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Density and Abundance of the Freshwater Pearl Mussel, *Margaritifera margaritifera*, in the Kennebecasis River, New Brunswick and Evidence of Recent Recruitment

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Freshwater Pearl Mussel, *Margaritifera margaritifera* (L., 1758) populations are endangered or threatened throughout Europe, and those in eastern Canada are believed to be some of the most abundant populations remaining worldwide. Although *M. margaritifera* occurs widely in Atlantic Canada, there is little information to allow its conservation status in the region to be assessed or to place these populations in a global context. Using 0.25 m² survey quadrats, maximum densities of *M. margaritifera* in six mussel beds on the Kennebecasis River and a tributary in southeastern New Brunswick were found to range from 12 to 200 m⁻². Mean densities at the five mainstem sites ranged from to 1.9 m⁻² (SE±0.4) to 16.0 m⁻² (±4.3). Mean density on the tributary stream was 1.2 m⁻² (SE±0.7). Abundance of *M. margaritifera* at the six sites ranged from 4,536 (SE±2,600) to 55,520 (SE±14,768) and together the six mussel beds supported an estimated 161,315 Freshwater Pearl Mussels. The presence of juvenile *M. margaritifera* as small as 11.5 mm at the most upstream site, and Freshwater Pearl Mussels <30 mm at all sites, indicates that there had been recruitment of *M. margaritifera* juveniles in the Kennebecasis River in the 4–6 years prior to the 2007–2008 study.

Key Words: Margaritifera margaritifera; Freshwater Pearl Mussel; Eastern Pearlshell; freshwater mussels; conservation; density; abundance; Kennebecasis River; recruitment; New Brunswick; Canada

The Freshwater Pearl Mussel, Margaritifera margaritifera (also known as the Eastern Pearlshell), is one of 10 extant species of freshwater mussels that occur in New Brunswick (Martel et al. 2010). The species is holarctic in distribution (Bauer 1997) but has been extirpated from much of Europe, where it was previously abundant (Young and Williams 1983). Elsewhere, although adults remain plentiful in some regions, populations are declining. The Freshwater Pearl Mussel is now considered among the most endangered of aquatic organisms worldwide (Beasley et al. 1998; Strayer et al. 2004; Araujo et al. 2009; Thomas et al. 2010). Margaritifera margaritifera populations in the United States are vulnerable, imperiled, critically imperiled, or in need of assessment (Strayer and Jirka 1997; Young et al. 2001). While Canadian *M. margaritifera* populations appear to be secure, the species is in need of conservation assessment in Canada. Although juvenile M. margaritifera (<50 mm) have been reported in the Petitcodiac River, New Brunswick (Hanson and Locke (2001) and in the Rivière du Gouffre, Quebec (Martel and McAlpine 2007), demonstration of recent recruitment into Canadian populations of this exceedingly

long-lived, salmonid-dependant, species are generally lacking (Martel *et al.* 2010).

Explanations offered for the decline of M. margaritifera, and Unionacea more broadly, include past commercial and current illegal harvest for pearls, loss of host fish species, habitat alteration, and pollution (Young et al. 2001; Strayer et al. 2004; Geist 2010; Hastie et al. 2010). Climate change may prove to be a serious threat to the Freshwater Pearl Mussel in the near future, dependant as it is on coldwater fish hosts (Hastie et al. 2003). In North America, Atlantic Salmon (Salmo *salar*) is believed to be the main host species. However, other salmonids, including Brook Trout (Salvelinus fontinalis), Brown Trout (Salmo trutta) and Arctic Charr (Salvelinus alpinus) are also reported to serve as hosts (Smith 1976; Thomas et al. 2010; Thomas 2011), although North American evidence for such is limited (Smith 1976; Martel et al. 2010).

Accounts from the late 19th C of freshwater pearls collected from the Saint John River basin (Ganong 1889) indicate *M. margaritifera* populations in the region are long standing, and eastern Canadian populations of the species may represent some of the largest

remaining stocks (Martel and McAlpine 2007). Nonetheless, the study reported here appears to be the first to estimate density in a Canadian *M. margaritifera* population using standardized survey methods for freshwater mussels (Strayer and Smith 2003).

Our objectives were to characterize a sample of mussel beds (area, water depth, flow, substrate, associated species) supporting *M. margaritifera* within the Kennebecasis River system; to determine the density and abundance of *M. margaritifera* in these beds; to determine whether density varied among sites; and to assess whether recent recruitment of *M. margaritifera* has taken place in this population. This information will provide the basis for any future conservation monitoring of *M. margaritifera* in the Kennebecasis River.

Methods

Selection of study sites

The Kennebecasis River is located within the Saint John River basin in southeastern New Brunswick. It is a 5th order river that includes nine 4th order tributaries. The river drains a basin of 1,110 km² (Hansen and Bray 1993) and flows approximately 103 km from Hamilton Lake to where it enters the Saint John River at Boars

Head, west of Saint John (Figure 1). The head of freshwater tidal influence is at Bloomfield, Kings County. The Kennebecasis is not impounded, with most of the river flowing over a late Devonianearly Carboniferous sedimentary basin (Miller and Brazeau 2007; St. Peter and Johnson 2009).

Six study sites occupying the mid-reaches of the river from Penobsquis (most upstream) to above Bloomfield (most downstream) were selected based on a search of New Brunswick Museum specimen records and site visits to assess the presence of *M. margaritifera* (Figure 1, Table 1). With the exception of a few small beds of *M. margaritifera* 1–2 km upstream of Penobsquis, searches of >20 km of river channel upstream of Penobsquis to above Portage Vale revealed no additional mussel beds. However, we observed numerous mussel beds between Penobsquis and Sussex that we did not survey.

The river course spanning our study sites passes through agricultural lands (primarily pasture), although a narrow wooded riparian zone borders much of the river, particularly in its upper mid-reaches (Figure 2). Mussel beds were delineated by three people snorkeling the width of the stream in a diagonal, criss-cross pattern, working downstream. The boundaries of any

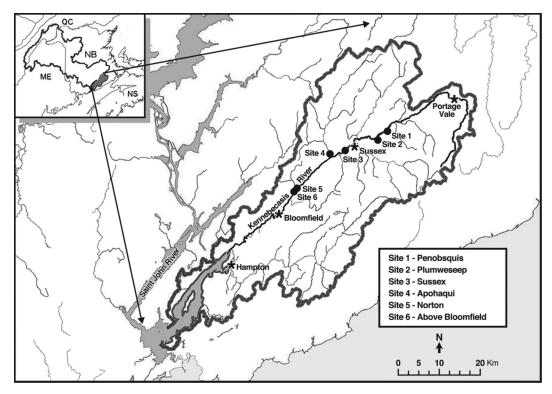


FIGURE 1. Map of the Kennebecasis River within the Saint John River basin (latter outlined in the inset map), New Brunswick, showing sites of *Margaritifera margaritifera* (Freshwater Pearl Mussel) sampling in 2007 and 2008. The Kennebecasis River drainage is outlined.

TABLE 1. *Margartifera margartifera* (Freshwater Pearl Mussel) beds at study sites on the Kennebecasis River, New Brunswick, in 2007 and 2008. Sites are arranged from most upstream (top) to most downstream (bottom). Site numbers are marked on Figure 1. Length of bed given is the maximum, width is the mean of four measures. Bed areas at Plumweseep and Above Bloomfield bed have been adjusted by subtracting areas of exposed vegetated islands that divided the bed. Bed areas are rounded to 3 significant figures.

Site	Latitude	Longitude	Length (m)	Width (m)	Area (m ²)	Mean water depth (m)	Mean Water velocity (m·s ⁻²)	Predominate substrate
Penobsquis	45.76461	-65.42220	169	15.3	2590	0.68	ND	cobble
Plumweseep	45.74147	-65.44705	200	17.8	3470	0.53	0.08	gravel
Sussex	45.72103	-65.54570	134	25.5	3420	0.50	0.28	cobble
Apohaqui*	45.70444	-65.59921	200	18.9	3780	0.28	0.10	sand/cobble
Norton	45.63615	-65.70009	150	37.9	5690	0.72	ND	cobble
Above Bloomfield	45.62853	-65.71112	200	42.3	6270	0.65	0.20	cobble

*On the Millstream River, a tributary of the Kennebecasis River



FIGURE 2. Most upstream (A: Penobsquis; 2007) and most downstream (B: Above Bloomfield; 2008) Margaritifera margaritifera (Freshwater Pearl Mussel) study sites on the Kennebecasis River, New Brunswick. Note the lack of forested riparian cover at the Above Bloomfield site. Photos: M. Sollows/NB Museum.

mussel bed located were considered to be 10 m beyond the first upstream and last downstream *M. margaritifera* sighted. Ten metres was chosen as a cut-off to allow for small gaps containing no mussels within a bed and follows the protocol used by Baird (2000) during study of the margaritiferid *Cumberlandia monodonta* (Spectaclecase).

Three mussel beds (Penobsquis, Sussex and Norton) were sampled from May to September 2007 and three beds (Plumweseep, Apohaqui and Above Bloomfield) were sampled from June to September 2008. Five of the sites were located on the mainstem of the Kennebecasis River, while the Apohaqui bed was located on the Millstream River, a tributary of the Kennebecasis.

Mussel bed characteristics

Individual beds were characterized on the basis of area (maximum length × width at 30 m intervals along the bed length, minus any exposed vegetated islands that divided the bed), mean water depth taken at the mid-point of 60 0.25 m² sampling quadrats (n = 60 samples for each bed), and mean water velocity taken at three points through the water column with a digital flowmeter (Model 6597 Flowatch flow meter, JDC Electronics SA, Waadt, Switzerland) at the mid-point

of each quadrat from ~5 cm above the substrate vertically to the surface (n = 180 samples for each bed). The predominant substrate type for 105 of the 169 quadrats that contained *M. margaritifera* was visually characterized as silt (<0.5 mm), sand (0.5–2 mm), gravel (2–4 mm), cobble (64–256 mm), or boulder (>256 mm). Substrates >4 mm and <64 mm were not present in quadrats occupied by *M. margaritifera*.

Sampling for Freshwater Pearl Mussels

Mussel beds were sampled using 0.25 m^2 quadrats, the recommended standard for surveys of freshwater mussels (Strayer and Smith 2003; Pooler and Smith 2005). Sixty randomly placed 0.25 m^2 quadrats (95% confidence interval with a desired precision of 30%) were searched at each of six beds (N = 360) to estimate the mean number of individuals in each mussel bed. The 30% precision rate was chosen as an intermediate level between the 25% precision that Dunn (2000) recommended for large rivers and the 50% precision she recommended for small streams.

Quadrats were surveyed for mussels by snorkeling (where water depth was <1 m) or by SCUBA (depths >1 m). Mussels visible at the substrate surface were removed from each quadrat and placed in a mesh bag. The entire quadrat was then excavated on the bottom by hand or with a metal scoop to a depth of 15 cm, and the substrate sorted through a quadrat-sieve fitted with 5 mm diameter screen (McAlpine and Sollows *in press*). Additional hand-held sieves (screen size 5 mm diameter) were also used where water velocity was low.

We followed Hastie and Cosgrove (2002) and accepted the presence of *M. margaritifera* <30 mm in length as evidence of recent juvenile recruitment and we used the approach of Hendelberg (1961) to estimate the age of juvenile mussels. Hendelberg (1961) reports that external annuli on the untreated surface (i.e. periostracum intact) of *M. margaritifera* shells can be counted (one increment = 1 year) and used to age mussels up to 15 years.

Statistical analyses

All data were examined for normality and equality of variance. The density of occurrence of Freshwater Pearl Mussels among sites was tested by non-parametric Kruskal-Wallis since the data were not normally distributed. Densities and abundances are reported as the mean and standard error of the mean (SE). Analyses were carried out using SYSTAT 11.0 (Systat Software, Inc., Chicago, Illinois).

Results

Mussel bed characteristics

The six mussel beds ranged from 2590 to 6270 m² and extended over as much as 200 m of the length of the stream channel. Mean water depth over beds during the sampling period ranged from 0.28 to 0.72 m and mean water velocity from 0.08 to 0.28 m s⁻¹ (Table 1). Quadrats in which *M. margaritifera* were present were dominated by cobble (Pearson χ^2 = 82.092, df = 25, *P* < 0.001), but *M. margaritifera* also occurred commonly on gravel and sand substrates; *M. margaritifera* were least common in quadrats dominated by silt or boulders. At three of the study sites (Apohaqui, Norton and Above Bloomfield) four additional mussel species were found in association with *M. margaritifera; Alasmidonta undulata, Anodonta implicata, Elliptio complanata,* and *Pyganodon cataracta.*

Density and abundance

Overall, 650 *M. margaritifera* were found on the Kennebecasis mainstem and Millstream River tributary, with 46.9% (n=169) of quadrats occupied by Freshwater Pearl Mussels. However, the percentage of quadrats occupied by *M. margaritifera* among sites was highly variable, ranging from 13.3% at Apohaqui to 60.0 % at Norton (Table 2). As expected, *M. margaritifera* were not evenly distributed across beds but were clumped, with maximum densities ranging from 12 to 200m⁻² (Table 2). Mean density of *M. margaritifera* was highest at Plumweseep (16.0 m⁻² (SE±4.3)) and lowest at Apohaqui (1.2 m⁻² (SE±0.7)), the tributary site.

There was no difference in the average density of *M.* margaritifera among beds at Penobsquis, Plumweseep, Sussex and Norton (P = 0.065, Kruskal-Wallis = 7.225, df = 3), the four most upstream mainstem sites. However, there were significant differences between sites when Above Bloomfield (P = 0.001, Kruskal-Wallis = 18.749, df = 4) or Above Bloomfield and Apohaqui, the most downstream mainstem and tributary sites respectively, were included (P = 0.001, Kruskal-Wallis = 20.888, df = 5). Our estimates of mean density suggest that the six mussel beds investigated on the Kennebecasis River system supported ~161,315 *M.* margaritifera, ranging from a low of 4,536 (SE±2,600) at Apohaqui to a high 55,520 (SE±14,768) at Plumweseep.

Recruitment

All live *M. margaritifera* <30 mm in length in the Kennebecais River were found completely buried, demonstrating the necessity of excavation to establish recruitment. Evidence of recent recruitment of *M. margaritifera* was detected at all six study sites, with

TABLE 2. Summary of *Margaritifera margaritifera* (Freshwater Pearl Mussel) density (number m⁻²), estimated abundance, and associated data at sampling locations along the mid-reach of the Kennebecasis River, New Brunswick in 2007 and 2008. Sites are arranged from most upstream (left)to most downstream (right). Total number of *M. margaritifera* encountered in the 60 0.25 m² quadrats sampled at each mussel bed is shown as *n*. The percentage of quadrats occupied by *M. margaritifera* at each site is shown as Percentage of quadrats occupied. Densities of *M. margaritifera* are reported as the mean number across the 60 quadrats and standard error of the mean with the minimum, maximum, and median in parentheses. Abundance is the estimated total/bed with standard error of the mean. See Table 1 for total areas of individual mussel beds. N = <30 mm refers to the number of individual *M. margaritifera* <30 mm total length in each bed and follows Hastie and Cosgrove (2002) as evidence of recent juvenile recruitment.

	Penobsquis (n=135)	Plumweseep (n=240)	Sussex (n=139)	Apohaqui* (n=18)	Norton (n=89)	Above Bloomfield (n=29)
% occupied Density	53.3 9.0±1.7 (0,52,4)	55.0 16.0±4.3 (0,200,4)	51.7 9.3±2.0 (0,68,4)	13.3 1.2±0.7 (0,40,0)	60.0 6.0±0.9 (0,24,4)	48.3 1.9±0.4 (0,12,0)
Abundance $N < 30 \text{ mm}$	23,310±4,434 22	55,520±14,768 14	31,696±6,771 8	4,536±2,600 1	34,140±5,258 2	12,113±2,633 1

*On the Millstream River, a tributary of the Kennebecasis River

the smallest *M. margaritifera*, collected at Penobsquis, being 11.5 mm total length. External annuli on the shells of Kennebecasis River *M. margaritifera* of <30 mm shell length suggest these mussels are 4–6 years of age.

However, recruitment appeared to be uneven. The greatest number of *M. margaritifera* <30 mm total length across the 60 quadrats per site sampled were found at the most upstream study sites (Penobsquis, Plumweseep, Sussex; n = 22, 14, 8 respectively). Only 1 or 2 Freshwater Pearl Mussels <30 mm were collected at each of the other three sites downstream (Table 2).

Discussion

Study sites and mussel bed characteristics

Many North American rivers have been impounded and this has had a deleterious effect on numerous freshwater mussel populations and distributions and those of their fish hosts (Vaughn and Taylor 1999). The lack of impoundments on the Kennebecasis River has been important in ensuring the persistence of the *M. margaritifera* population on this river, even in the face of serious declines in Atlantic Salmon stocks in the Saint John River basin (Cunjack and Newbury 2005).

Mean water velocities recorded at mussel beds on the Kennebecasis River (0.08 to 0.28 m·s⁻¹) were comparable to optimum current velocities reported for M. margaritifera habitat in Europe (0.25--0.75 m·s⁻¹; Hastie et al. 2000b and references cited therein). The presence of *M. margaritifera* is often reported to be associated with low water depth (Gittings et al. 1998; Morales et al. 2004). However, the mean summer water depths over mussel beds in the Kennebecasis River (0.28–0.72 m) in 2007 and 2008 were lower than the optimum (0.3-0.4 m) computed from habitat suitability curves for this species (Hastie et al. 2000a), suggesting that drier summers could pose a threat to at least some of the M. margaritifera population in the Kennebecasis River. Hastie et al. (2003) identified changing weather patterns leading to prolonged dry periods as a threat to Margaritifera populations.

Many investigators report the preference of *M.* margaritifera for sandy, gravelly, or cobble bottoms (Nedeau et al. 2000; Martel et al. 2010) and Hastie et al. (2000a) found *M.* margaritifera density more closely related to characteristics of the substrate than other features. Although *M.* margaritifera on the Kennebecasis River occurred most frequently in quadrats dominated, in descending order, by cobble, gravel, or sand, and although Freshwater Pearl Mussels appeared to avoid areas of boulder bottom, there is evidence that mussel beds occur where sediments are relatively stable. Boulders in a watercourse may play an important role in providing this stability (Layzer and Madison 1995; Strayer 1999).

Geist and Auerswald (2007) found that stream beds in which the interstitial spaces of the substrate had become clogged with mud, and subsequently compacted, were unsuitable for *M. margaritifera*. This emphasizes the importance of controlling sedimentation in the Kennebecasis River from upstream agricultural and forestry operations and the value of maintaining forested riparian zones.

Density

Maximum densities of *M. margaritifera* for each of the six beds in this study (12 to 200 m⁻²) are within the range of 10–50⁺ m⁻², categorized as high by Martel and McAlpine (2007), but much lower than historic densities reported by others. Densities of 400 m⁻² are cited for Scottish streams in the mid-1980s and it is speculated that historic densities exceeded 1000 m⁻² (Bauer 1987). Hanson and Locke (2001) surveyed freshwater mussel species at various sites on the Petitcodiac River (New Brunswick) and categorized *M. margaritifera* as "abundant" (>1 mussel m⁻²) at only 13% of 52 sites examined.

Mean densities of M. margaritifera have been reported to be highly variable among sites, even within a single river (Outeiro et al. 2008; Hastie et al. 2010). Hastie et al. (2004) considered mussel densities >1 m⁻² as indicative of "optimal mussel habitat". According to Young et al. (2003), densities of Freshwater Pearl Mussels >10 m⁻² indicate conditions favorable for the viability of *M. margaritifera* beds (i.e. for producing juveniles). While this might suggest that only the Plumweseep bed of the six mussel beds studied is viable, the presence of *M. margaritifera* <30 mm at all sites suggests this is not the case. Mean densities of M. margaritifera in two Iberian streams ranged from 0.27 to 6.55 m⁻² (Outeiro et al. 2008). Although these densities are relatively low compared to densities recorded in Scotland (1.8-37.4 m⁻²; Hastie et al. 2010) and Sweden (maximum ~ 24 m⁻² Arvidsson et al. 2012), populations in the Spanish streams were judged to be viable. Given that the lowest mean density/bed recorded in the Kennebecasis River system was 1.2 m⁻² (Apohaqui) and the mean density at most sites was much higher, density alone would suggest that the M. margaritifera population in the Kennebecasis River is viable.

Arvidsson et al. (2012) surveyed 107 streams in Sweden and estimated total population sizes of M. margaritifera of 50-290,000 in individual streams, with a mean abundance of 27,281/stream (SE±5,383). While Arvidsson et al. (2012) found that mussel density was more important to recruitment than the density of host fish, population size in itself seems to be a poor predictor of recruitment in the Freshwater Pearl Mussel. Recruiting populations in Swedish streams had as few as 100 individuals and non-recruiting populations as many as 252,000 M. margaritifera. While it is not possible to provide an estimate of the total number of M. margaritifera in the entire Kennebecasis River, the estimate of ~161,315 for the six beds surveyed (extrapolated from the 15 m² sampled in each bed ($60 \times 0.25 \text{ m}^2$) to the entire bed) is well above the mean reported by Arvidsson et al. (2012) for Swedish streams.

Recruitment

Small *M. margaritifera* are notoriously difficult to find in the field (Young and Williams 1984; Hastie and Cosgrove 2002; Hastie *et al.* 2010) and individuals <10 mm, although present, may not be detected even with sieving (Hastie *et al.*, 2000a; Young *et al.*, 2001). Although Hastie *et al.* (2010) were able to detect *M. margaritifera* as small as 6 mm, Hastie and Cosgrove (2002) experimentally demonstrated a size-specific sampling bias towards Freshwater Pearl Mussels >50 mm. Hastie *et al.* (2010) found considerable withinriver variation in recruitment levels among sites, findings that seem to agree with ours.

As Hanson and Locke (2001) have noted, populations of non-reproducing *M. margaritifera* can persist for decades in this exceedingly long-lived species. Although many eastern Canadian rivers appear to host sizable populations of *M. margaritifera*, there are few data confirming recent recruitment in these rivers. Arvidsson *et al.* (2012) defined recruiting *M. margaritifera* populations as those where at least one mussel <50 mm was found, implying that recruitment had occurred in the last 15–20 years. On this basis, our data provide ample evidence that recent recruitment has occurred at all six sites sampled on the Kennebecasis River.

In conclusion, the population of *M. margaritifera* in the Kennebecasis River shows evidence of recent recruitment and densities of the Freshwater Pearl Mussel suggest a viable population. However, ensuring the persistence of *M. margaritifera* in the river in the future will require continuing attention to streamside habit so that host fish populations do not decline, sedimentation does not become a problem, and summer water temperatures do not increase. Considering that *M. margaritifera* is at risk globally, and the potential importance of eastern North American populations, determining the viability of the Freshwater Pearl Mussel in other salmonid river systems in eastern Canada should be a priority.

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Literature Cited

- Araujo, R., C. Toledo, D. Van Damme, M. Ghamizi, and A. Machordom. 2009. *Margaritifera marocana* (Pallary, 1918): a valid species inhabiting Moroccan Rivers. Journal of Molluscan Studies 75: 95–101.
- Arvidsson, B. L., J. Karlsson, and M. E. Österling. 2012. Recruitment of the threatened mussel *Margaritifera margaritifera* in relation to mussel population size, mussel density and host density. Aquatic Conservation: Marine and Freshwater Ecosystems 22: 526–532.

- Baird, M. 2000. Life history of the Spectaclecase, *Cumberlandia monodonta* Say, 1829 (Bivalvia, Unionoidea, Margaritiferidae). M.Sc. thesis. Biology Department, Southwest Missouri State University, Springfield, Missouri.
- Bauer, G. 1987. Reproductive strategy of the Freshwater Pearl Mussel, *Margaritifera margaritifera*. Journal of Animal Ecology 56: 691–704.
- Bauer, G. 1997. Host relationships at reversed generation times: *Margaritifera* (Bivalvia) and salmonids. Ecological Studies 130: 69–79.
- Beasley, C. R., D. Roberts, and T. G. Mackie. 1998. Does the Freshwater Pearl Mussel, *Margaritifera margaritifera* L., face extinction in Northern Ireland? Aquatic Conservation: Marine and Freshwater Ecosystems 8: 265–272.
- Cunjack, R. A., and R. W. Newbury. 2005. Atlantic coast rivers of Canada. Pages 939–980, *in* Rivers of North America. *Edited by* A. C. Benke and C. E. Cushing, Elsevier Academic Press, Boston, Massachusetts.
- Dunn, H. L. 2000. Development of strategies for sampling freshwater mussels (Bivalvia: Unionidae). Pages 161–167 *in* Proceedings of the First Freshwater Mollusk Conservation Society Symposium, Chattanooga, Tennessee, in 1999, Part II of Freshwater Mollusk Symposium Proceedings. *Edited by* R. A. Tankersley, D. I. Warmolts, G. T. Watters, B. J. Armitage, P. D. Johnson and R. S. Butler. Ohio Biological Survey, Columbus, Ohio. xxi + 274 pages.
- Ganong, W. F. 1889. Economic mollusca of Acadia. Bulletin of the Natural History Society of New Brunswick 7: 6–14.
- Geist, J. 2010. Strategies for the freshwater conservation of endangered Freshwater Pearl Mussels (*Margaritifera margaritifera* L.): a synthesis of conservation genetics and ecology. Hydrobiologia 644: 69–88.
- Geist, J., and K. Auerswald. 2007. Physiochemical stream bed characteristics and recruitment of the Freshwater Pearl Mussel (*Margaritifera margaritifera*). Freshwater Biology 52: 2299–2316.
- Gittings, T., D. O'Keefe, F. Gallagher, J. Finn, and T. O'Mahony. 1998. Longitudinal variation in abundance of a Freshwater Pearl Mussel, *Margaritifera margaritifera*, population in relation to riverine habitats. Biology and Environment: Proceedings of the Royal Irish Academy 98B: 171–178.
- Hanson, D., and D. I. Bray. 1993. Single-station estimates of suspended sediment loads using sediment rating curves. Canadian Journal of Civil Engineering 20: 133–143.
- Hanson, J. M., and A. Locke. 2001. Survey of freshwater mussels in the Petitcodiac River drainage, New Brunswick. Canadian Field-Naturalist 115(2): 329–340.
- Hastie, L. C., and P. J. Cosgrove. 2002. Intensive searching for mussels in a fast-flowing river: an estimation of sampling bias. Journal of Conchology 37: 309–316.
- Hastie, L. C., P. Boon, and M. R. Young. 2000a. Physical microhabitat requirements of Freshwater Pearl Mussels, *Margaritifera margaritifera* (L.). Hydrobiologia 429: 59– 71.
- Hastie, L. C., M. R. Young, and P. Boon. 2000b. Growth characteristics of Freshwater Pearl Mussels, *Margaritifera margaritifera* (1.) Freshwater Biology 43: 243–256.
- Hastie, L. C., P. J. Cosgrove, and M. J. Gaywood. 2003. The threat of climate change to Freshwater Pearl Mussel populations. Ambio 32: 40–46.
- Hastie, L. C., S. L. Cooksley, F. Scougall, M. R. Young, P. J. Boon, and M. J. Gaywood. 2004. Applications of extensive survey techniques to describe Freshwater Pearl Mussel distribution and macrohabitat in the River Spey, Scotland. River Research and applications 20: 1001–1013.

- Hastie, L. C., E. C. Tarr, B. al-Mousawi, and M. R. Young. 2010. Medium-term recruitment patterns in Scottish Freshwater Pearl Mussel, *Margaritifera margaritifera*, populations. Endangered Species Research 11: 21–33.
- Hendelberg, J. 1961. The Fresh-water Pearl Mussel, Margaritifera margaritifera (L.). Report of the Institute of Freshwater Research Drottningholm 4: 149–171.
- Layzer, J.B. and L.M. Madison. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. Regulated Rivers: Research and Management 10: 329–345.
- Martel, A. L., and D. F. McAlpine. 2007. Freshwater bivalves in North America — Assessing the conservation status of the Eastern Pearlshell, *Margaritifera margaritifera* (Linnaeus, 1758), in Canada: the need to examine recruitment success among rivers. Tentacle: Newsletter of the Mollusc Specialist Group, Species Survival Commission, IUCN (World Conservation Union) 15: 18–19.
- Martel, A. L., D. F. McAlpine, J. Madill, D. L. Sabine, A. Paquet, M. Pulsifer, and M. Elderkin. 2010. Freshwater mussels (Bivalvia: Margaritiferidae, Unionidae) of the Atlantic Maritime Ecozone. Pages 551–598 in Assessment of Species Diversity in the Atlantic Maritime Ecozone *Edited by* D. F. McAlpine and I. M. Smith. NRC Research Press, Ottawa, Ontario.
- McAlpine, D. F., and M. C. Sollows. In press. A quadratsieve system for sampling freshwater unionoids using SCUBA. Northeastern Naturalist.
- Miller, R. F., and M. D. Brazeau. 2007. A late Devonian Porolepiform fish (*Holoptychius*) and the age of the Kennebecasis Formation, southern New Brunswick, Canada. Atlantic Geology 43: 187–196.
- Morales, J. J., A. I. Negro, M. Lizana, A. Martinez, and J. Palacios. 2004. Preliminary study of the endangered populations of Pearl Mussel, *Margaritifera margaritifera*, in the River Tera (north-west Spain): habitat analysis and management considerations. Aquatic Conservation: Marine and Freshwater Ecosystems 14: 587–596.
- Nedeau, E. J., M. A. McCollough, and B. I. Swartz. 2000. The freshwater mussels of Maine. Maine Department of Inland Fisheries and Wildlife, Augusta, Maine.
- Outeiro, A., P. Ondina, C. Fernandez, R. Amaro, and E. San Miguel. 2008. Population density and age structure of the Freshwater Pearl Mussel, *Margaritifera margaritifera*, in two Iberian rivers. Freshwater Biology 52: 485–496.
- Pooler, P. S., and D. R. Smith. 2005. Optimal sampling design for estimating spatial distribution and abundance of a freshwater mussel population. Journal of the North American Benthological Society 24: 525–537.
- Smith D. G. 1976. Notes on the biology of *Margaritifera* margaritifera (L.) in central Massachusetts. American Midland Naturalist 96: 252–256.

- St. Peter, C. J., and S. C. Johnson. 2009. Stratigraphy and structural history of the late Paleozoic Maritimes Basin in southeastern New Brunswick, Canada. New Brunswick Department of Natural Resources; Mineral Policy, and Planning Division, Memoir 3, 348 pages.
- Strayer, D. L. 1999. Use of flow refuges by unionid mussels in rivers. Journal of the North American Benthological Society 12: 236–246.
- Strayer, D. L., and K. J. Jirka. 1997. The pearly mussels of New York State. New York State Education Department, Albany, New York.
- Strayer, D. L., J. A. Downing, W. R. Haag, T. L. King, J. B. Layzer, T. J. Newton, and S. J. Nicholos. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. BioScience 54: 429-439.
- Strayer, D. L., and D. R. Smith. 2003. A guide to sampling freshwater mussel populations. American Fisheries Society Monograph 8, American Fisheries Society, Bethesda, Maryland. 103 pages.
- Thomas, G. R. 2011. Conservation ecology of the endangered Freshwater Pearl Mussel, *Margaritifera margaritifera*. Ph.D. thesis, University of Swansea, Wales.
- Thomas, G. R., J. Taylor, and C. Garcia de Leaniz. 2010. Captive breeding of the endangered Freshwater Pearl Mussel, *Margaritifera margaritifera*. Endangered Species Research 12: 1–9.
- Vaughn, C. C., and C. M. Taylor. 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. Conservation Biology 13: 912–920.
- Young, M., and J. Williams. 1983. The status and conservation of the Freshwater Pearl Mussel, *Margaritifera margaritifera* Linn. in Great Britain. Biological Conservation 25: 35–52.
- Young, M. and J. Williams. 1984. The reproductive biology of the Freshwater Pearl Mussel, *Margaritifera margaritifera* (Linn.) in Scotland I. Field Studies. Archives of Hydrobiology 99: 405–422.
- Young, M. R., P. J. Cosgrove L. C. Hastie, and B. Henniger. 2001. A standardized method for assessing the status of freshwater mussels in clear, shallow rivers. Journal of Molluscan Studies 67: 395–396.
- Young, M. R., L. C. Hastie, and S. L. Cooksley. 2003. Monitoring the Freshwater Pearl Mussel, *Margaritifera margaritifera*. Conserving Natura 2000 Rivers Monitoring Series No. 2, Published by Life in UK Rivers (English Nature, the Countryside Council for Wales, the Environment Agency, the Scottish Environment Protection Agency, Scottish Natural Heritage, and the Scotland and Northern Ireland Forum for Environmental Research) and distributed by English Nature, Peterborough.

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