

NOTE

ARE PARASITES AND DISEASES CONTRIBUTING TO THE DECLINE OF FRESHWATER MUSSELS (BIVALVIA, UNIONIDA)?

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ABSTRACT

Freshwater mussels (Mollusca: Bivalvia: Unionida) consist of 843 species in six families, but many are imperiled. Significant causes of mussel declines include contaminants and loss of substrate. Potentially, etiological agents are also contributing factors, but parasites and pathogens of freshwater mussels are understudied relative to those affecting marine bivalves. Published accounts of viral pathogens have been reported exclusively from *Hyriopsis cumingii* (Unionidae) in China. There are limited records of possible bacterial and fungal pathogens from unionids in the USA and Finland. Parasitic and commensal organisms generally include ciliates (Ciliophora), trematodes (Platyhelminthes: Aspidogastrea and Digenea), roundworms (Nematoda), moss animals (Ectoprocta, Entoprocta), oligochaetes and leeches (Annelida: Sedentaria: Clitellata), mites (Arthropoda: Acari), copepods (Arthropoda: Copepoda), insects (Arthropoda: Insecta), and fish eggs (Chordata: Actinopterygii). Parasites injure the host through attachment or feeding or when they invade host tissue to complete their life cycles (e.g., digeneans). Commensals are small organisms living in or on mussels that may use the mantle cavity or shell as a refuge or substrate, and commensals also may feed on particulates that have been gathered by their molluscan host. Typically, however, the relationship between the two parties is subject to speculation (e.g., leeches). We are in the midst of a biodiversity crisis, and this minireview highlights the relationships among these organisms and the need to understand the health of wild and captive mussels.

KEY WORDS: freshwater mussels, Unionida, parasites, diseases, gross pathology, histopathology

Freshwater mussels are a globally distributed group of about 843 species in six families (Graf and Cummings 2007; Williams et al. 2017). Approximately 29 species have gone extinct in the USA as a result of human activities and many other mussel species have declining populations (Haag 2012).

These declines are thought to result primarily from human activities that fall into one of four general categories. The first includes activities (such as dam construction) that change the physical habitat of rivers and lakes. The second includes activities that contaminate the benthos with chemical and physical waste from industrial and municipal sources (e.g., Hornbach 2001; Grabarkiewicz and Davis 2008). The third category is the extensive harvesting of mussels for the button and pearl industries, which has contributed to declines in some species, especially in the USA (Haag 2012). The fourth category is the introduction of nonnative aquatic molluscs, such as the zebra mussel (*Dreissena polymorpha*) or Asian clam (*Corbicula fluminea*), which compete with native mussels for food and available substrate or which foul waters, harming indigenous species (Cummings and Graf 2010). Additionally, nonnative molluscs potentially can introduce nonnative etiological agents that might negatively affect native molluscs (Prenter et al. 2004). Although we lack data on the presence of nonnative etiological agents in freshwater mussels, *Perkinsus marinus* and *Haplosporidium nelsoni* are good examples of introduced pathogens that have affected significantly the USA marine shellfish industry (Bureson and Ford 2004; Villalba et al. 2004). Because of declining populations and mass mortality events known as “die-offs” and “mussel kills,” the health of wild and hatchery-reared mussels is a growing concern (Neves 1987; Fleming et al. 1995; Lydeard et al. 2004).

In an effort to shed light on the possibility of etiological agents as causative factors of mussel declines, Grizzle and Brunner (2009) reviewed the literature regarding parasites and infectious diseases reported from freshwater bivalves. Most of the cited literature are observations of single-celled eukaryotic organisms and metazoans that may engage in either a commensal or parasitic relationship with unionids or margaritiferids in North America and Europe. The other four families in Unionida are underrepresented in the parasite and disease

literature. Additionally, there appears to be almost no peer-reviewed literature on viral, bacterial, or fungal infections in freshwater mussels. A few exceptions include reports of RNA and DNA viruses infecting the digestive system of *Hyriopsis cumingii* in China (Grizzle and Brunner 2009; Lei et al. 2011). In 1931 mussel propagation personnel reported “adult mussels became sterile through bacterial attacks on larval mussels” (Pritchard 2001). Intracellular microorganisms have been observed in histological sections of the digestive gland of *Elliptio complanata* in the USA, but it was unclear if they were prokaryotic or eukaryotic (see Fig. 5 in Chittick et al. 2001). Fungal hyphae were observed in the marsupia of *Unio pictorum*, *U. tumidus* (Pekkarinen 1993a), and *Pseudoanodonta complanata* in Finland (Pekkarinen 1993b). These latter three studies or observations appear to have been overlooked by Grizzle and Brunner (2009). It is possible that some parasite or disease records may be missed because they appear in literature in which characterizing parasites or diseases was not the primary objective, such as reports on surveys that detail population or community structure. Pekkarinen (1993a) reported fungi and ciliates in the marsupium associated with degenerating glochidia, but it was unclear if the fungi were pathogenic or saprophytic. Overall, parasitic or commensal organisms have been reported primarily in wild mussels; there is little information about disease problems that may occur in a hatchery.

Ciliates (Ciliophora), trematodes (Platyhelminthes: Aspidogastrea, and Digenea), moss animals (Ectoprocta, Entoprocta), roundworms (Nematoda), oligochaetes and leeches (Annelida: Sedentaria: Clitellata), mites (Arthropoda: Acari), copepods (Arthropoda: Crustacea: Copepoda), insects (Arthropoda: Insecta), and fish eggs (Chordata: Actinopterygii) are associated with the soft tissues or shells of freshwater mussels (Grizzle and Brunner 2009; Wisniewski et al. 2013). Aspidogastreans, digeneans, nematodes, mites, insect larvae, and fish eggs either infect mussels or have been reported as injurious agents. Interestingly, the eggs of both mites (*Najadicola ingens*) and fishes (*Rhodeus sericeus*) sometimes may obstruct the water tubes of a marsupium and prevent or hinder the development of glochidia (Stadnichenko and Stadnichenko 1980; McElwain et al. 2016 and references therein). Ciliates, oligochaetes, leeches, insect larvae, and copepods have been found in the mantle cavity of mussels, but the relationship between these organisms and their hosts is poorly understood. Perhaps their presence was not associated with tissue damage or perhaps the authors did not provide many supporting details concerning injuries. For example, the larvae of several midge species (Chironomidae) have been found in the mantle cavity of unionids (Roback et al. 1979). Some species, such as *Baeoctenus bicolor*, appear to injure gill and mantle tissue, whereas others, such as *Orthocladus doreus*, do not (Gordon et al. 1978; Roback et al. 1979). Other noteworthy examples include the observations of Antipa and Small (1971). Transmission electron microscopy revealed the remnants of unionid gill cells in the food vacuoles of *Conchophthirus curtus*, but there was no evidence of tissue

damage associated with attached ciliates. Curiously, Coker et al. (1921) reported *Chaetogaster limnaei* feeding on mussel parasites but provided no other supporting details. Overall, few studies have used light or electron microscopy to document the pathological changes to tissues associated with pathogens, parasites, or commensals.

Since the publication of the work of Grizzle and Brunner in 2009, a few noteworthy studies have been published regarding parasites in freshwater mussels. Levine et al. (2009) reported *Gomphus militaris* (Arthropoda, Insecta, Odonata) as potentially feeding on the gills of *Popenaias popeii* (Unionidae), a critically endangered species restricted to two populations in the Rio Grande basin (Carman 2007). Some mussels were missing the entire outer gills or all four gills. It is unclear how often odonates occur in the mantle cavity of mussels, as there appears to be no other literature on this topic (Grizzle and Brunner 2009). Lopes et al. (2011) found third-stage larvae of *Hysterothylacium* sp. (Nematoda, Anisakidae) in the pericardial cavity of *Diplodon suavidicus* (Hyriidae) in Brazil and presented photographs of nematodes coiled in the pericardial cavity. In the early 20th century, *Ascaris* sp. or *Ascaris*-like worms were reported in the digestive tract of unspecified unionids in the USA, but there were no accompanying species descriptions, no information about pathology, and no indication that any specimens were deposited in a museum (Clark and Wilson 1912; Wilson and Clark 1912; Coker et al. 1921). McElwain et al. (2016) described histopathological changes associated with the eggs and larvae of *Unionicola* sp. from *Strophitus connasaugaensis* and provided a literature review regarding pathologies associated with *Unionicola* spp. in unionids. Similarly, Abdel-Gaber et al. (2018) described injuries to the tissues of *Coelatura aegyptiaca* (Unionidae), *Mutela rostrata*, and *Chambardia rubens* (Mutelidae) associated with eggs and larvae of *Unionicola tetrafurcatus*. Müller et al. (2015) described histopathological changes to the gonad and hepatopancreas associated with *Rhipidocotyle campanula* and *Phyllodistomum* sp. Few studies have demonstrated tissue damage associated with digeneans in unionids.

Parasite-induced pearl formation, shell deformities, and neoplasms received little or no treatment by Grizzle and Brunner (2009). Mussels may form pearls in response to digeneans (Clark and Wilson 1912; Wilson and Clark 1912; Gentner and Hopkins 1966; Hopkins 1934), mites (Dallas 1858; Baker 1928; Edwards and Vidrine 2013), and midge larvae (Forsyth and McCallum 1978; Pekkarinen 1993a), and pearls may occur in various soft tissues, especially the mantle. Interestingly, some small organisms can become embedded in the nacre or may otherwise cause an increased localized deposition of nacre, and such protuberances are referred to as blister pearls (Jameson 1902). Shell deformities of freshwater mussels include protuberances, infoldings, and misshapen shells. Some anomalies are thought to be the result of an injury to the mantle that disrupts the normal process of shell formation, such as a small animal traveling between the shell and mantle. Some deformities may be the result of damage to the shell that is later repaired (Beedham 1971; Forsyth and

McCallum 1978; Roper and Hickey 1994; Parmalee and Bogan 1998; Strayer 2008). There are also reports of shell erosion as a result of friction or a low pH (Kat 1982; Roper and Hickey 1994; Parmalee and Bogan 1998; Nedeau 2008; Haag 2012). However, some shell deformities are more difficult to explain (Pekkarinen 1993a; Strayer 2008). Pekkarinen (1993a) reported a pustular disease affecting the posterior portion of the periostracum and nacre of *Anodonta anatina*, *Unio pictorum*, and *U. tumidus* in the Vantaa River, Finland. The author speculated that some of the pustules may have formed in response to chironomid larvae, but it is unclear how these invaders might cause protuberances of the periostracum. Pustules commonly occurred among *A. anatina* and were occasionally observed among *U. pictorum* and *U. tumidus*. Strayer (2008) reported a widespread shell deformity affecting *E. complanata*, *Alasmidonta undulata*, *Pyganodon cataracta*, *Lasmigona costata*, and *L. compressa* in streams in New York's Hudson River valley and Southern Tier regions. Affected mussels displayed a truncated posterior shell margin (the exposed portion of a mussel shell when the animal is normally buried), but the causative agent/mechanism behind this aberration remains indeterminate. Possible agents/mechanisms include: (1) the exposed portion of the shell was worn down, (2) the shell formation process was corrupted by a chemical contaminant or a pathogen that damaged the mantle, or (3) the mussels were irritated by a chemical contaminant that caused the mantle to periodically retract. Strayer (2008) estimated the prevalence of the deformity to be >10% at some sites. Several authors have reported tumors arising from tissues in the mantle cavity, mostly among *Anodonta* spp. Williams (1890) reported an adenomyoma from the mantle of *A. cygnea*. Collinge (1891) reported a tumor arising from the mantle–gill junction in *A. cygnea*. The tumor seemed to impair nacreization since the affected animal lacked nacre in the posterior portion of the shell. Butros (1948) reported a connective tissue tumor from the labial palp of *A. imbecata*. Pauley (1967a, 1967b) observed adenomas from the foot of *A. californiensis*. Pekkarinen (1993b) described hyperplastic lesions that grossly resembled tumors in the marsupial gill. Overall, the literature indicates that neoplasms may occur in <1% of mussels in a given population.

Some metazoans may damage somatic tissues or more directly impair fecundity by infecting the gonad or by obstructing the marsupial water tubes, but these appear to be isolated or rare events (Pauley and Becker 1968; Gordon et al. 1978; Huehner and Etges 1981; Grizzle and Brunner 2009; Levine et al. 2009; Müller et al. 2015; McElwain et al. 2016). Parasites typically exhibit an aggregated distribution among hosts; most hosts are infected with a small number of parasites, whereas only a small number of hosts in a given population are colonized by large numbers of parasites (Poulin 2011). Therefore, it seems unlikely that metazoan parasites would be responsible for widespread declines. Furthermore, the literature does not provide a clear indication as to the cause of die-offs and or mussel kills. It seems more likely that a microbial pathogen, rather than a metazoan parasite, would be

a causative agent of, or a contributing factor to, a mussel kill or die-off, but there is little evidence of this in the published literature aside from viral diseases affecting *H. cumingii* in China (Grizzle and Brunner 2009). Furthermore, our understanding of mussel health is limited because the primary literature contains few documented examples of microscopy used to characterize the gross and histopathological changes to tissues associated with parasites, commensals, or diseases.

To unravel the potential causes of mussel kills or die-offs, I recommend that gross anatomical and histological characteristics of normal and infected or diseased mussels be compared and photographed during health assessments. To this end, investigators should consult Löw et al. (2016) for a detailed description of the periostracum and nacre of a normal shell and the gross external and internal anatomy of healthy soft tissues. Gross pathology studies visually documented the following: insects (Beedham 1971; Forsyth and McCallum 1978; Levine et al. 2009), mites (Humes and Jamnback 1950; McElwain et al. 2016), tumors (Butros 1948; Pauley 1967b), and die-offs (Pauley 1968; Neves 1987). Images of aberrant shells have been published in Beecher (1883), Baker (1901), Williams (1969), Forsyth and McCallum (1978), Kat (1982), Pekkarinen (1993a), Roper and Hickey (1994), Parmalee and Bogan (1998), Nedeau (2008), Strayer (2008), Haag (2012), and Edwards and Vidrine (2013). Regarding histology, McElwain and Bullard (2014) is a comparative and comprehensive histological atlas for Unionidae. Correspondingly, several studies have included images of histopathological changes to tissues associated with pathogens, parasites, commensals, tumors, and die-offs. These are as follows: viruses (Zhiguo et al. 1986; Jianzhong et al. 1995; Lei et al. 2011), intracellular microorganisms (Chittick et al. 2001), aspidogasters (Pauley and Becker 1968; Bakker and Davids 1973; Fredericksen 1972; Huehner and Etges 1981; Huehner et al. 1989; Rosen et al. 2016), digeneans (Kniskern 1952; Chittick et al. 2001; Müller et al. 2015), insects (Beedham 1971), mites (Mitchell 1955; Baker 1976; McElwain et al. 2016; Abdel-Gaber 2018), fish eggs (Stadnichenko and Stadnichenko 1980), tumors (Butros 1948; Pauley 1967a; Pauley 1967b; Pekkarinen 1993b), and die-offs (Pauley 1968).

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LITERATURE CITED

- Abdel-Gaber, R., M. Fol, and S. Al Quraishy. 2018. Light and scanning electron microscopic studies of *Unionicola tetrafurcatus* (Acari: Unionicolidae) infecting four freshwater bivalve species and histopathological effect on its hosts. *Journal of Parasitology* 104:359–371.

- Antipa, G. A., and E. B. Small. 1971. The occurrence of *Thigmotrichous* ciliated protozoa inhabiting the mantle cavity of unionid molluscs of Illinois. *Transactions of the American Microscopical Society* 90:463–472.
- Baker, F. C. 1901. Some interesting molluscan monstrosities. *Transactions of the Academy of Science of St. Louis* 11:143–146.
- Baker, F. C. 1928. The Fresh Water Mollusca of Wisconsin, Part II. Pelecypoda. Bulletin 70 of the Wisconsin Geological and Natural History Survey. 495 pp.
- Baker, R. A. 1976. Tissue damage and leukocytic infiltration following attachment of the mite *Unionicola intermedia* to the gills of the bivalve mollusc *Anodonta anatina*. *Journal of Invertebrate Pathology* 27:371–376.
- Bakker, K. E., and C. Davids. 1973. Notes on the life history of *Aspidogaster conchicola* Baer, 1826 (Trematoda: Aspidogastrea). *Journal of Helminthology* 47:269–276.
- Beecher, C. E. 1883. Some abnormal and pathologic forms of fresh-water shells from the vicinity of Albany, New York. Thirty-Sixth Annual Report of the New York State Museum of Natural History 51–55.
- Beedham, G. E. 1971. The extrapallial cavity in *Anodonta cygnea* (L.) inhabited by an insect larva. *Journal of Conchology* 26:380–385.
- Burreson, E. M., and S. E. Ford. 2004. A review of recent information on the Haplosporidia, with special reference to *Haplosporidium nelson* (MSX disease). *Aquatic Living Resources* 17:499–517.
- Butros, J. 1948. A tumor in a fresh-water mussel. *Cancer Research* 8:270–271.
- Carman, S. M. 2007. Texas hornshell *Popenaia popeii* recovery plan. New Mexico Game and Fish, Conservation Services Division, Santa Fe, New Mexico.
- Chittick, B., M. Stoskopf, M. Law, R. Overstreet, and J. Levine. 2001. Evaluation of potential health risks to eastern elliptio (*Elliptio complanata*) (Mollusca: Bivalvia: Unionida: Unionidae) and implications for sympatric endangered freshwater mussel species. *Journal of Aquatic Ecosystem Stress and Recovery* 9:35–42.
- Clark H. W., and C. B. Wilson. 1912. The mussel fauna of the Maumee River. Bureau of Fisheries Document 757, U.S. Department of Commerce and Labor, Washington, D.C.
- Coker, R. E., A. F. Shira, H. W. Clark, and A. D. Howard. 1921. Natural history and propagation of fresh-water mussels. Bulletin of the U.S. Bureau of Fisheries 37:75–181.
- Collinge, W. E. 1891. Note on a tumour in *Anodonta cygnaea*, Linn. *Journal of Anatomy and Physiology* 25:154.
- Cummings, K. S., and D. L. Graf. 2010. Mollusca: Bivalvia. Pages 309–385 in J. H. Thorp and A. P. Covich, editors. *Ecology and Classification of North American Freshwater Invertebrates*. Elsevier, Amsterdam.
- Dallas, W. S. 1858. On the natural history of the Cingalese pearl oyster and on the production of pearls. *Annals and Magazine of Natural History* 3rd series 1:81–100.
- Edwards, D. D., and M. F. Vidrine. 2013. Mites of freshwater mollusks. Malcolm F. Vidrine, Eunice, Louisiana.
- Fleming, W. J., T. P. Augspurger, and J. A. Alderman. 1995. Freshwater mussel die-off attributed to anticholinesterase poisoning. *Environmental Toxicology and Chemistry* 14:877–879.
- Forsyth, D. J., and I. D. McCallum. 1978. *Xenochironomus canterburyensis* (Diptera: Chironomidae), a commensal of *Hyridella menziesi* (Lamellibranchia) in Lake Taupo; features of pre-adult life history. *New Zealand Journal of Zoology* 5:759–800.
- Fredericksen, D. W. 1972. Morphology and taxonomy of *Cotylogaster occidentalis* (Trematoda: Aspidogastrea). *Journal of Parasitology* 58:1110–1116.
- Gentner, H. W., and S. H. Hopkins. 1966. Changes in the trematode fauna of clams in the Little Brazos River, Texas. *Journal of Parasitology* 52:458–461.
- Gordon, M. J., B. K. Swan, and C. G. Paterson. 1978. *Baeoetenus bicolor* (Diptera: Chironomidae) parasitic in unionid bivalve molluscs, and notes on other chironomid–bivalve associations. *Journal of the Fisheries Research Board of Canada* 35:154–157.
- Grabarkiewicz, J. D., and W. S. Davis. 2008. An introduction to freshwater mussels as biological indicators. EPA-260-R-08-015. U.S. Environmental Protection Agency, Office of Environmental Information, Washington, D.C.
- Graf, D. L., and K. S. Cummings. 2007. Review of the systematics and global biodiversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies* 73:291–314.
- Grizzle, J. M., and C. J. Brunner. 2009. Infectious diseases of freshwater mussels and other freshwater bivalve mollusks. *Reviews in Fisheries Science* 17:425–467.
- Haag, W. R. 2012. North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, Cambridge, U.K.
- Hopkins, S. H. 1934. The parasite inducing pearl formation in American freshwater Unionidae. *Science* 79:385–386.
- Hornbach, D. J. 2001. Macrohabitat factors influencing the distribution of naiads in the St. Croix River, Minnesota and Wisconsin, USA. Pages 213–232 in G. Bauer and K. Wächtler, editors. *Ecological Studies* 145, Ecology and Evolution of the Freshwater Mussels Unionoida. Springer-Verlag, Berlin.
- Huehner, M. K., and F. J. Etges. 1981. Encapsulation of *Aspidogaster conchicola* (Trematoda: Aspidogastrea) by unionid mussels. *Journal of Invertebrate Pathology* 37:123–128.
- Huehner, M. K., K. Hannan, and M. Garvin. 1989. Feeding habits and marginal organ histochemistry of *Aspidogaster conchicola* (Trematoda: Aspidogastrea). *Journal of Parasitology* 75:848–852.
- Humes, A. G., and H. A. Jamnback. 1950. *Najadicola ingens* (Koenike), a water-mite parasitic in fresh-water clams. *Psyche* 57:77–87.
- Jameson, H. L. 1902. On the origin of pearls. *Proceedings of the Zoological Society of London* 1:140–166.
- Jianzhong, S., X. Lixin, L. Yanan, Z. Minzhou, and M. Shujian. 1995. Histopathological studies on the plaque diseases of bivalve mussel *Hyriopsis cumingii* Lea. *Journal of Fisheries of China* 19: 1–7.
- Kat, P. W. 1982. Shell dissolution as a significant cause of mortality for *Corbicula fluminea* (Bivalvia: Corbiculidae) inhabiting acidic waters. *Malacological Review* 15:129–134.
- Kniskern, V. B. 1952. Studies on the trematode family Bucephalidae Poche, 1907, Part II: The life history of *Rhipidocotyle septapapillata* Krull, 1934. *Transactions of the American Microscopical Society* 71:317–340.
- Lei, Z., X. Tiao-Yi, H. Jie, D. Liang-Ying, and L. Xiao-Yan. 2011. Histopathological examination of bivalve mussel *Hyriopsis cumingii* Lea artificially infected by virus. *Acta Hydrobiologica Sinica* 35:666–671.
- Levine, T. D., B. K. Lang, and D. J. Berg. 2009. Parasitism of mussel gills by dragonfly nymphs. *American Midland Naturalist* 162:1–6.
- Lopes, L., D. M. Pimpão, R. M. Takemoto, J. C. O. Malta, and A. M. B. Varella. 2011. *Hysterothylacium* larvae (Nematoda, Anisakidae) in the freshwater mussel *Diplodon suavidicus* (Lea, 1856) (Mollusca, Unioniformes, Hyriidae) in Aripuanã River, Amazon, Brazil. *Journal of Invertebrate Pathology* 106:357–359.
- Löw, P., K. Molnár, and G. Kriska. 2016. Atlas of animal anatomy and histology. Springer International Publishing, Cham, Switzerland.
- Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Hershler, K. E. Perez, B. Roth, M. Seddon, E. E. Strong, and F. G. Thompson. 2004. The global decline of nonmarine mollusks. *Bioscience* 54:321–330.
- McElwain, A., and S. A. Bullard. 2014. Histological atlas of freshwater mussels (Bivalvia, Unionidae): *Villosa nebulosa* (Ambleminae: Lampsilini), *Fusconaia cerina* (Ambleminae: Pleurobemiini) and *Strophitus connasugaensis* (Unioninae: Anodontini). *Malacologia* 57:99–239.
- McElwain, A., R. Fleming, M. Lajoie, C. Maney, B. Springall, and S. A. Bullard. 2016. Pathological changes associated with eggs and larvae of *Unionicola* sp. (Acari: Unionicolidae) infecting *Strophitus connasau-*

- gaensis* (Bivalvia: Unionidae) from Alabama creeks. *Journal of Parasitology* 102:75–86.
- Mitchell, R. D. 1955. Anatomy, life history, and evolution of the mites parasitizing fresh-water mussels. Miscellaneous Publications, Museum of Zoology, University of Michigan, No. 89, 52 pp.
- Müller, T., M. Czarnoleski, A. M. Labecka, A. Cichy, K. Zając, and D. Dragosz-Kluska. 2015. Factors affecting trematode infection rates in freshwater mussels. *Hydrobiologia* 742:59–70.
- Nedea, E. J. 2008. Freshwater mussels and the Connecticut River watershed. Connecticut River Watershed Council.
- Neves, R. J. 1987. Proceedings of the workshop on die-offs of freshwater mussels in the United States, June 23–25, 1986, Davenport, Iowa. U.S. Fish and Wildlife Service, Upper Mississippi Conservation Committee.
- Parmalee, P. W., and A. E. Bogan. 1998. The freshwater mussels of Tennessee. The University of Tennessee Press, Knoxville.
- Pauley, G. B. 1967a. A tumorlike growth on the foot of a freshwater mussel (*Anodonta californiensis*). *Journal of the Fisheries Research Board of Canada* 24:679–682.
- Pauley, G. B. 1967b. Four freshwater mussels (*Anodonta californiensis*) with pedunculated adenomas arising from the foot. *Journal of Invertebrate Pathology* 9:459–466.
- Pauley, G. B. 1968. A disease of the freshwater mussel, *Margaritifera margaritifera*. *Journal of Invertebrate Pathology* 12:321–328.
- Pauley, G. B., and C. D. Becker. 1968. *Aspidogaster conchicola* in mollusks of the Columbia River system with comments on the host's pathological response. *Journal of Parasitology* 54:917–920.
- Pekkarinen, M. 1993a. Reproduction and condition of unionid mussels in the Vantaa River, South Finland. *Archiv für Hydrobiologie* 127:357–375.
- Pekkarinen, M. 1993b. A hyperplastic growth involving glandular and nervous tissues in the marsupial gill of *Pseudoanodonta complanata* in southern Finland. *Journal of Invertebrate Pathology* 61:326–327.
- Poulin, R. 2011. *Evolutionary Ecology of Parasites*, 2nd ed. Princeton University Press, Princeton, New Jersey. 331 pp.
- Prenter, J., C. MacNeil, J. T. A. Dick, and A. M. Dunn. 2004. Roles of parasites in animal invasions. *Trends in Ecology and Evolution* 19:385–390.
- Pritchard, J. 2001. An historical analysis of mussel propagation and culture: Research performed at the Fairport Biological Station. Iowa State University Digital Repository, Natural Resource Ecology and Management Publication 58, Iowa State University, Ames.
- Roback, S. S., D. J. Bereza, and M. F. Vidrine. 1979. Description of an *Ablabesmyia* [Diptera: Chironomidae: Tanypodinae] symbiont of unionid fresh-water mussels [Mollusca:Bivalvia:Unionacea], with notes on its biology and zoogeography. *Transactions of the American Entomological Society* 105:577–620.
- Roper, D. S., and C. W. Hickey. 1994. Population structure, shell morphology, age and condition of the freshwater mussel *Hyridella menziesi* (Unionacea: Hyriidae) from seven lake and river sites in the Waikato River system. *Hydrobiologia* 284:205–217.
- Rosen, R., H. Abe, O. Adejumo, K. Ashami, L. Ballou, K. Montgomery, S. Toe, E. Berg, and L. Peng. 2016. Mean intensity and prevalence of *Cotylaspis insignis* (Trematoda: Aspidogastridae) infections in the fat mucket, *Lampsilis radiata luteola* (Bivalvia: Unionidae), from North Elkhorn Creek, a tributary of the Kentucky River in Central Kentucky, U.S.A. *Comparative Parasitology* 83:1–5.
- Stadnichenko, A. P., and Y. A. Stadnichenko. 1980. The effect of bitterling larvae on the Lamellibranchia mollusk *Unio rostratus gentilis* Haas. *Gidrobiologicheskii Zhurnal* 1980:57–61.
- Strayer, D. L. 2008. A widespread morphological deformity in freshwater mussels from New York. *Northeastern Naturalist* 15:149–151.
- Villalba, A., K. S. Reece, M. C. Ordás, S. M. Casas, and A. Figueras. 2004. Perkinsosis in molluscs: A review. *Aquatic Living Resources* 17:411–432.
- Williams, J. C. 1969. Mussel fishery investigation Tennessee, Ohio and Green Rivers final report. State of Kentucky Project No. 4-19-R.
- Williams, J. D., A. E. Bogan, R. S. Butler, K. S. Cummings, J. T. Garner, J. L. Harris, N. A. Johnson, and G. T. Watters. 2017. A revised list of the freshwater mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. *Freshwater Mollusk Biology and Conservation* 20:33–58.
- Williams, J. W. 1890. A tumour in the fresh-water mussel (*Anodonta cygnea*, Linn.). *Journal of Anatomy and Physiology* 24:307–308.
- Wilson, C. B., and H. W. Clark. 1912. The mussel fauna of the Kankakee Basin, U.S. Bureau of Fisheries Document 758. U.S. Department of Commerce and Labor, Bureau of Fisheries, Washington, D.C.
- Wisniewski, J. M., K. D. Bockrath, J. P. Wares, A. K. Fritts, and M. J. Hill. 2013. The mussel–fish relationship: A potential new twist in North America? *Transactions of the American Fisheries Society* 142:642–648.
- Zhiguo, Z., D. Sufang, X. Yumin, and W. Jie. 1986. Studies on the mussel *Hyriopsis cumingii* plague I. A new viral infectious disease. *Acta Microbiologica Sinica* 26:308–312.