to low temperatures tend to have low reproductive rates making them more vulnerable to other disturbances.

New Zealand mudsnails are euryhaline organisms and in both their native and introduced ranges are found in saline, brackish, or freshwater habitats. Studies of European clones indicated that mudsnails were able to feed, grow, and reproduce at salinities ranging from 0 to 15 ppt with salinity optima at 5 ppt (NZMMCWG 2007). In New Zealand, Winterbourn (1970) found acute salinity tolerance for mudsnails to be 21 ppt in the laboratory although he collected them from some New Zealand locations where salinities approached 27 ppt. The clone in the Columbia River estuary in Astoria, OR must be able to tolerate salinities that vary daily from 0 to 32 ppt (Dybdahl and Kane 2005).

In their native habitats, New Zealand mudsnail individuals can tolerate scouring events (Winterbourn et al. 1981). High flows tend to redistribute the snails rather than kill them (Holomuzuki and Biggs 1998). Laboratory studies found that only 8 percent of mudsnails were dislodged when subjected to scouring flows in an experimental flume (Holomuzuki and Biggs 2000).

Mudsnails are highly tolerant to a variety of substrates in habitats of various depths and water qualities. In the Great Lakes, mudsnails have been collected at depths ranging from 4 to 45 m (Zaranko et al. 1997; Levri et al. 2007). They occur in silt, sand, cobble, riffle, run, and on submersed vegetation in the United States (Richards 2002; Zaranko et al. 1997; NZMMCWG 2007). Kerans et al. (2005) found them in very high densities in cobble habitat in Yellowstone National Park. In New Zealand densities were highest in areas with an abundance of fine substrate, aquatic vegetation, and low velocities (Cunha and Moreira 1995; Savage 1996; Jowett et al. 1991) and lowest in streams prone to sediment-moving flood flows (Winterbourn 1997; Holomuzki and Biggs 2000). There are inconsistent reports of mudsnail survival in waters with high nutrient loads. Duggan et al. (2002) reported that in New Zealand mudsnails dominated invertebrate communities in streams with high nutrient loads and abundant macrophytes. Likewise, in Australia they seem consistently associated with waters with high agricultural runoff and nutrient inputs (Schreiber et al. 2003). However, there have been some reports that high nutrient levels adversely affect population densities and individual survival (Tomkins and Scott 1986; Hickey and Vickers 1994).

Data gaps: DNA information on each clonal type, temperature ranges, salinity tolerances, flow rates, substrates, water quality tolerances, combined environmental effects.

Killer shrimp (*Dikerogammarus villosus*)

Current distribution: Presently not in the United States.

Killer shrimp and zebra mussels both evolved in the Ponto-Caspian region in and around the Black and Caspian Seas. For this reason several authors have suggested that habitat alteration caused by the settlement of zebra mussels may facilitate establishment of co-evolved killer shrimp, which appears to be the case in Europe (Devin et al. 2003; Ricciardi et al. 1997; Casellato et al. 2006; Lods-Crozet and Reymond 2006). Thus, it is likely that if killer shrimp are introduced into North American waters they will rapidly expand into areas that have already been invaded by zebra mussels.

Killer shrimp are euryhaline eurythermic species that can survive a diverse range of salinities and temperatures. They can tolerate salinities between 0 and 20 ppt but cannot tolerate salinities >24 ppt (Bruijs et al. 2001; Dick and Platvoet 2000; van der Velde et al. 2000). Because killer shrimp survived salinities up to 10 ppt and adapted to salinities of up to 20 ppt in laboratory studies, Bruijs et al. (2001) concluded that the species could be transported over large distances in ballast water and is thus capable of developing large populations in temperate areas on a global scale. Lower temperature tolerances have not been documented for killer shrimp, but if they are similar to tolerances recorded for zebra mussels there should be no survival when temperatures reach -2 °C, and poor growth at temperature ranges from 0 to 8 °C (Claudi and Mackie 1994). Preliminary research has indicated that killer shrimp prefer temperatures between 20 to 30 °C with upper limits of 30 to 35 °C (Dick and Platvoet 2000; van der Velde et al. 2000).

Upon invading a new water body, killer shrimp exhibit a high dispersal and adaptability to new habitats and compete and sometimes displace other invertebrates. In Lake Léman, Switzerland, the spatial and bathymetric dispersion of killer shrimp down to a depth of 10 m led to displacement of native gammarid species (Lods-Crozet and Reymond 2006). After invasion, two native gammarids, *Dikerogammarus pulex* and *D. fossarum*, were no longer found at depths between 0 and 5 m where they were previously abundant. Likewise, in Lake Garda Italy, Casellato et al. (2006) determined that killer shrimp dispersed to depths between 4 to 11 m and were displacing the native species, *Echinogammarus stammeri*, in portions of the lake. The researchers admitted that only constant monitoring of the lake over time would determine what depths might be inhibitory to invasion.

A wide range of substrate types can be colonized by killer shrimp. In Lake Léman, Lods-Crozet and Reymond (2006) found them on cobbles, gravel, and sand/clay with zebra mussel aggregates. Devin et al. (2003) examined killer shrimp populations on a mesohabitat scale in the Moselle River, France. The research indicated that the amphipod was capable of colonizing a wide range of substratum types but not sand. They predicted that densities would probably peak where rivers had cobbles as a substratum and tree roots along the banks to provide protection for juveniles.

Grabowski et al. (2007) critically reviewed life histories of several invasive and native gammarids in central Europe to define traits that may promote invasion of aliens in comparison to native species. Their findings suggested that type of life history is as important to invasion as ecological tolerance. Invasive species like killer shrimp have very high reproductive potential, which is expressed by high fecundity, early maturity, and repeated reproduction each year. In contrast, native gammarid species of central Europe are characterized by relatively small brood size, lower partial fecundity, and late reproductive ability (one generation per year). Grabowski et al. concluded that the life history traits of invasive gammarids facilitated invasion into European waters. Additionally Grabowski et al. (2007) suggested that predation may also be a factor in rapid establishment and spread of killer shrimp in Europe as it is a voracious predator responsible for the extermination of other macroinvertebrate species (Dick and Platvoet 2000; Krisp and Maier 2005).

Data gaps: Temperature ranges, water depths, pH, life cycle habitat requirements.

Swamp Eel (*Monopterus albus*)

Current distribution: Florida, Georgia, and Hawaii.

Swamp eels have the potential to survive in diverse habitats. They thrive in shallow wetlands, marshes, swamps, streams, ditches, and ponds (Prok 2000), mostly less than 3 m in depth (Froese and Pauly 2008). Although they prefer freshwater, swamp eels have been reported to be capable of tolerating brackish and slightly saline waters (Nichols 1943). In their native range, they live in muddy ponds, swamps, canals, and rice fields (Ip et al. 2003). During dry seasons, swamp eels burrow into moist earth to survive long periods without flowing water (Cheng et al. 2003) or food (Prok 2000).

Temperature amplitudes for swamp eels are currently unknown. In their native range, they are found in Southeast Asia between 34 °N to 6 °S (Froese and Pauly 2008). Froese and Pauly (2008) list them as being a tropical species existing optimally where temperatures are between 25 to 28 °C. However, in the United States they have been reported to survive freezing conditions in Georgia (Starnes et al.

1998). Based on observations of the species in Georgia, Starnes et al. (1998) predicted that swamp eels could establish populations from Texas to the Chesapeake Bay. If this were the case, swamp eels would likely become common in the rice-growing areas of the southeast.

Swamp eels have developed many adaptations for survival under harsh conditions. They are obligate air breathers with young that possess a vascular system that enables them to survive in poorly oxygenated environments (Liem 1961, 1981; Graham 1997). If not using gills underwater, they can obtain up to 25 percent of oxygen cutaneously from air. They sometimes travel short distances over land to escape over-population and food scarcity (Liem 1987; Tay et al. 2003).

Swamp eels are nocturnal and secretive (Prok 2000). During the day, they hide in thick aquatic vegetation in small burrows near the water's edge. For this reason, their presence in a water body may go unnoticed until populations reach high densities, impairing management efforts and increasing the chances of spread to nearby water bodies.

Data gaps: Temperature ranges, salinity tolerances, water depth, pH, reproductive potential in U.S. waters, impacts on native fauna.

Golden alga (*Prymnesium parvum*)

Current distribution: Texas and other parts of southwestern and coastal United States.

Predictions as to whether a specific site will be susceptible to harmful blooms by the golden alga may be difficult because environmental tolerances differ depending on the strain. While present in many U.S. water bodies, it is unclear what factors specifically induce the organism to produce the toxins that can cause fish kills. Contributing factors that led to a massive fish kill from a golden alga bloom in Finland were sunny weather, high water pH, high oxygen saturation, and high N:P ratio (Lindholm et al. 1999).

Golden algae have been recorded worldwide in coastal and inland waters of varying salinity (Baker et al. 2007). Tolerance to low salinity has enabled the species to spread to inland waters and into fish ponds. Baker et al. (2007) summarized published information from marine studies on golden alga tolerances to temperature and salinity. Their summary indicated that the species could grow in water salinities that varied from 0 to 34 psu (practical salinity units) and temperatures between 5 and 30 °C. Unfortunately, similar in situ studies of the species have not been conducted in inland waters.

Using a strain of golden alga isolated from inland waters in Texas, Baker et al. (2007) attempted to define the ecological response and toxic potential of the species in relation to temperature, light, and salinity. In their laboratory studies, they found the exponential growth rate of the golden alga was a unimodal function of temperature lacking interactions with light or salinity with rapid growth at temperatures between 25 and 30 °C. These results were consistent with studies using strains derived from saline waters, leading the authors to conclude that the temperature optima for golden alga occurs between 25 and 30 °C and growth inhibition occurs at approximately 10 °C. Subsequent studies indicated that the exponential growth rate, population density, and toxicity to fish were highest when the golden alga was grown at 20 °C (Grover et al. 2007). The Texas strain was insensitive to salinity over a wide range, with optimum growth near 22 psu and greatly reduced growth only

below ~1 psu whereas the salinity optima for the strains derived from saline habitats ranged from 8 to 34 psu (Baker et al. 2007).

Laboratory studies that examined stationary cell concentrations of the golden alga strain from inland Texas indicated growth and abundance were highest at temperatures between 25 and 28 °C and salinities between 20 to 25 psu, conditions that are not typical for the time of year (autumn and winter) when golden alga blooms often occur in Texas (Baker et al. 2007). Looking at toxicity, the researchers found that maximum toxicity to fish was observed at extreme (low and high) values of salinity and for lower temperatures. They noted that blooms in Texas inland waters occur at low salinities and lower temperatures. In light of the contradiction between high predicted growth and abundance under summer conditions and the occurrence of inland blooms in winter, Baker et al. (2007) concluded that additional unknown seasonal factors must limit the species.

Data gaps: temperature and salinity tolerances in inland waters, pH, conditions that stimulate toxin production.

Round Goby (*Neogobius melanstomus*)

Current distribution: In and around the Great Lakes and Illinois River.

Round gobies are benthic fish that co-evolved with the zebra mussels in the Ponto-Caspian region in and around the Black and Caspian Seas (Jude et al. 1992). Because the two species co-occur in their native water bodies, it might be anticipated that round gobies could exist in the same sites in the United States where zebra mussels have already invaded.

Round gobies are eurythermal (i.e. adaptable to a wide range of temperatures). In their native habitat round gobies have been reported to survive in temperatures between -1 and 30 °C (Moskal'kova 1996). Similar amplitudes have been recorded in the United States. Great Lakes' fishermen report that the fish is seemingly unaffected by rapid temperature fluctuations because round gobies caught in 16 °C lake water can be placed immediately in 32 °C water with no apparent harm (Charlebois et al. 1997). In the profundal zone of Lake Ontario, round gobies have been caught at depths of 55, 95, and 130 m where temperatures were recorded to be 3.9, 3.4, and 3.2 °C, respectively, and photo-synthetically active radiation was negligible (Walsh et al. 2007).

The threshold oxygen concentration of round gobies ranges between 0.3 and 0.9 ml l⁻¹ depending on the size of the fish (Charlebois et al. 1997). Skin respiration comprises 13 percent of the total respiration (Moskal'kova 1996). If dissolved oxygen becomes less than 50-60 percent of saturation, the fish reportedly will leave an area (Charlebois et al. 1997).

Although round gobies have been reported to prefer shallow waters from <1 m up to 20 m in depth (Sapota 2004), they are found at greater depths both in their native and introduced ranges. For example, they have been reported in the Caspian Sea at depths up to 70 m (Moskal'kova 1996), in Lake Huron up to 73 m (Schaeffer et al. 2005), and in Lake Ontario up to 150 m (Walsh et al. 2007). In its native habitat, round gobies are found in slow rivers, lagoons, and brackish coastal waters (Jude and DeBoe 1996). They tolerate flow rates of 0.34 m/s for 3-4 minutes but at higher rates remain close to the bottom using their pelvic fins to brace against the current (Charlebois et al. 1997). Overall, round gobies seem to prefer littoral zones where wave action results in high

dissolved oxygen levels and reduces the amount of decayed material. In their introduced range, round gobies have been reported to flourish in areas with substrates of coarse gravel, rock cobble, riprap, shells, sand, and vegetation (Jude and DeBoe 1996; Charlebois et al. 1997; Eros et al. 2005). Unfortunately, some habitat enhancement projects that are built to restructure fish communities may also provide ideal habitat for reproduction and expansion of round gobies (Jude and DeBoe 1996).

Few laboratory studies have addressed salinity tolerances of round gobies. Moskal'kova (1996) determined that embryonic development proceeded normally at salinities between 4.2 and 19.5 ppt. In Eurasia, round gobies have been collected in waters where salinities vary from 1 ppt to 40.6 ppt (Charlebois et al. 1997). These waters also support successful reproducing colonies.

Data gaps: Water depths, salinity tolerance, flow rates, substrates.

Ruffe (*Gymnocephalus cernuus*)

Current distribution: Western Great Lakes and tributaries.

The distribution of ruffe in North America is presently limited to the western Great Lakes and tributaries; however, their widespread occurrence in Europe and Asia suggests that the potential distribution of the species could be extensive in North America (Drake and Lodge 2006). Ruffe have been reported to tolerate a variety of environmental conditions from fresh to brackish waters at various depths and temperatures under oligotrophic to eutrophic conditions (Brazner et al. 1998; Gunderson et al. 1998; Popova et al. 1998). Studies by Lappalainen and Kjellman (1998) led them to conclude that adult ruffe are an r-selected species with no special ecological requirements. In an effort to predict their potential North American distribution, Drake and Lodge (2006) used eight ecological and climate variables (annual precipitation, elevation, ground frost frequency, maximum annual air temperature, mean annual air temperature, minimum annual air temperature, slope, and wet day frequencies). Their results indicated that ruffe will likely invade large areas from northeast North America westward to the Pacific Ocean and northward from Oregon to Alaska (Drake and Lodge 2006). Invasion into the southeastern and southwestern United States and Mexico appeared unlikely. Drake and Lodge emphasized that availability of more aquatic variables (e.g., water quality and water temperature data) would improve accuracy of the generated maps. These data, however, are very limited for almost all aquatic species.

Ruffe are demersal freshwater and brackish species (Froese and Pauly 2008; Drake 2005). Although the fish has been extensively studied, Hölker and Thiel (1998) also pointed out the need for additional detailed life history studies of the ruffe to determine how different life history stages change in relation to environmental factors. Only with this knowledge can fish biologists hope to control populations of the ruffe. Such information would also contribute greatly to the ability to predict whether specific sites are susceptible to invasion.

Froese and Pauly (2008) report the temperature tolerances for ruffe are between 10 and 20 °C. Hölker and Thiel (1998) described ruffe as having a relatively low water temperature optimum (i.e. between 5 and 20 °C) for food consumption. Subsequent studies by Henson and Newman (2000) in North America found that maximum growth of ruffe occurred at 14 °C. In Lake Võrtsjärv, Estonia, Kangur et al. (1999) noted that ruffe have an advantage over percid fish species in that they can maintain high activity at low temperatures allowing them to take food in late autumn and winter.

The maximum depth at which ruffe can occur is not presently known (Froese and Pauly 2008). In their native range, ruffe were found 30 km offshore at a depth of 50 m although densities were very low (Lehtonen et al. 1998). In Loch Lomond, one of the deepest water bodies in Great Britain, ruffe were one of the most common species in the littoral zone (Adams and Maitland 1998). Studies undertaken in the former Soviet Union documented that ruffe larvae usually inhabit the whole water column but at night were concentrated near the surface from 0 to 1 m and during the day migrated to a depth of 5 to 6 m (Popova et al. 1998). As adults, ruffe were reported to move to deep sites in summer and autumn and migrate in winter and spring to shallow waters. Ruffe were found in all of 67 lakes in Germany sampled for fish communities (Mehner et al. 2005).

Ruffe seem to prefer water bodies with pH ranges between 7.0 and 7.5 (Froese and Pauly 2008). Eggs develop normally at pH 6.5 to pH 10.5, one of the widest ranges from a broad set of fish tested (Kiyashko and Volodin 1978).

Ruffe have been reported from both fresh and brackish waters. Albert et al. (2006) undertook laboratory studies that examined reproductive success of ruffe collected from freshwater and brackish lakes in Estonia. Eggs of freshwater females hatched in salinities up to 7.7 ppt and eggs from brackish water females hatched in salinities up to 9.9 ppt. Females from brackish water had significantly larger eggs. The authors concluded that survival in all tested salinities depended on female origin, with brackish water females showing a higher salinity tolerance. Popova et al. (1998) reported that the most important abiotic factor influencing ruffe distribution in estuaries was tolerance to salinity.

Because responses of adult ruffe to eutrophication are sometimes inconsistent, Lehtonen et al. (1998) examined fish populations in areas with different trophic levels near Helsinki. Their results suggested that ruffe could be one of the most successful benthic feeders in hypereutrophic waters. However, the low oxygen content of such waters in winter might be a restricting factor for ruffe abundance. Seasonal movements of ruffe are related to spawning, deterioration of oxygen conditions, and dense aggregations of food (Popova et al. 1998). Kangur et al. (2003) observed an increase in ruffe in two lakes in Estonia with increasing eutrophication until hypereutrophy was reached.

Ruffe can inhabit lakes, quiet pools, and margins of streams with various substrates (Froese and Pauly 2008). In lakes and reservoirs, they seem to prefer sand and silty well-aerated sites with or without vegetation (Popova et al. 1998). In such sites, water current seems to be the most limiting abiotic factor.

Data gaps: Water depths, temperature and salinity tolerances.

SUMMARY: Hundreds of exotic plants and animals have become established in aquatic habitats over the past few centuries (Cohan and Carlton 1998) and additional invasions are likely to occur due to expanding global trade and travel (Ricciardi and Rasmussen 1998). Additionally, changes in climate may provide opportunities for many nonindigenous species to expand their ranges and invade new habitats. In order to lessen their impact, it would be highly desirable to know which sites are susceptible to invasion by a nonindigenous species. Unfortunately, published accounts of the physiological ecology of many invaders and potential invaders are not sufficient to support robust predictions of their potential range or practical insight into how aspects of their biology, life history,

and biotic and abiotic environmental requirements might be used to manage their spread. In most cases it is not until the invader becomes a serious problem that extensive research is undertaken and then the research usually focuses on control measures, not intervention or prevention. One of the aquatic invasive species that has been extensively studied is the zebra mussel. By monitoring certain environmental variables, sites that are susceptible to invasion can now be predicted with relatively good accuracy and appropriate actions can be taken to minimize the chances of infestation. Unfortunately, these data are not currently available for most aquatic species and it is those gaps that must be filled before predicting which sites will be susceptible to invasion by other nonindigenous species.

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