Biological Synopsis of Dark Falsemussel (*Mytilopsis leucophaeata*)

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ABSTRACT

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Dark Falsemussel, *Mytilopsis leucophaeata*, is an invasive macrofouling pest that has had significant impacts in its invaded range. This species originates from the southern coast of the USA and the Gulf of Mexico but has invaded various non-native regions of the United States, Brazil and Europe. Dark Falsemussel is found in brackish warm–temperate waters within its native range; however, the species can survive within very broad environmental limits. Once introduced in non-native regions through industrial shipping, the high temperature and salinity tolerance of the species favors its establishment. Extensive knowledge of the species biology is crucial to better understand the risk of invasion in Canada.

RÉSUMÉ

Duhaime, J. and Cudmore, B. 2012. Biological Synopsis of Dark Falsemussel (*Mytilopsis leucophaeata*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2980: iv + 18 p.

Mytilopsis leucophaeata est une espèce envahissante de macro-encrassement ayant des impacts significatifs dans les cours d'eau qu'elle envahit. Cette espèce, originaire de la côte Sud des États-Unis et du golfe du Mexique, a maintenant été introduite dans différentes régions des États-Unis, du Brésil et de l'Europe, à l'extérieur de sa distribution d'origine. *Mytilopsis leucophaeata* évolue dans des habitats tempérés et saumâtres au sein de sa distribution d'origine mais elle peut survive dans des conditions environnementales très larges. Une fois introduite dans une région exotique par les voies de la navigation industrielle, la grande tolérance de l'espèce aux variations de température et de salinité favorise sont établissement. Une connaissance approfondie de la biologie de l'espèce est cruciale afin de mieux comprendre les risques posés par une potentielle invasion au Canada.

1.0 INTRODUCTION

Dark Falsemussel (*Mytilopsis leucophaeata*) is an epifaunal bivalve of brackish habitats known as an important invading pest. The species occurs in low abundance throughout its native distribution on the southern coast of the USA and the Gulf of Mexico (Nuttall 1990, Therriault et al. 2004, GISD 2005, Verween et al. 2006); however, the species can attain densities of up to 28,000 individuals per m^2 in its introduced range (Laine et al. 2006). As with other members of the Dreissenidae, Dark Falsemussel has become a serious biofouling species in its invaded range (Verween et al. 2005, Kennedy 2011a). Invasions are related to important ecological impacts associated with the species high filtration rate (Bergstrom et al. 2009). *Dreisenna polymorpha,* a species in the same family (Therriault et al. 2004), produced important food web perturbations and ecosystem shifts in its invaded range (Nicholls et al. 2011), and the presence of *M. leucophaeata* may cause similar affects.

The species has now extended its range to multiple non-native regions of America (i.e., Hudson River, Southern New England, Mississippi River, and Brazil) and Europe (i.e., Belgium, Finland**,** France**,** Germany**,** Netherlands**,** Spain**,** Ukraine, Russia**,** and Britain) (Jacobson 1953, Smith and Boss 1996, Therriault et al. 2004, de Souza et al. 2005, Kennedy 2011a). The principal vectors for its introduction into new areas are associated with the industrial shipping pathway. Larvae and adults are transported via hull fouling and ballast water (Smith and Boss 1996, Oliver et al. 1998, Bamber and Taylor 2002, Verween et al. 2005, Farrapeira et al. 2010).

Dark Falsemussel can survive and reproduce in a wide range of salinity and temperature conditions and invade most brackish waterbodies (Sidall 1980, Verween et al. 2007a, 2007b, Mackie and Claudi 2010, Verween et al. 2010). No occurrence of the species in the wild has been recorded in Canada; however, given its very broad environmental limits, Canadian waters may be at risk of invasion. Extensive understanding of Dark Falsemussel biology is crucial to the development of sound scientific advice on the ecological risk associated with a potential invasion in Canada.

2.0 NAME AND CLASSIFICATION

From Integrated Taxonomic Information System (2011) and Rosenberg and Gofas (2011).

Kingdom: Animalia
Phylum: Mollusca
Class: Bivalvia Linnaeus, 1758

Subclass: Heterodonta Neumayr, 1884
Order: Veneroida H. Adams and A. Adams, 1856
Superfamily: Dreissenoidea Gray, 1840
Family: Dreissenidae Gray, 1840
Genus: *Mytilopsis* Conrad, 1857
Species: *Mytilopsis leucophaeata* Conrad, 1831

Common scientific name: *Mytilopsis leucophaeata*
Synonyms: *Congeria cochleata*
Congeria leucophaeta
Mytilus americanus Recluz, 1858
Mytilus cochleatus Kickx, 1835
Mytilus leucophaeatus Conrad, 1831

Common English name: Dark Falsemussel
Vernacular names: Brakwatermossel, Dutch
Brackish Water Mussel, English
Dark False Mussel, English
Dark Falsemussel, English
Brackwasser-Dreikantmuschel, German
Conrad's False Mussel, English

3.0 DESCRIPTION

3.1 MORPHOLOGY

Dark Falsemussel is a dark brown mussel (Figure1) ranging between 1.3 and 2.7 cm in length (Abbott 1974, Bamber and Taylor 2002). The species has an elongated shell that is dorsally flattened and ventrally convex (Verween et al. 2010). *Mytilopsis leucophaeata* also has a round ventroposterior side and umbone (Nyst 1835, Pathy and Mackie 1993). The ventrolateral shoulder (or ridge) is absent (Pathy and Mackie 1993). The internal shell is grey with a weakly developed pallial sinus and a very short pallial line (Verween et al. 2010). Juveniles have very smoothly curved shells and their shape is more elongated (rectangular) than the adults (Verween et al. 2010). Young specimens display a cream-like colour and occasionally have stripes (Pathy and Mackie 1993, Verween et al. 2010). *Mytilopsis leucophaeata* is often confused with the Zebra Mussel which displays similar stripes and, occasionally, uniform dark shell coloring (Pathy and Mackie 1993, Smith and Boss 1996, Verween et al. 2010).

The shell of Dark Falsemussel is composed of tubules ranging from 1 to 5 μm in size (Sidall 1980, Pathy and Mackie 1993). Tubules appear at the juvenile stage and are restricted to the older regions of the shell (i.e., delimited by the pallial line) (Siddall 1980, Pathy and Mackie 1993). The aragonite crystal shell (Pathy and Mackie 1993) is composed of three shell structural types: the outer crossed-lamellar, the inner complex crossed-lamellar, and the middle pallial myostracum

(Pathy and Mackie 1993). The presence of an apophysis on *M. leucophaeata* is an important character to distinguish between Zebra and Quagga mussels (Pathy and Mackie 1993). The apophysis is a slightly triangular or rounded projection of the shelf located near the umbone that serves as an attachment point for the anterior retractor muscles (Abbott 1974, Verween et al. 2010). This feature differs from hinge teeth, which are absent from early life stages (Siddall 1980).

3.2 GENETICS

Therriault et al. (2004) described the phylogeny of the Dreissenidae by comparing the genetics of *Dreissena rostriformis, D. bugensis, D. polymorpha, D. stankovici, Congeria kusceri, and M. leucophaeata* based on the DNA sequence of two mitochondrial gene fragments. Intraspecific variations represented differences smaller than 1.2% and interspecific variations ranged between 6.0% and 11.5%. Differences of 9.7% and 11.5% were reported between *M. leucophaeata* and *D. polymorpha* specimens. A smaller genetic difference of 6.0% was observed when comparing with *Congeria kusceri. Mytilopsis leucophaeata* intraspecific variations of 0.7 and 0.9% were also reported.

4.0 DISTRIBUTION

4.1 NATIVE DISTRIBUTION

Mytilopsis leucophaeata usually occurs in low abundance throughout its native habitat (Therriault et al. 2004, Kennedy 2011b). Tampico, Mexico, is known as the southern limit of the species native range (Marelli and Gray 1983); however, the northern limit of its native distribution is not consistent among publications. Some authors consider its native range to include Chesapeake Bay (Conrad 1857, Johnson 1934, Smith and Boss 1996) or the Hudson River (Marelli and Gray 1983); whereas, other authors suggest that it is limited to the southern coast of the USA and the Gulf of Mexico (Therriault et al. 2004, GISD 2005, Verween et al. 2006). Based on the lack of fossil records on the eastern coast of the United States, Nuttall (1990) concluded that the presence of the species in this region was the result of an introduction. Therefore, based on those findings, it was determined that the native distribution of Dark Falsemussel was limited to the southern coast of the USA and the Gulf of Mexico (Figure 2).

4.2 NON-NATIVE DISTRIBUTION

Based on Nuttall (1990), the eastern coast of the United-States, from Florida to Chesapeake Bay, is part of the non-native distribution of *M. leucophaeata* (Figure 2). Various authors have also reported the introduction of this species in Housatonic, Hudson and Mississippi Rivers (Rehder 1937, Jacobson 1953, Koch 1989, Smith and Boss 1996) (Figure 2). Moreover, recent records showed evidence of the introduction of *M. leucophaeata* in South America (northeastern Brazil) (de Souza et al. 2005).

Mytilopsis leucophaeata introduction to Europe was reported as early as 1835 in Belgium (Nyst 1835). Subsequently, the species was found in Finland (Laine et al. 2006)**,** France (Le Mao 2003)**,** Germany (Nehring and Leuchs 2000)**,** Netherlands (Wolff 1969, 2005)**,** Spain (Escot et al. 2003)**,** Ukraine (Therriault et al. 2004)**,** Russia (Therriault et al. 2004), and England (Bamber and Taylor 2002).

5.0 BIOLOGY AND NATURAL HISTORY

5.1 REPRODUCTION

Fertilization is accomplished through the release of sperm and eggs into the water column (Verween et al. 2010). Spawning is initiated in late May – early June and lasts approximately 4 to 5 months (Verween et al. 2005, Verween 2010). Multiple larval peaks are observed during the year (Verween et al. 2010) with the greatest peaks in late August–September (Verween et al. 2005). The interaction of temperature, salinity and food availability regulates the duration and intensity of spawning (Verween et al. 2007a). The onset of spawning requires temperatures of 15– 0 °C (Schütz 1969 as cited by Verween et al. 2007b, Verween et al. 2005) and salinity of 2.6–4.9 PSU (Verween et al. 2005). Food availability also regulates the reproductive behaviour of *M. leucophaeata* as gametogenesis is controlled by chlorophyll *a* concentration (Verween et al. 2009). The Dark Falsemussel is a slow colonizer; however, its long spawning period increases its probability of successful establishment. Species with continuous spawning periods are expected to represent more stable adult populations (Verween et al. 2009).

5.2 LIFE CYCLE

The life history (Table 1) of *M. leucophaeata* is composed of two phases: the pelagic larval form and the benthic mussel form. Life stages (Figure 3) were described by Verween et al. (2010) who noted that the first stage after fertilization is the trochophora (<63 µm), a larva characterized by a ring of cilia and a prototroch. The trochophore then transforms into a D-shaped veliger (50–91 µm) which has a soft, bilateral, symmetric bivalve shell. The veliger has a straight dorsal hinge and rounded ventral valve margins. Later, additional secretion of ornamented larval shell initiates the veliconcha stage (109–150 µm) which develops an umbo and displays a clam-like profile. During this stage, the mussel also develops new organs such as a muscular foot and gill filaments. Primary settlement of the larvae and the loss of velum mark the onset of the postveliger stage (220–480 µm). Later, benthic mussels transform into juveniles (>580 µm) which are rounded posteriorly and have a pronounced anterior shoulder.

Juveniles are morphologically similar to adult mussels, but still immature. Fertilization to metamorphosis can be accomplished within 9 days (Kennedy 2011b) and the species has a minimum longevity of approximately 5 years (Verween et al. 2006).

5.3 GROWTH

Verween et al. (2006) studied the growth of *M. leucophaeata* and reported the species was characterized by an oscillatory growth. The principal growing period was late spring to summer with maximum growth being observed in June and July. Temperature constituted the principal regulator of Dark Falsemussel growth. Shell increment was reduced during autumn and winter but never ceased; even at temperatures as low as 6.3 ˚C. Annual growth ranged between 3 and 6 mm per year. Growth rate was dependent on shell length with smaller individuals growing at higher rates than larger individuals. Growth decreased with increasing size until lengths greater than 15 mm were reached.

5.4 PHYSIOLOGICAL TOLERANCE

The native range of the Dark Falsemussel is characterized by oligohaline (0.5–5 PSU) to mesohaline (5–18 PSU) conditions (Kennedy 2011a). The species has a warm–temperate native range with annual water temperature ranging between 24 and 27˚C in the Gulf of Mexico (Verween et al. 2010). However, *M. leucophaeata* can tolerate a range of salinity and thermal water conditions ranging between 0 and 32 PSU (Sidall 1980, Verween et al. 2007a, Verween et al. 2010), and 5 and 43˚C, respectively (Verween 2007b, von Reshöft et al. 1961 as cited by Kennedy 2011a). Although survival is possible within these ranges, environments at the limits of favourable conditions are not suitable for reproduction (Verween et al. 2007b). Physiological tolerance of adult and larval stages to various chalk, nutrient and physical variables and invasion potential have been summarized by Mackie and Claudi (2010) (Table 2).

A temperature-salinity interaction was reported by Verween et al. (2007b) who observed higher survival rates at low salinities (5–10 PSU) when water temperature was high (30˚C) compared to lower temperatures (10˚C). Variation in salinity tolerance reported in the literature can also be attributed to high efficiency in hyperosmotic regulation, a typical adaptation of brackish water mussels (Verween et al. 2010).

5.5 PREDATORS

Various fishes, waterfowl and crab taxa were identified as predators of the Dark Falsemussel. *Mytilopsis leucophaeata* was present in the stomach content of Sheepshead (*Archosargus probatocephalus*), Pinfish (*Lagodon rhomboids*), and Blue Catfish (*Ictalurus furcatus*) (Gunter and Shell 1958, Odum and Heald 1972). Known waterfowl predators are Canvasback (*Aythya valisineria*), the Lesser

Scaup (*Aythya affinis*), Greater Scaup (*Aythaya marila*), and Ring-necked Duck (*A. collaris*) (Perry and Uhler 1982, 1988, Perry et al. 2007). Crab predators include Flatback Mud Crab (*Eurypanopeus depressus*), Harris Mud Crab (*Rhithropanopeus harrisii*), and Blue Crab (*Callinectes sapidus*) (Odum and Heald 1972, Milke and Kennedy 2001). Larvae planktonic stages are vulnerable to filter-feeding predators preying on planktonic larvae (e.g., ctenophores) (Purcell et al. 1991, Kennedy 2011a).

5.6 FEEDING AND DIET

Dark Falsemussels are filter-feeding organisms capable of ingesting particles as small as 4 μm (Verween et al. 2010). Phytoplankton is their principal nutritional source with occasional ingestion of detritus, bacteria, and organic matter (Verween et al. 2010). Stomach contents of 84 Dark Falsemussels were composed of inorganic particles (36%), vascular plant detritus (31%), epiphytic diatoms (7%) and phytoplankton (4%) (Odum and Heald 1972). A maximum filtration rate of 55 ml $mussel^{-1} \bullet h^{-1}$ was observed by Rajagopal et al. (2005) for 20 mm specimens at a temperature ranging between 20 ˚C and 35˚C. Filtration rate varied as a function of size and water temperature. Filtration rate increased with size, and maximum rates were observed at temperatures between 20˚C and 28˚C.

5.7 HABITAT REQUIREMENTS

Despite the native estuarine distribution of Dark Falsemussel (Kennedy 2011a), its broad environmental tolerance allow establishment in most brackish environments (Verween et al. 2010).

Dark Falsemussel attaches byssally to rocks, macrophytes, and wood debris in low densities (Jacobson 1953, Wolff 1969, Verween et al. 2010). The species can also attach to oysters, hydrozoans, tube worms, sponges, barnacles, mussels, clams, and snails (Conrad 1831, Gunter and Shell 1958, Koch 1989, Smith and Boss 1996, Oliver et al. 1998), or settle in the interstice of clumps formed by the Hooked Mussel (*Ischadium recurvum*) (Hinkley 1907). *Mytilopsis leucophaeata* also occasionally forms clusters on artificial surfaces such as sticks, bottles, pilings, walls, and water cooling installations (Oliver et al. 1998, Bamber and Taylor 2002, Verween et al. 2005, Kennedy 2011a).

5.8 PARASITES

Infection of the Dark Falsemussel by two parasites has been reported in the literature. *Mytilopsis leucopheata* infection from the flatworm, *Paravortex gemellipara* was first observed by Wardle (1980a) in Galveston Bay, USA. Wardle (1980a) noted that the incidence of the parasite seemed to be closely related to its host population density indicating high abundance of *M. leucopheata* might be required for their proliferation. Cross contamination with other host species, such as the Hooked Mussel, is possible where the two species coexist. Another parasite, *Proctoeces maculates*, a trematode species infecting fishes and molluscs, has been reported in 10 of 254 *M. leucopheata* specimens in Galveston Bay (Wardle 1980b). This parasite can have significant impacts on aquaculture species and was identified as the probable causative agent of a massive mortality of *Mytilus edulis* stocks in Laguna Veneta, Italy (Munford et al. 1981). However, its abundance seems to vary over time and no occurrence of the species has been recorded in Canada (Fisheries and Oceans Canada 2009).

6.0 PATHWAYS OF INTRODUCTION AND TRANSFER

Ballast water transfer and hull fouling have been the main vectors of Dark Falsemussel introduction and transfer to non-native regions (Smith and Boss 1996, Oliver et al. 1998, Bamber and Taylor 2002, Verween et al. 2005, Farrapeira et al. 2010). The high resistance of *M. leucopheata* larvae and post larvae to salinity levels as high as 32 PSU increases the probability of successful transfer, particularly in ballast water of high salinity (Siddall 1980, Therriault et al. 2004, Verween et al. 2010). Canal construction also represents a potential route of expansion of the species range. *Mytilopsis leucophaeata* planktonic larvae can disperse by passive movement through water current (Heiler et al. 2010) and by attaching to other organisms (e.g., waterfowl) (Johnson 1994). The Dark Falsemussel is thought to have been introduced into the Hudson River (NY) through its attachment to the Eastern Oyster (*Crassostrea virginica*), a species that has been moved around the world for open water oyster bed planting (Carlton and Mann 1996, Kennedy 2011a).

In 2007, Dark Falsemussel was found on a boat at an international border crossing into Saskatchewan (J. Shead, Manitoba Conservation and Water Stewardship and T. Johnston, Saskatchewan Ministry of the Environment, pers. comm.). Although the boat was cleaned and did not enter into natural waterbodies in Canada, the incidence brought into light the ability for this species to attach to watercraft, and raised questions about its potential to survive and establish in Canadian inland waters.

7.0 IMPACTS

The ecological effects of Dark Falsemussel population explosion in Chesapeake Bay were quantified by Bergstrom et al. (2009). The high filtration rates of *M. leucophaeata* increased water clarity markedly and resulted in the proliferation of submerged aquatic vegetation biomass due to increased light penetration. An increase in dissolved oxygen concentration was also observed due to a decline in the decomposition of planktonic algae. Little is known on other ecological impacts of Dark Falsemussel and further studies are required.

Some authors stipulated the ecological impact of *M. leucophaeata* is likely to be similar to that of Zebra Mussels (Verween et al. 2006, Sousa et al. 2009). *Dreissena polymorpha* has led to important food web perturbations and ecosystem shifts in its introduced range. The important filtering capacity of the species alters ecosystem energy flow by producing significant transfer of biomass from pelagic to benthic environments, and by reducing the proportion of energy available to the pelagic food web (MacIsaac et al. 1992, Gergs et al. 2009). High filtration rates also result in the alteration of phytoplankton and zooplankton assemblages by reducing abundance and altering species composition (Bastviken et al. 1998, Jack and Thorp 2000, Wilson 2003, Caraco et al. 1997). *Dreissena polymorpha* also have an important effect on light penetration by reducing water turbidity which results in an important increase in macrophyte biomass and overall benthic primary productivity (Zhu et al. 2006). Ultimately, Zebra Mussel invasions result in important ecosystems alterations and unavoidable biological regime shifts (Nicholls et al. 2011). Biofouling may also have an important impact on native unionid mussels which may lead to mortality and extirpation (Schlosser et al. 1996, Riccardi et al. 1998).

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Table 1. *Mytilopsis leucophaeata* development stages (adapted from Kennedy et al. 2011a).

	Development Stages		
0 days	Fertilization		Pelagic larvae
0.5 days	20% trochophores	< 63 µm	
1 day	Predominantly D-shaped veliger	50-91 µm	
4 days	Umbo in most larvae	109-150 µm	
9 days	Metamorphosed individuals present	220-480 µm	
15 days	Moving juveniles	> 580 µm	Benthic
	Adult		

Table 2. Survival and invasion potential of Dark Falsemussel in relation to chalk, nutrient and physical variables (from Mackie and Claudi 2010).

		No Potential for Adult Survival	**Little Potential for Larval Development**	**Good Potential for Long-term Survival**	**Good Potential for Long-term Survival**
		No potential for infestation	*Little potential for infestation*	*Moderate potential for infestation*	*High potential for infestation*
Chalk Variables	Calcium (mg Ca/L)	<8	8-12	12-30	30-120
	pH	<7.0, >9.5	7.0-7.8, 9.0-9.5	7.8-8.2 or 8.8-9.0	8.2-8.8
	Total alkalinity (mg $CaCO^3$/L)	<30	30-45	45-100	100-420
	Total hardness (mg $CaCO^3$/L)	<30	30-45	45-100	100-420
Nutrient Variables	Dissolved oxygen (mg/L) (% saturation)	<2	2-4	5-6	≥6
	Chlorophyll *a* (µg/L)	<5 or >25	5-10	10-20	20-25
	Total phosphorus (µg/L)	<10 or >50	10-25	25-35	35-50
	Total nitrogen (µg/L)	<150 or >750	150-375	375-525	525-750
	Secchi depth (m)	<0.5, >6	4-6	3.0-4.0	0.5-3.0
Physical Variables	Temperature (˚C)	<10, >30	10-13 or 28-30	15-20 or 24-28	20-24
	Conductivity (µS/cm), 25˚C	<450	450-3400	3400-6600	5100-15,400
	TDS (mg/L)	<300	300-2300	2300-4400	3400-10,300
	Salinity (mg/L)(ppt)	<0.2 or >30	0.2-2, 25-30	2-4, 12-25	5-12
	Turbidity (NTU)	>80	20-80	5-20	<5
	TSS (mg/L)	>96	28-96	8-28	<8

Figure 1. Dark Falsemussel (*M. leucophaeata*). (Photo credit: Francisco Welter Schultes, Zoologisches Institute).

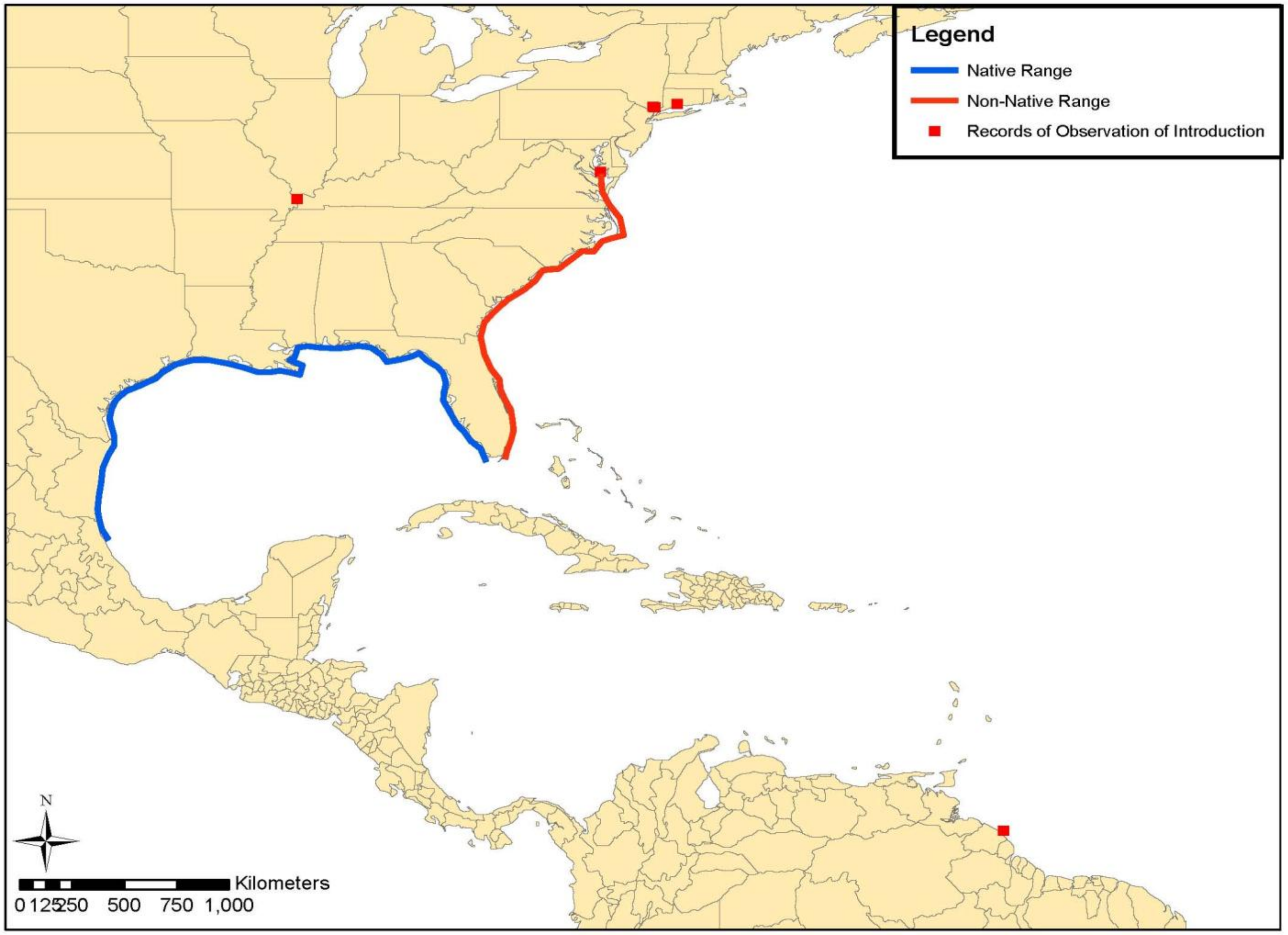

Figure 2. Native and non-native distribution of Dark Falsemussel in North and South America. Records of observation of introduction from: Redher (1937), Jacobson (1953), Koch (1989), Smith and Boss (1996), and de Souza (2005).

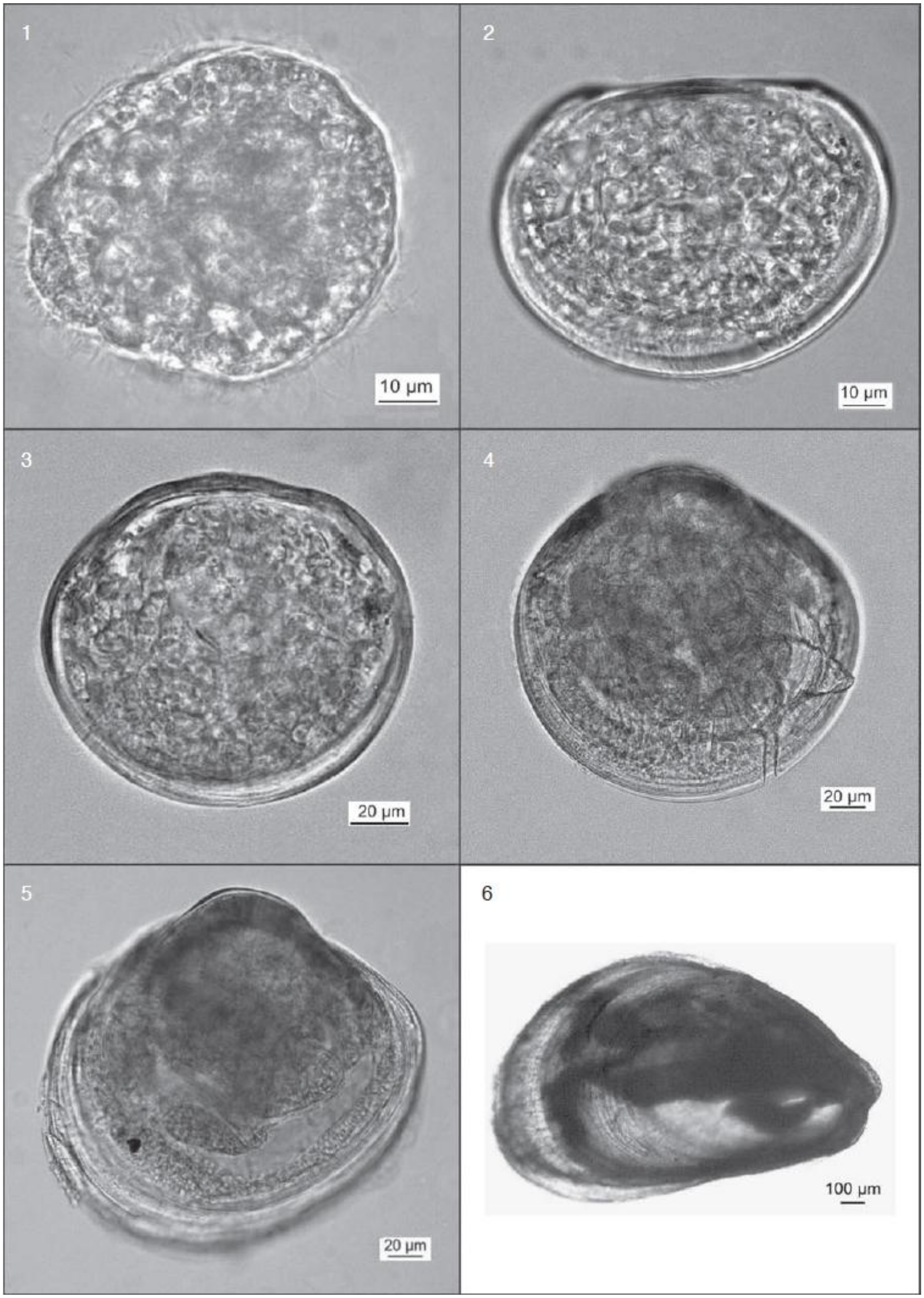

Figure 3. Larval stages of *Mytilopsis leucophaeata:* 1) trochophore; 2) D-shaped veliger; 4) pediveliger; 5) postveliger; and, 6) juvenile. (Photo credit: Annick Verween, Ghent University).