

## Chapter 12

# A Snail, a Clam, and the River Jordan: *A Revealing Novel*



The river Rhine, it is well known,  
Doth wash your city of Cologne;  
But tell me, Nymphs, what power divine  
Shall henceforth wash the river Rhine?

Samuel Taylor Coleridge 1772-1834

Cover photos:

Asian clam: <http://www.corpi.ku.lt/databases/index.php/aquanis/species/view/id/1018>

New Zealand mud snail: Dr. Dan Gustafson, Montana State University.

Technical Report

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Ancient Chinese Fortune Cookie Proverb: Unexpected good luck sometimes comes in small packages that are often hard to see unless you are willing to open your eyes.

## Summary

For better or worse, the invasive ‘good luck’ clam, *Corbicula fluminea* and New Zealand mudsnail, *Potamopyrgus antipodarum* are well established in the Jordan River, UT. Both the snail and the clam reach some of the highest densities recorded ( $>>5000 \text{ m}^{-2}$  for *Corbicula*; 250,000 to 500,000  $\text{m}^{-2}$  for *Potamopyrgus*). Based on literature review presented in this report and recent mollusk surveys conducted in the Jordan River by OreoHelix Consulting and the Wasatch Front Water Quality Council; it is now apparent that the filter-feeder/pedal-feeder *Corbicula* and the grazer, *Potamopyrgus* dominate ecosystem functions in the Jordan River. *Corbicula* can filter out the entire water column FPOM (including algae, bacteria, nutrients) in the Jordan River in about a day in locations where its densities are high, as it does in many rivers. *Corbicula* filtration rates can range from about 0.4 to 3.0 cubic meters of water  $\text{m}^{-2} \text{ hr}^{-1}$ , depending on temperatures. It has also been suggested that *Corbicula* can decrease the likelihood of cyanoHABS and increase water clarity that promote reestablishment of native aquatic vegetation. On good days, *Corbicula*’s organic matter consumption rates in the Jordan River can be from 0.33 to 6.2 metric tons  $\text{km}^{-1} \text{ day}^{-1}$ . The ‘good luck’ clam is also likely responsible for among other things: enhancing nutrient cycling, reducing turbidity, increasing light penetration, and reducing phytoplankton abundance; all of which are improvements in the degraded Jordan River’s water quality. However, these benefits performed free of monetary expenditure come with some ecological and water quality costs, primarily dissolved oxygen consumption and ammonia respiration. *Corbicula*  $\text{O}_2$  consumption rates can range from 1 to 16  $\text{mg m}^{-2} \text{ hr}^{-1}$  and  $\text{CO}_2$  respiration rates range from 1 to 14  $\text{mg m}^{-2} \text{ hr}^{-1}$ . *Corbicula*’s consumption rates of nitrogen and phosphorus in the Jordan River range between 0.75 to 2.12  $\text{mg m}^{-2} \text{ day}^{-1} \text{ N}$  and 0.27 to 0.95  $\text{mg m}^{-2} \text{ day}^{-1} \text{ P}$ . Excretion rates were calculated to be from 75 to 1,426  $\mu\text{mol m}^{-2} \text{ day}^{-1} \text{ NH}_4$  and from 15 to 286  $\mu\text{mol m}^{-2} \text{ day}^{-1} \text{ P}$  in the river. As with all mollusks, *Corbicula* contributes to the reduction of the greenhouse gas  $\text{CO}_2$  in the production of  $\text{CaCO}_3$  based shells. It is quite feasible that *Corbicula* sequesters  $\approx 10$  metric tons  $\text{C km}^{-1} \text{ year}^{-1}$  in sections of the Jordan River, via shell production.

The New Zealand mudsnail, *Potamopyrgus* can have production rates  $\approx 1500 \text{ mg AFDM m}^{-2} \text{ day}^{-1}$ ; excretion rates  $\approx 8 \text{ mg N m}^{-2} \text{ day}^{-1}$ ; and egestion rates  $\approx 200 \text{ mg N m}^{-2} \text{ day}^{-1}$  in the Jordan River. Although much is still to be learned about its role in the Jordan River, it likely has similar rates as *Corbicula* but on a smaller scale.

*Corbicula* and *Potamopyrgus* are undoubtedly the most important and dominant biota in the now **novel** Jordan River ecosystem and together co-regulate seasonal nitrogen, phosphorus, and carbon cycling, microbial community structure, and stream metabolism. The snail and clam are almost certainly seasonally controlling most other ecosystem functions as well, (e.g. water quality), despite their roles being unnoticed to most researchers and managers.

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## Introduction

Over the millennia, physical and chemical conditions in the Jordan River, Utah drainage have created a freshwater mollusk hotspot in an otherwise depauperate western United States, providing ideal habitat for mussels, clams, and snails, including the globally invasive Asian clam<sup>4</sup>, *Corbicula fluminea* and New Zealand mudsnail, *Potamopyrgus antipodarum* (Richards 2017a; 2017b). *Corbicula fluminea* densities and biomass in the now highly regulated and degraded Jordan River<sup>5</sup>, UT often occur at greater levels than have been reported elsewhere in the world (Richards 2017a, Richards 2017b, Phelps 1994; Karatayev et al. 2003; Ilarri et al. 2011; Beaver et al. 1991). This species of clam often reaches densities  $\gg 5000/m^2$  in several sections of the Jordan River, particularly downstream of its confluence with Mill Creek (Richards 2017a, Richards 2017b). Invasive New Zealand mudsnails, *Potamopyrgus antipodarum* are extremely abundant throughout the Jordan River and have been estimated to exceed densities  $\gg 250,000 m^{-2}$ , particularly in upstream sections (Richards personal observation).

When bivalves (mussels and clams) such as *Corbicula*<sup>6</sup> or snails such as *Potamopyrgus*<sup>7</sup> reach high enough densities and biomass, they transition into ecosystem engineers and keystone species (Prins and Escaravage 2005). They then control and oft times transform most ecological functions by:

- altering water quality;
- enhancing nutrient cycling;
- reducing turbidity and increase light penetration;
- reducing phytoplankton abundance
- regulating bacteria and fungi assemblages;
- controlling key processes such as oxidation of organic matter; and
- altering N:P ratios, nutrient chemistry, sediment oxygen demand (SOD), and; biological oxygen demand (BOD)(see following sections for citations).

Thus, their dominance in an aquatic ecosystem is considered by ecologists and managers to be a double-edged sword; on one side, ecosystem altering invasive species that may cause certain types of water quality degradation; on the other side, naturalized resident species such as

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<sup>4</sup> *Corbicula* is known as the 'good luck clam' in many parts of Asia.

<sup>5</sup> The Jordan River, UT was named after the Biblical 'River Jordan' in the Mideast.

<sup>6</sup> The species of *Corbicula* found in the Jordan River is *Corbicula fluminea* but in this report will be referred to as *Corbicula*.

<sup>7</sup> The New Zealand mudsnail found in the Jordan River is *Potamopyrgus antipodarum* but in this report will simply be referred to as *Potamopyrgus*.

*Corbicula* and *Potamopyrgus*, that replace inefficient natives and that may vastly improve overall water quality, depending on conditions, and doing so with zero monetary expenditures by citizens.

The effects of *Corbicula* and *Potamopyrgus* on ecosystem processes are well known throughout the world. It is also known that these clams and snails have occupied most sections of the Jordan River at unbelievably high densities/biomass for well over a decade, undoubtedly having huge ecological and water quality effects. However, *Corbicula* and *Potamopyrgus* and their role in the ecological functioning of the Jordan River continues to be ignored and their effects are all but invisible to most Jordan River researchers and managers, despite this knowledge. Jordan River managers and scientists studying the effects of nutrient loads on water quality and ecosystem processes in the river always seem to come up short explaining inconsistencies in data interpretation, typically resulting in conclusions that are mostly vague, unsatisfactory, incomplete, and on occasion, wrong (e.g. Follstad Shah et al. 2017; others). The most likely explanation for these incorrect assessments is the failure to include the effects of *Corbicula* and *Potamopyrgus*.

## Justification

Researchers and managers have been blind to the very large effects that the ecosystem engineers, *Corbicula* and *Potamopyrgus* are having on nutrient cycling, water quality, and ecosystem functions in the Jordan River. This has often resulted in misinformed and erroneous conclusions, and likely misdirected management decisions. This technical report describes known effects of *Corbicula* and other bivalves (used as surrogates for *Corbicula*) and *Potamopyrgus* on ecological processes and water quality in waters outside of Utah based on literature review. This knowledge is then applied to the most recent and only intensive surveys of *Corbicula* distribution and abundance in the Jordan River, as reported by Richards (2017a; 2017b) and the Wasatch Front Water Quality Council and by personal observations by Richards while conducting ecological studies, including mollusk surveys on the Jordan River. The review and analyses validates the large effect that *Corbicula* and *Potamopyrgus* are having on the river's nutrient cycle, water quality, and ecosystem function and will guide scientists and managers to a better understanding of the river and their ability to manage the river accordingly.

## Report Sections

This report is presented in several sections. The first section of the review focuses on *Corbicula*'s water column filter feeding ecology and its ecosystem effects. The second section of the review focuses on the clam's pedal feeding ecology and its ecosystem effects. The third section focuses on *Potamopyrgus* ecology and ecosystem effects and the fourth section applies what was learned in the first three sections to *Corbicula* and *Potamopyrgus* populations in the Jordan River. This fourth section on effects of *Corbicula* in the Jordan River is primarily focused on portions of the mid-Jordan River downstream of its confluence with Mill Creek to about 900

South. This portion of the river contained the highest *Corbicula* densities found by Richards 2017a and 2017b and members of the Wasatch Front Water Quality Council, and is likely where *Corbicula* has the most influence. The fourth section addressing the effects of *Potamopyrgus* on the Jordan River ecosystem focuses more on sections upstream of its confluence with Mill Creek, where its known densities are highest.

## Review of *Corbicula* Ecology and Ecosystem Effects

*Corbicula*, a keystone species, ecosystem engineer is well known to alter food web structure, often times shifting the structure towards a microbial based food web (Prins and Escaravage 2005). *Corbicula* are self-fertilizing, simultaneous hermaphrodites and release up to 2,000 juveniles per day, and more than 100,000 in a lifetime. Juveniles are  $\approx 1$  mm in length and take from one to four years to reach maturity and reach a length of about 5 cm. Table 1 is a summary of *Corbicula* life history characteristics.

Table 49. Summary of some *Corbicula* life history characteristics. From Sousa et al. 2008 Table 1 (and adapted from McMahan 2002).

<i>Life history characteristics</i>	<i>C. fluminea</i>
Life span	1 to 5 years
Age at maturity	3 to 9 months
Reproductive mode	Hermaphroditic
Growth rate	Rapid
Fecundity	68 678
Juvenile size release	250 $\mu$ m
Position of broods	Inner demibranchs
Type of released larvae (juveniles)	D-shaped configuration
Type of brooding	Synchronous
Juvenile survivorship	Low
Adult survivorship	Usually low
Number of reproductive events	Usually two but may vary
Assimilated energy respired	11 - 42 %
Non-respired energy transferred to growth	58 - 71 %
Non-respired energy transferred to reproduction	5 - 15 %
Turnover time	73 - 91 days
Habitat requirements	Intolerant to high salinity values and even moderate hypoxia conditions (this species is usually restricted to well-oxygenated areas). Tolerate low water temperatures and prefer sandier sediments mixed with silt and clay (which enhance the organic matter content). However, in some ecosystems this species can be found in all types of sediments (with or without submerged vegetation) (Sousa et al. 2008)

*Corbicula* filter large amounts of water and thus process large amounts of suspended materials (FPOM) and nutrients, which are used by the clams for growth and reproduction or excreted in

dissolved form or deposited as feces or pseudofeces<sup>8</sup> (Ostroumov 2005; Cohen et al. 1984; Beaver et al. 1991; Arnott and Vanni 1996; Newell et al. 2005). As a result, *Corbicula* enhances nutrient cycling (Lauritsen and Mozley 1989, Cohen et al. 1984; Boltovskoy et al. 1995). Not only does *Corbicula* alter water column processes, it also alters benthic/sediment processes. This is because *Corbicula* has two distinct feeding mechanisms: 1) filtering- feeding water column particulate organic matter (POM) (Lauritsen 1986a; Leff et al. 1990; Boltovskoy et al. 1995) and, 2) pedal feeding sediment organic matter (OM) using cilia on their foot to collect subsurface organic matter (Cleland 1988; Reid et al. 1992, Hakenkamp and Palmer 1999).

*Corbicula* can influence nutrient fluxes through one of five main pathways:

1. regeneration of dissolved nutrients directly into the water column;
2. sequestration of nutrients bound up in tissue and shell;
3. burial of particulate in sediments;
4. regeneration of dissolved nutrients from sediments; or,
5. denitrification from sediments (Konrad 2013).

#### Water Column Filter-feeding

*Corbicula* often dominate the benthic invertebrate community both numerically and in terms of biomass (Lauritsen and Mozley 1989; Poff et al. 1993). *Corbicula* perform both the function of removing particles from the water column and regulating other biota involved in water purification, including algae, bacteria, and fungi in the sediments (Ostroumov 2002a; Newell 1988; Newell & Ott 1998). They thus control the key process of oxidation of organic matter in an aquatic system when clams occur at high densities, particularly the major oxidizer, bacteria, (Wetzel 2001; Sorokin et al. 1997; Ostroumov 2005). *Corbicula* can directly reduce the amount of particulate organic matter (POM) available to be remineralized by pelagic consumers and bacterioplankton (Cloern 1982; Officer et al. 1982; Newell et al. 2005). *Corbicula* also actively select particles to digest or reject as pseudofeces as illustrated in Figure 65.

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<sup>8</sup> Pseudofeces are mucous-enveloped, partially or undigested filtered POM.

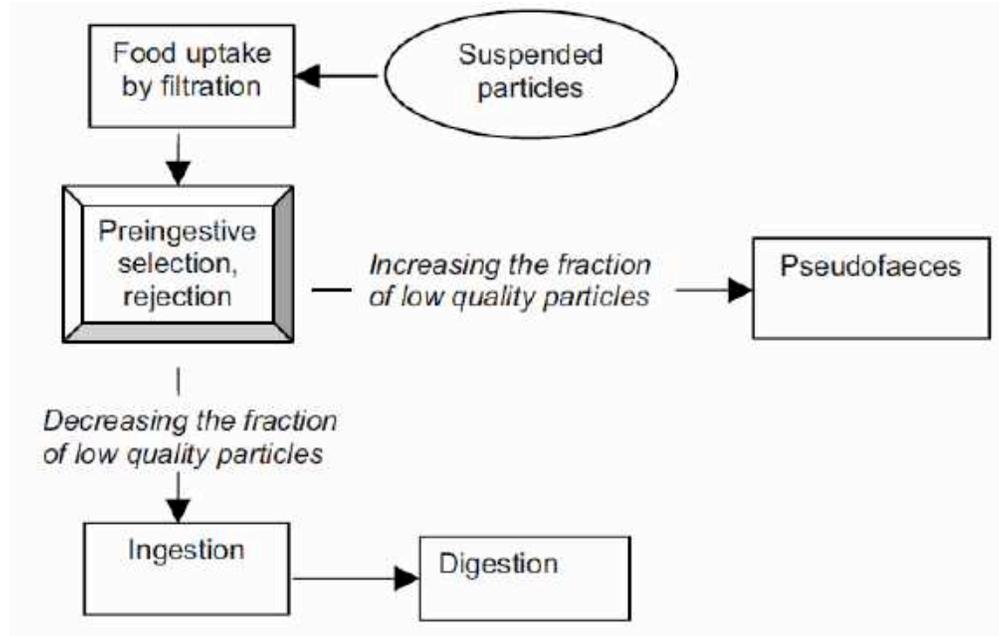


Figure 65. A conceptual model of food processing by *Corbicula* actively filter feeding and particle selecting for rejection as pseudofaeces or digestion (from Dame and Olenin (2005)).

#### Filtration Rates

Bivalves are world renowned for the ability to filter large volumes of water (Table 50) and *Corbicula* filtration rates are some of the highest recorded for filter feeders (Cohen et al. 1984; Beaver et al. 1991; Lauritsen 1986) ( Table 51; Table 52).

Table 50. Estimates of filter feeder clearance times (number of days for water column to be filtered). Note: Only 4 of the taxa in table are non- bivalves. From Ostroumov (2005).

System	Organism	% vol	Time (d)	References; comments
Lake Baikal, Russia	<i>Baikalospongia bacillifera</i> , <i>B. intermeda</i> , <i>Lubomirskia baikalensis</i>	100	1.2	Savarese et al., 1997; littoral zone, 12-m depth
Lake Punnusjarvi, Russia	Zooplankton (various)	100	3	Andronikova (1976, 1978) – cit. in Gutelmaher (1986)
Lake Tuakitoto, New Zealand	<i>Hyridella menziesi</i> (bivalve)	100	1.4	Ogilvie and Mitchell, (1995)
<i>Sphagnum</i> bog-pond; Wisconsin, USA	<i>Spongilla lacustris</i> (sponge)	130	1	Frost (1978); areas of high biomass 31.8 g m <sup>-2</sup>
Laholm Bay in the Kattegat, Denmark	<i>Cardium edule</i> , <i>Mya arenaria</i>	50-100	3	Loo and Rosenberg (1989); area 60 km <sup>2</sup>
Northern San Francisco Bay, USA	<i>M. arenaria</i>	100	ca. 1	Nichols (1985)
South San Francisco Bay, USA	<i>Potamocorbula amurensis</i>	100	0.6	Cloern (1982); water volume 2500·10 <sup>6</sup> m <sup>3</sup>
North Inlet (South Carolina, USA)	<i>Crassostrea virginica</i>	100	0.8-6.1	Dame et al. (1980); volume 22 ·10 <sup>6</sup> m <sup>3</sup>
Carlingford Lough, Ireland	<i>C. gigas</i> , <i>Tapes semidiscussata</i> , <i>Mytilus edulis</i>	100	87.5	Ball et al. (1997); cit. in Dame et al. (2001); volume of water 196·10 <sup>6</sup> m <sup>3</sup>
Narragansett Bay (Rhode Island, USA)	<i>Mercenaria mercenaria</i>	100	32.1	Pilson (1985); volume of water 2724·10 <sup>6</sup> m <sup>3</sup>
Oosterschelde, The Netherlands	<i>Mytilus edulis</i> , <i>Cerastoderma edule</i>	100	3.7	Smaal et al. (1986); volume of water 2740·10 <sup>6</sup> m <sup>3</sup>
Western Wadden	<i>M. edulis</i> , <i>C. edule</i>	100	5.8	Dame et al. (1991a); Van

Sea, The Netherlands					Stralen (1995); cit. in Dame et al. (2001); volume of water $4020 \cdot 10^6$ $m^3$
Ria de Arosa, Spain	<i>M. edulis</i>	100	12.4		Tenore et al.(1982); cit. in Dame et al. (2001); volume of water $4335 \cdot 10^6$ $m^3$
Chesapeake Bay, USA	<i>C. virginica</i>	100	87.5		Newell (1988) ; volume $27300 \cdot 10^6$ $m^3$
Marina da Gama	several species	100	1.1		Davies et al. (1989) volume $0.025 \cdot 10^6$ $m^3$
Kertinge Nor, Denmark	<i>Ciona intestinalis</i> (ascidian)	100	0.8-5		Petersen and Riisgård (1992) ; volume $11\ 000 \cdot 10^6$ $m^3$
Bay of Brest, France	multiple species	100	2.8-6		Hily (1991); volume $1480 \cdot 10^6$ $m^3$
Marennes-Oléron, France	<i>C. gigas</i> , <i>M. edulis</i>	100	2.9		Héral et al. (1988); Bacher (1989) - cit. in Dame et al. (2001); volume $675 \cdot 10^6$ $m^3$
Königshafen, Germany	<i>M. edulis</i> , <i>C. gigas</i>	100	0.9-2.8		Asmus and Asmus (1991); volume $7.2 \cdot 10^6$ $m^3$

Table 51. Filtration rates *Corbicula fluminea* clearance time (amount of days for the water column to be filtered) from Karatayev et al. (2005)

Water body	Days	Source
Potamac River, USA	3-4	Cohen et al. 1984
Upper Chowan River, USA	1-1.5	Lauritsen 1986
Meyers Branch Stream, USA	1	Leff et al. 1990
Clear Fork of the Trinity River, USA	0.01	McMachon and Bogan 2001

Table 52. *Corbicula* filtration rates (from Lauritsen (1986) Table 1).

	Algal Volume (mm <sup>3</sup> /L)				
	0.33	0.67	1.33	2.00	2.67
Mean filtration rate (ml/hr)	782.3	656.5	489.0	420.2 <sup>a</sup>	277.8
1 SE	69.6	55.5	53.6		82.5
Mean volume ingested (mm <sup>3</sup> )	0.23	0.41	0.64		0.80
1 SE	0.01	0.03	0.06		0.07

A clearance rate model developed by Fulford et al. (2007) predicted that at historic oyster biomass levels oysters would be able to filter the entire volume of Chesapeake Bay in about 27 d (annual average), and in about 9 d at peak summer clearance rates. This is consistent with previous estimates of water filtration by oysters reported by Newell (1988) but likely much less than would occur from the better filter-feeder, *Corbicula*. Cohen et al. (1984) showed that *Corbicula* at moderate densities ( $\approx 1400 \text{ m}^{-2}$ ) compared to mid-Jordan River densities (section: *Corbicula* and *Potamopyrgus* in the Jordan River) were able to filter the entire volume of water in a reach of the Potomac River ( $3.0 \times 10^7 \text{ m}^3$ ) in 3 to 4 days or an estimated  $8.9 \times 10^6 \text{ m}^3 \text{ day}^{-1}$ . Cohen et al. (1984) also showed that on average, one *Corbicula* was able to remove 30% of phytoplankton chlorophyll *a* from a 2 -L river water sample in 2 hours. Beaver et al. (1991) reported that *Corbicula* filtrations rates in a hypereutrophic lake were approximately  $0.5$  to  $0.7 \text{ L hr}^{-1} \text{ clam}^{-1}$  and at moderate densities ( $1310$  to  $2621 \text{ m}^{-2}$ ) reduced chlorophyll *a* concentrations  $> 60\%$  in 7 days.

#### Particle Size Ingestion

*Corbicula* typically have a lower ingestion size limit of  $< 1 \mu\text{m}$  and upper size limit of about  $20 \mu\text{m}$  for filtered POM (McMahon and Bogan 2001; Way et al. 1990) but can consume algae with a spherical diameter from  $50 \mu\text{m}$  up to  $170 \mu\text{m}$  (Boltovskoy et al. 1995). However, larger sized POM or higher concentrations of POM favor the production of pseudofeces and/or reduced filtration rates (Beaver et al. 1991; Lauritsen 1986; Way et al. 1990). Because of this particle ingestion size range, they can effectively remove a large majority of or even completely deplete detritus, bacteria and algae from the water column when they occur at high densities/biomass (Mikheev 1994, McMahon 1999, Boltovskoy et al. 1995; Cloern, 1982 Fr chet and Bourget 1985; Dame and Olenin 2005). Consequently, *Corbicula* play a key role in the stability of aquatic ecosystems (Herman and Scholten 1990; Kotta et al 2005; Dame and Olenin 2005). *Corbicula* has been shown to initiate pseudofeces production at  $17$  to  $20 \text{ mg l}^{-1}$  TSS (Fuji 1979, Hornbach et al. 1984, Way et al. 1990; Appendix 37). See Appendix 37 for a detailed description of the effects of inorganic suspended matter on bivalves, including *Corbicula* and native mussels in the Jordan River.

## Filter-feeding Selectivity

*Corbicula* is considered to be mostly a non-selective, filter-feeder (Lauritsen 1986; Way et al. 1990; Beaver et al. 1991). Several feeding studies have suggested that *Corbicula* grow equally well on green algae and diatoms and assimilation and net production efficiencies of *Corbicula* fed the cyanobacteria, *Anabaena oscillaroides* were not significantly different than those fed chlorophytes (Lauritsen 1986; Beaver et al. 1991). The Lauritsen (1986) study found that the lowest filtration rates and the highest assimilation efficiencies were with another cyanobacteria, *Anabaena flos-aquae*. *Corbicula* are even thought to have reduced the severity of cyanoHABs in the Potomac River (Phelps 1994).

## Nutrient Ingestion and Excretion

*Corbicula* can digest and assimilate N from different sources of POM with efficiencies from  $\approx 20$  to 90% (Newell et al. 2005). Some nitrogen and phosphorus regeneration is a direct result of *Corbicula* excretion from filter feeding on phytoplankton (Newell et al. 2005). High densities of *Corbicula* in eutrophic systems are completely capable of reducing water column phosphorus (TP) levels (Beaver et al. 1991). Boltovskoy et al. suggested that *Corbicula* needed roughly 66 to 673 mg C m<sup>-2</sup> h<sup>-1</sup> (mean: 289) for respiration only and that phytoplankton ingestion alone may only supply 2 to 51% of organic matter C required for respiration.

Nutrients excreted into the water column by *Corbicula* in dissolved inorganic form may be readily available to phytoplankton and periphyton (Arnott and Vanni 1996; Hakenkamp and Palmer 1999). Nitrogen excretion (g<sup>-1</sup> dry weight) is size dependent; smaller bivalves excrete less than larger bivalves however, smaller bivalves may excrete more P per gram dry weight than larger bivalves (Arnott and Vanni 1996; Hakenkamp and Palmer 1999). Thus small clams relative to medium or large clams can excrete at significantly lower N:P ratios, however, excreted N:P in all size classes can often be lower than that which occurs in the water column and may shift phytoplankton towards N limitation (Arnott and Vanni 1996). This can have direct effects on species-specific phytoplankton growth rates, which may allow cyanobacteria to outcompete algal phytoplankton. However, *Corbicula* filter feed both cyanobacteria and algae and net effects need to be calculated.

Newell et al. (2005) reported average ammonium excretion rates of *Corbicula*:

$$\cong 6.0 \mu\text{mol NH}_4^+ \text{ g}^{-1} \text{ DW h}^{-1} \text{ (DW = dry tissue weight)}$$

and average phosphorus excretion rates

$$\cong 1.2 \mu\text{mol P g}^{-1} \text{ DW h}^{-1} \text{ (DW = dry tissue weight)}$$

Lauritsen and Mozley (1989) reported  $\text{NH}_3$  excretion rates between 357 and 8642  $\mu\text{mol m}^{-2} \text{day}^{-1}$  and  $\text{PO}_4$  (orthophosphate) rates between 161 and 3924  $\mu\text{mol m}^{-2} \text{day}^{-1}$  in a coastal plain river in Virginia-North Carolina. They estimated that an average size clam of 20 mg DFW would excrete 2.06  $\mu\text{mol NH}_3 \text{hr}^{-1}$  in summer and 0.95  $\mu\text{mol NH}_3 \text{hr}^{-1}$  in winter and 0.36  $\mu\text{mol PO}_4 \text{hr}^{-1}$  in summer and 0.02  $\mu\text{mol PO}_4 \text{hr}^{-1}$  in winter. Thus, P recycling by *Corbicula* can be greater than all other sources including; zooplankton, point sources, tributary loading, atmospheric inputs, sediments, and macrophytes (Arnott and Vanni 1996).

Konrad (2013) discussed approaches for evaluating the effects of bivalve filter feeding on nutrient dynamics. A summary of these is provided in Appendix 36.

### $\text{O}_2$ consumption and $\text{CO}_2$ respiration

Hokenkamp and Palmer 1999 reported that *Corbicula* consumes high rates of  $\text{O}_2$  and respire high rates of  $\text{CO}_2$ , which contributes strongly to total metabolism in streambeds and significant utilization of OM resources. However, the benefit of *Corbicula* on reducing hypoxia depends on a reduction in the flux of organic detritus to benthic sediments that creates biochemical oxygen demand (BOD) through heterotrophic respiration and decomposition of organic material (Konrad 2013). With respect to carbon dynamics, *Corbicula* may be the single most important species in a stream.

Boltovskoy et al. (1995) estimated *Corbicula* densities between 450 and 4500  $\text{m}^{-2}$  (mean 2000  $\text{m}^{-2}$ ) and 66 to 673  $\text{mg C m}^{-2} \text{h}^{-1}$  (mean: 289  $\text{mg C m}^{-2} \text{h}^{-1}$ ) required for respiration only, which translates to approximately 16 to 162 (mean 69)  $\text{g C m}^{-2} \text{day}^{-1}$ . These densities were similar to those found by Richards 2017a in the Jordan River.

### Turbidity

Filter feeding by *Corbicula* also reduces turbidity, increases water clarity, and thereby increases nutrient mineralization rates and light availability to microphytobenthos and SAV (Buttner 1986; Lauritsen and Mozley 1989; Phelps 1994; Newell et al. 2005; Buttner 1986; Lauritsen and Mozley 1989; Phelps 1994; Beaver et al. 1991; Newell 2004; Newell & Koch 2004). Phelps (1994) suggested that it was *Corbicula* filter feeding at high clearance rates that reduced turbidity, increased light availability to bottom sections of the Potomac River, and allowed aquatic vegetation to reestablish.

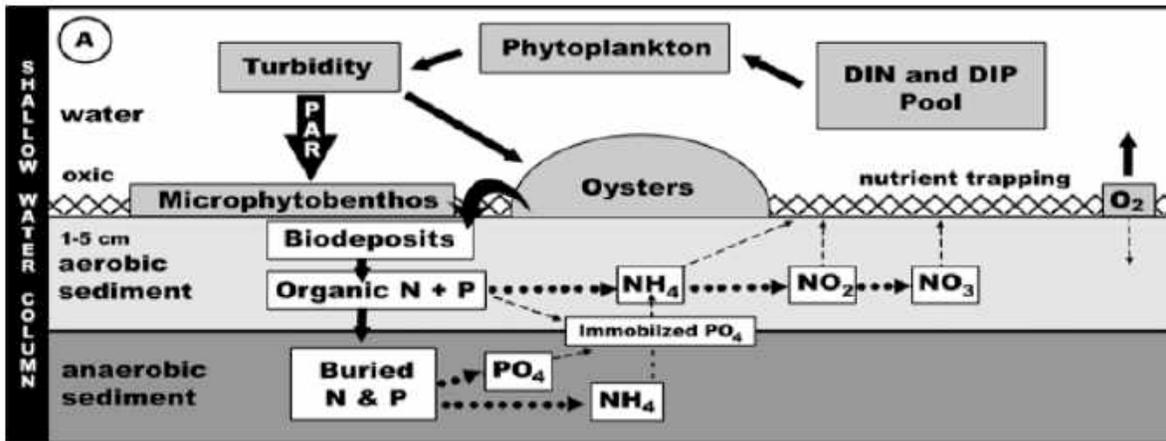


Figure 66. An additional conceptualization of bivalves (oysters) on nutrient cycling (from Newell et al. 2005). The Jordan River is a shallow, often eutrophic water body and this figure is a good representation by replacing ‘oysters’ with *Corbicula* in the illustration.

### Sediments and Biodeposition

Most researchers focus on nutrient regeneration of bivalve filter-feeding, however one of the more important effects of bivalve feeding is the repackaging of small seston particles into large aggregates of feces and pseudofeces, known as biodeposition (Newell et al. 2005; more). Particles in bivalve feces are tightly bound in a mucoid matrix and voided as pelleted strings that can be as long as several millimeters (Kautsky and Evans 1987, Widdows et al. 1998; Newell et al. 2005). Feces and pseudofeces sinking velocities can be up to 40 times faster than that of non-aggregated particles, although pseudofeces are less tightly bound in mucus than feces and may disaggregate when voided (Kautsky and Evans 1987, Widdows et al. 1998; Newell et al. 2005). Table 5 displays the enormous amount of biodeposits and bio-sediment formation rates that bivalves are capable of. Table 6. shows how a bivalve (oyster) was seasonally capable of removing up to several metric tons (5%) of N inputs and more than a ton (35%) of P inputs to a watershed per month (based on oysters at 1 g dry weight m<sup>-2</sup>). *Corbicula* is assumed to be a much more efficient filterer than most oysters and can occur in the Jordan River up to 9.9 g dry weight m<sup>-2</sup>, which suggests it could be removing N and P at much greater rates than shown in Table 6.

Table 53. Biosediments formation by suspension-feeders. From Ostroumov 2005.

System	Organisms	Amount	Comments	References
Laholm Bay	<i>Cardium edule</i>	N: 199 t y <sup>-1</sup> C: 1449 t y <sup>-1</sup>	per 60 km <sup>2</sup> ; 0-10 m depth	Loo and Rosenberg (1989)
	<i>M. arenaria</i>	N: 36 t y <sup>-1</sup> C: 262 t y <sup>-1</sup>		
	<i>C. edule</i> + <i>M. arenaria</i>	N: 235 t y <sup>-1</sup> C: 1711 t y <sup>-1</sup> C: 29 g m <sup>-2</sup> y <sup>-1</sup>		
Rocky shores	<i>Mytilus edulis</i>	11.9 kg m <sup>-2</sup> y <sup>-1</sup> (dry weight),	of 11.9 kg, faeces 9.2 kg, pseudofaeces 2.7	Tsuchiya (1980)
Norwegian-Greenland Sea, depth 2020-2630 m	sponge <i>Thenea abyssorum</i> , biomass up to 1524 mg AFDW m <sup>-2</sup>	0.6-2.2 mg C m <sup>-2</sup> d <sup>-1</sup>	The poriferan community possibly adds up to 10% to the vertical particle flux	Witte et al. (1997)
	<i>T. abyssorum</i>	up to 0.7 g C m <sup>-2</sup> y <sup>-1</sup>	-	author's estimate based on the data (Witte et al. 1997)
Baltic coastal ecosystem	<i>M. edulis</i>	1092 g m <sup>-2</sup> y <sup>-1</sup> dry weight, including C 80.7 g m <sup>-2</sup> y <sup>-1</sup>	Total sedimentation (total amount of all types of sedimenting material) was 3521 g m <sup>-2</sup> y <sup>-1</sup> dry weight	Kautsky and Evans, 1987;
		N 10.4 g m <sup>-2</sup> y <sup>-1</sup> P 1.6 g m <sup>-2</sup> y <sup>-1</sup>		
Marine/estuarine NETHERLANDS	<i>M. edulis</i>	60 g m <sup>-2</sup> h <sup>-1</sup>	-	Widdows et al., 1998
Marine/estuarine	bivalves	25 g m <sup>-2</sup> h <sup>-1</sup>	-	Smaal et al. 1986
Marine/estuarine	<i>M. chilensis</i>	18 g m <sup>-2</sup> h <sup>-1</sup>	-	Jaramillo et al., 1992; cit. in Ostroumov et al., 2001

Table 54. Newell et al. 2005: Total monthly N and P (kg) inputs and removal by oysters in an estuary. Note: This table was based on oysters but exemplifies the contribution bivalves (such as *Corbicula*) have

on nutrient removal. Also note that the nutrient removal values are for 1 bivalve (Oyster) = 1.0 g DW. *Corbicula* in the Jordan River range from mean = 1.1 g DW m<sup>-2</sup> up to 9.9 g DW m<sup>-2</sup> (see section: *Corbicula* and *Potamopyrgus* in the Jordan River).

	Total-N inputs (kg)	Total-P inputs (kg)	Monthly nutrient removal for oysters at a density of 1 m <sup>-2</sup> on 1,736 ha oyster bottom			
			N (kg)	P (kg)	% N inputs	% P inputs
Jan	281,450	5,245	0	0	0.0	0.0
Feb	261,970	4,837	0	0	0.0	0.0
Mar	312,350	5,351	106	38	0.0	0.7
Apr	292,500	5,338	226	82	0.1	1.5
May	243,930	6,022	552	200	0.2	3.3
Jun	148,250	4,641	1,207	436	0.8	9.4
Jul	75,480	4,059	3,887	1,405	5.1	34.6
Aug	80,810	4,274	4,038	1,460	5.0	34.2
Sep	99,140	4,587	2,331	843	2.4	18.4
Oct	97,940	4,015	449	162	0.5	4.0
Nov	114,500	4,344	218	79	0.2	1.8
Dec	254,270	6,373	66	24	0.0	0.4
<b>Total</b>	<b>2,262,580</b>	<b>59,085</b>	<b>13,080</b>	<b>4,728</b>	<b>0.6</b>	<b>8.0</b>

*Corbicula* biodeposits have been shown to contain ≈ 2 to 3 times as much C, N, and P per unit weight as particles settling-out naturally from the water column (Newell et al. 2005)(Table 55).

Table 55. Example of Bivalve (oyster) Carbon, nitrogen, and phosphorus biodeposits vs. seston (From Newell et al. 2005, Table 1).

	Biodeposits	Seston Material
Carbon (mg C g <sup>-1</sup> )	34.8 ± 3.15	14.6 ± 1.19
Nitrogen (mg N g <sup>-1</sup> )	4.8 ± 0.44	2.1 ± 1.19
Phosphorus (mg P g <sup>-1</sup> )	0.58 ± 0.085	0.32 ± 0.028
C:N:P ratio (molar)	154:18:1	117:14:1

Although some algae are undigested and passed as feces or pseudofeces (Hill and Knight 1981; Galtsoff 1964, Cohen et al. 1984), overall, “*Corbicula* biodeposition enhances net ecosystem losses of N and P via sediment burial and bacterially mediated, coupled nitrification-denitrification” (Newell et al. 2005). Microphytobenthos may then compete with nitrifying bacteria for N, potentially reducing coupled nitrification-denitrification, they retain N and P within sediments, further reducing net regeneration to the water column. (Newell et al. 2005).

Biodeposition can stimulate microbial metabolism sufficiently to cause the sediments to become anaerobic when *Corbicula* are at very high population densities or in locations with low water circulation (Newell 2004). When this occurs, nutrients are regenerated primarily as NH<sub>4</sub><sup>+</sup> and

$\text{PO}_4^{3-}$ , with little or no loss due to burial and denitrification (Newell et al. 2005). Also, under these conditions, *Corbicula* may show several signs of density dependence because it has low tolerance of hypoxia relative to other freshwater bivalves of North America (Johnson & McMahon, 1998; Matthews & McMahon, 1999).

As reported in the Water Column section of this report, Cohen et al. (1984) showed that *Corbicula* removed vast quantities of phytoplankton from Potomac River water. They also demonstrated that pheopigment concentration in the sediment was proportional to clam biomass, thus verifying that *Corbicula* deposit some partially digested phytoplankton on the bottom as feces or pseudofeces. Cohen et al. (1984) also reported that Prokopovich (1969) found that the mucoidlike mass of the pseudofeces of *Corbicula* was a strong binding agent of sediment and that it would probably require a bottom-scouring storm to resuspend the excreted, partially decomposed algae.

Clams can experience variation in oxygen availability depending on the habitats occupied (e.g. pools versus riffles), diel or seasonal factors, and/or location. Additionally, clams in streams can be exposed to low oxygen waters during periods of low flow, during the release of water from dams, and/or a significant effect of DO level on final burial depth (Saloom and Duncan 2005).

Newell et al. (2005) described the major chemical pathway of bivalve deposits as they relate to benthic-water column coupling and the inter relationship between aerobic and anaerobic microbe communities that have evolved in association with bivalve deposits:

“Natural sediments have well-developed microbial communities inhabiting distinct zones of oxygen content (Henriksen and Kemp 1988). Therefore, bivalve biodeposits that settle on sediments with an oxic surface layer are subject to initial decomposition by aerobic bacteria. Organic materials are oxidized to  $\text{CO}_2$ ,  $\text{PO}_4^{3-}$ , and  $\text{NH}_4^+$ , and other aerobic bacteria further oxidize  $\text{NH}_4^+$  to  $\text{NO}_2^-$  and  $\text{NO}_3^-$ . Some of the  $\text{NO}_2^-$  and  $\text{NO}_3^-$  diffuses down into underlying anaerobic sediments, and some diffuses out of the sediment and enters the water-column nutrient pool. In the underlying anaerobic sediments, denitrifying bacteria use the oxidized forms of N as terminal electron acceptors, reducing the  $\text{NO}_2^-$  and  $\text{NO}_3^-$  to  $\text{N}_2$  gas (Henriksen and Kemp 1988, Seitzinger 1988, Risgaard-Petersen et al. 1994). Absent N fixation,  $\text{N}_2$  is unavailable to plants and passes to the atmosphere. Denitrification can only occur where there is a close juxtaposition between oxygenated sediments that support nitrifying bacteria and anaerobic sediments that support denitrifying bacteria (Kristensen 1988). Bacterial degradation of particulate organic N and P from bivalve biodeposits that settle to anoxic sediments is solely via anaerobic pathways. Because the initial nitrification step is precluded, all regenerated N remains as  $\text{NH}_4^+$ , and there is negligible sorption of  $\text{PO}_4^{3-}$  to iron complexes (Krom and Berner 1981). The microbial communities associated with sediments are a crucial element mediating nutrient regeneration processes from biodeposits.”

In addition, total N flux from bivalve respiration and deposits can range from  $\approx 1$  to  $5 \text{ mmol N m}^{-2} \text{ h}^{-1}$  (Dame et al. 1989; 1991a; Asmus and Asmus 1991; Magni et al. 2000; Newell et al.

2005). Dame et al. (1989) estimated that oyster biodeposits transferred  $\approx 189 \text{ g N m}^{-2} \text{ y}^{-1}$  from the water to the sediments, most of which was regenerated as  $\text{NH}_4^+$  ( $125 \text{ g N m}^{-2} \text{ y}^{-1}$ ) (Newell et al. 2005). Dame et al. (1989) also calculated that bivalves were responsible for a net retention of  $98 \text{ g P m}^{-2} \text{ yr}^{-1}$ , which was either incorporated into fauna and flora or buried in the sediments, with little P release (Newell et al. 2005; Konrad 2013). Newell et al. (2005) concluded that because sediment N and P regeneration are less than 100% efficient due to burial and denitrification, bivalve feeding reduces recycling and reduces system-level phytoplankton production and biomass.

### Body tissue and Shell Carbon Consumption and Fixation Rates

*Corbicula* is an extremely fast growing bivalve. It can grow from a 1 mm juvenile to a 5 cm adult within a year and develop very thick shells. These clams require constantly large amounts of carbon to incorporate into their shells ( $\text{CaCO}_3$ ) during their growth. Carbon sources for shell development include organic carbon filtered from the water column or pedal fed from the substrate or from  $\text{CO}_2$  dissolved in the water (Baker 2010). By now everyone is aware that  $\text{CO}_2$  is a major greenhouse gas that effects many stream functions, including metabolism and water quality. *Corbicula* fix carbon into refractory proteins that are part of their shells but more importantly they fix carbon in the shells themselves, which are approximately 12% carbon by weight (Baker 2010). Unlike the carbon contained in plant and animal tissue that can return to  $\text{CO}_2$  to the atmosphere in a few years or less, carbon fixed as  $\text{CaCO}_3$  can persist for tens to hundreds of years as shells or indefinitely as limestone. Shell decay rates are mostly dependent on water chemistry and flow (Strayer and Malcom 2007).

Several studies have measured freshwater bivalve shell production, including *Corbicula* (Aldridge & McMahon, 1978; Strayer et al., 1981; Vincent, Vaillancourt and Lafontaine, 1981; Vincent and Lafontaine, 1984). Only a few have measured shell decay (Strayer et al., 1981; Strayer and Malcom 2007). Aldridge & McMahon (1978) found that shell production was approximately 30 times organic production, suggesting that the populations of *Corbicula* that have been studied had shell production rates of  $18\text{--}400 \text{ g shells m}^{-2} \text{ year}^{-1}$ . Dense populations of *Corbicula* might therefore produce more than  $1 \text{ kg shells m}^{-2} \text{ year}^{-1}$  and are capable of producing large amounts  $>10 \text{ kg m}^{-2} \text{ year}^{-1}$  of spent shells (Strayer and Malcom 2007). C, N, and P concentrations in bivalve tissues can vary seasonally and differ between body tissue and shells (Arnott and Vanni 1996). Zebra mussels are about 5 to 10% dry weight as tissue compared to shell dry weight.

### *Corbicula* and water quality

Bivalves, including *Corbicula*, are a severely underestimated key component for maintaining and improving water quality in an aquatic ecosystem (Huang et al. 2005; Fulford et al. 2007)(Table

56 and Table 57). Their role is powerful, labile, and subject to subtle adjustment and regulation (Ostroumov 2005). However, their role in maintaining Jordan River water quality is overlooked by every agency other than the Council.

Table 56. Water filtration by suspension-feeders may influence other biotic and abiotic processes that are involved in water purification. From Ostroumov 2005.

<b>Water purification</b>	<b>Biotic/ Abiotic</b>	<b>Suspension-feeders influence</b>
Chemical oxidation by oxygen	Abiotic	Suspension-feeders remove some suspended matter from water column; by increasing light penetration, they help benthic algae to carry out photosynthesis and to produce oxygen; availability of oxygen is especially important at the bottom where the organic matter is accumulated
Photodegradation of organic matter and pollutants	Abiotic	Suspension-feeders via filtration increase the water transparency and light penetration into water
Pollutant sorption by sediments	Abiotic	The sorption of pollutants by sediments depends on the percentage of organic matter in the sediments; suspension-feeders produce pellets rich in organics and by doing so increase the percentage and amount of organic matter in the sediments; as a result, the capacity of sediments to adsorb pollutants increases.
Pollutant sorption by pellets	Abiotic	Suspension-feeders produce pellets (faeces, pseudofaeces) which are the additional centers for adsorption of pollutants
Sedimentation of particles of seston	Abiotic	Suspension-feeders remove small particles from water and aggregate them into bigger particles of pellets; the latter sediment faster than the small particles
Material accumulation by aquatic organisms	Biotic	Suspension-feeders produce shells, which contain C and other elements that stay on the bottom for long time. It is important in terms of biomineralization and cycling of carbonates bound in shells.
Oxidative biodegradation of organic molecules by bacteria and fungi	Biotic	By removing bacteria and fungi from water suspension-feeders participate in regulating the abundances of many species in the ecosystem. As a result, suspension-feeders contribute to the control of the rate of processes performed by bacteria and fungi (e.g., Ostroumov, 2000 e, 2001 d)
Recycling nutrients making them available to organisms involved in water purification	Biotic	Suspension-feeders actively participate in recycling nutrients. E.g., they excrete N and P. By doing so they contribute to recycling.
Decreasing sediment erodibility	Biotic/ Abiotic	Sediment erodibility depends on the epifaunal bivalves (Widdows et al. 2000)

Table 57. Some key facts and principles that characterize suspension-feeders as part of water- filtering biomachinery maintaining water quality and some features of aquatic ecosystem. From Ostroumov 2005.

<b>Key facts</b>	<b>Comment / Consequences</b>	<b>Fundamental principles concerning the role of suspension-feeders</b>
The amount of water filtered (per unit of biomass of animals or per unit of area or per unit of time) is very significant There are several taxa of suspension-feeders which filter water	Significant contribution to the removal of particles (seston) from water; contribution to water purification  Increase in reliability of the biomachinery of water filtration	Large-scale repair of water quality  Contribution to the stability of water quality in ecosystem; maintaining stability of habitats of many aquatic species
The higher the concentration of particles, the lower the filtration rate and relative grazing pressure	Positive feedbacks that in turn may lead to the increase in heterogeneity of parts of the water column	Suspension-feeders have a potential to contribute to creating habitat heterogeneity (in terms of patchiness of concentrations of suspended matter in water)
The amount of suspension that is being filtered out of water is usually more than needed for metabolism	A significant amount of the formerly suspended matter is finally packed, ejected and/or excreted as pellets	Suspension-feeders provide some ecological services to the system (by upgrading water quality); ecological taxation: suspension-feeders pay ecological tax to the community (ecosystem)
Suspension-feeders produce pellets	The pellets gravitate towards the bottom or the lower layers	Acceleration of migration of elements through the water
	of the water column	column of the ecosystem; pellets-mediated acceleration of the removal of particles (seston) from water column
Suspension-feeders remove bacteria and fungi	Regulatory effect (control) on planktonic bacteria and fungi; regulatory impact on benthos benthic community	Contribution to the regulation of ecosystem metabolism

### Review of *Potamopyrgus* Ecology and Ecosystem Effects

*Potamopyrgus* densities in the western U.S. can often exceed 300,000 m<sup>-2</sup> (Richards et al. 2001; Richards 2004; Cross et al. 2010; Arango et al. 2009) and have been reported as high as 500,000 m<sup>-2</sup> in a tributary of the Snake River in Yellowstone National Park (Hall et al. 2003). Richards (personal observations) has estimated that this snail can far exceed 250,000 m<sup>-2</sup> in the Jordan River, particularly on submerged aquatic vegetation where they can be 500,000 m<sup>-2</sup>. Although it is thought to be primarily a parthenogenic livebearer in the western USA (M. Dybdahl, Washington State University, personal communication), males have been found to comprise from 1- 3% of a population in SW Montana. In the western USA, adult *Potamopyrgus* are typically 4 to 5 mm shell length. *Potamopyrgus* often comprises 85% to 95% of the invertebrate assemblages both in biomass and abundance in many rivers in the western USA (Bowler 1991, Richards et al. 2001, Shannon et al. 2003), although for unknown reasons this snail undergoes widely varying 'boom and bust' population density cycles (Richards unpublished data, Moore et al. 2012).

Hall et al. (2003) and Hall et al. (2006) documented *Potamopyrgus* diverting > 75% of gross primary production in a river in Yellowstone National Park. Their data showed that *Potamopyrgus* consumed nearly 100% of the algal primary production and that algal growth rates were slower with increased *Potamopyrgus* biomass, which suggested that *Potamopyrgus* was consuming high-turnover algal taxa and that its impacts on the aquatic environment were comparable to that of the zebra mussel (*Dreissena polymorpha*) in the eastern USA (Hall et al. 2003). Hall et al. (2003) also showed that *Potamopyrgus* can dominate carbon and nitrogen cycles in productive streams, which the Jordan River certainly is. See Table 58 for values generated by (Hall et al. 2003). Arango et al. (2009) showed that heavy grazing by *Potamopyrgus* dominated the nitrogen cycle in a stream of similar size to the Jordan River and changed periphyton composition by reducing the proportion of green algae and increasing the proportion of nitrogen-fixing diatoms. Arango et al. (2009) also showed that nitrogen fixation rates increased disproportionately to nitrogen-fixing algal cells, indicating that these snails increased nitrogenase efficiency, probably by improving light and (or) nutrient availability to nitrogen fixers. Thus, *Potamopyrgus* has the potential to alter ecosystem function and affect whole ecosystem processes wherever it occurs in high densities (Alonso and Castro-Diez 2012), including the Jordan River.

Table 58. Hall et. al (2003) Table 1 *Potamopyrgus* production values.

Table 1. Mean abundance, biomass, secondary production, and scaled excretion and egestion fluxes of <i>Potamopyrgus antipodarum</i> relative to native invertebrates in Polecat Creek, WY, during July and August 2001						
	Abundance	Biomass	Production	Excretion	Egestion	
	indiv/m <sup>2</sup>	gAFDM/m <sup>2</sup>	mgAFDM/m <sup>2</sup> /d	mgN/m <sup>2</sup> /h	gAFDM/m <sup>2</sup> /d	mg/Nm <sup>2</sup> /d
<i>Potamopyrgus</i>	48 3000	34.5	1490	7.8	4.1	190
Native primary consumer taxa	950	0.95	41	0.17*	**	8.7*

\*Estimates based on Grimm (1988)    \*\*Not estimated

### *Corbicula* and *Potamopyrgus* in the Jordan River

The Jordan River is fairly shallow (< 2 m), eutrophic, and the water column is well mixed. It is also, heavily urbanized, degraded, and regulated (Richards 2017b). However, its water chemistry continues to be ideal for mollusk production, including the now resident clam, *Corbicula* and snail, *Potamopyrgus*. Both *Corbicula* and *Potamopyrgus* reach much higher than average densities and biomass in sections of the Jordan River than elsewhere in the world (Table 59; other citations throughout this report). The following sections discuss rate estimates and effects of the snail and clam in the Jordan River<sup>9</sup>.

#### *Corbicula* in the Jordan River

*Corbicula* densities and biomass are both spatially and temporally variable in the Jordan River (Richards 2017a; 2017b; Table 59). Results in this section were based on density estimates from mostly riffle and run habitats between the Jordan River’s confluence with Mill Creek and 900 S, the area intensively surveyed by Richards (2017a). However, *Corbicula* densities upstream of Mill Creek confluence are within the range reported in Table 59. Pool habitats almost always have very low densities of live clams.

Table 59. Descriptive statistics of live *Corbicula* m<sup>-2</sup> in the Jordan River. Based on Richards 2017a.

11a. Live clams and empty shells m<sup>-2</sup> in run habitat

	N	Mean	Std. Error	Median	25 <sup>th</sup>	75 <sup>th</sup>	Maximum

<sup>9</sup> Note: All of the values in all of the tables for Jordan River are rough estimates. Values in tables should be considered reasonably accurate but not precise. There were many variables that effected these estimates. Some estimates were based on data for other bivalve taxa (e.g.oysters). Temperature effects, seasonal effects, and individual *Corbicula* biomass variability, etc. need to be accounted for. Field data collection is critically needed to verify and adjust.

54 <sup>th</sup> South to Mill Creek	7	271	76	297	85	444	575
Mill Creek to 21 <sup>st</sup> South	12	449	279	122	79	348	3,502
17 <sup>th</sup> South to 13 <sup>th</sup> South	9	4,175	1,670	2,180	1,245	4,880	16,400
13 <sup>th</sup> South to 9 <sup>th</sup> South	13	1,014	467	250	39	1,366	6,100
Total	41	1,416	453	353	85	1,366	16,400

11b. Live clams m<sup>-2</sup> in run habitat

	N	Mean	Std. Error	Median	25 <sup>th</sup>	75 <sup>th</sup>	Maximum
54 <sup>th</sup> South to Mill Creek	7	175	49	150	53	275	367
Mill Creek to 21 <sup>st</sup> South	12	179	66	99	33	258	837
17 <sup>th</sup> South to 13 <sup>th</sup> South	9	2,635	1,287	956	650	3,420	12,400
13 <sup>th</sup> South to 9 <sup>th</sup> South	13	676	295	130	13	1,100	3,700
Total	41	875	323	262	40	837	12,400

11c. Empty shells m<sup>-2</sup> in run habitat

	N	Mean	Std. Error	Median	25 <sup>th</sup>	75 <sup>th</sup>	Maximum
54 <sup>th</sup> South to Mill Creek	7	97	38	78	17	147	300
Mill Creek to 21 <sup>st</sup> South	12	271	218	43	28	90	2,665
17 <sup>th</sup> South to 13 <sup>th</sup> South	9	1,540	432	1,224	595	1,712	4,000
13 <sup>th</sup> South to 9 <sup>th</sup> South	13	338	179	110	25	350	2,400
Total	41	541	149	110	31	512	4,000

11d. Live clams and empty shells m<sup>-2</sup> in pool habitat. N = 7 samples

	Mean	Std. Error	Median	25 <sup>th</sup>	75 <sup>th</sup>	Maximum
Live clams	4	1	6	1	6	8

Empty shells	5	1	6	3	7	10
Live clams and empty shells	10	2	10	4	15	16

*Corbicula* prefer well oxygenated sediments (Belanger et al. 1985; Richards 2017a; 2017b) and their populations are often much lower or absent in sediments of high organic and low oxygen content (Aldridge and McMahon 1978; McMahon 1979; Eng 1979). This is similar to what Richards 2017a and 2017b reported; high abundances in run habitat, low to absent abundances in slower pool habitats with high organic and low oxygen contents.

#### Estimated Water Column Filtration Rates for *Corbicula* in the Jordan River

Karatayev et al. (2005) stated that in small water body streams (e.g. Jordan River), *Corbicula* could filter the volume of water equivalent to that of the entire waterbody from 16 min to 4 days (see Table 3).

Based on Karatayev et al. (2005) estimates, **it should only take *Corbicula* ≤ 1 day to filter the entire water column in sections of Jordan River where the clam is at high densities and less than a week in other locations.** Lauritsen (1986) estimated average sized *Corbicula* water column filtering rates at three temperatures shown in Table 60.

Table 60. *Corbicula* filtrations rates reported by Lauritsen (1986) at three temperatures (Similarly sized clams (mean shell length=22.4 mm) were used for testing. At 8<sup>0</sup> C, only data from clams that opened their shells were analyzed).

	Temperature		
	8°C	20°C	31°C
Mean filtration rate (ml/hr)	245.9	905.8	951.3
1 SE	47.4	43.6	78.9
n	4	4	4

Filtration rates were estimated for *Corbicula* in the Jordan River using Lauritsen (1986) rates (Table 60) and density estimates from Table 59. Results are presented in Table 61.

Table 61. Estimated filtration rates of *Corbicula* in the Jordan River at 3 temperature means and standard errors from rates published by Lauritsen (1986).

<i>Corbicula</i> Density	8° C	20 °C	21° C
--------------------------	------	-------	-------

(m <sup>-2</sup> )	m <sup>3</sup> m <sup>-2</sup> hr <sup>-1</sup>	m <sup>3</sup> m <sup>-2</sup> hr <sup>-1</sup>	m <sup>3</sup> m <sup>-2</sup> hr <sup>-1</sup>
Median = 650	0.16 (± 0.01)	0.59 (± 0.03)	0.62 (± 0.05)
Mean = 1,435	0.35 (± 0.02)	1.301 (± 0.06)	1.37 (± 0.10)
75 <sup>th</sup> = 1,223	0.30 (± 0.01)	1.11 (± 0.05)	1.16 (± 0.09)
95 <sup>th</sup> = 3,700	0.91 (± 0.04)	3.35 (± 0.15)	3.52 (± 0.28)
99 <sup>th</sup> = 12,400	3.05 (± 0.16)	11.23 (± 0.50)	11.80 (± 0.93)

Estimated N and P consumption rates for *Corbicula* in the Jordan River

Table 14 contains monthly and daily nitrogen and phosphorus consumption rates based on Newell et al. 2005.

Table 62. Monthly and daily Nitrogen and Phosphorus consumption rates (mg m<sup>-2</sup>) for *Corbicula* in the Jordan River during summer months (June-September = 122 days) based on Newell et al. (2005). See Table 6 from Newell et al. (2005) monthly consumption rates adjusted by mean and se for *Corbicula* density adjusted biomass.

<i>Corbicula</i> Biomass <sup>1</sup> (g m <sup>-2</sup> )	<i>Month</i>		<i>Day</i>	
	<i>N</i> mg m <sup>-2</sup> (± SE)	<i>P</i> mg m <sup>-2</sup> (± SE)	<i>N</i> mg m <sup>-2</sup> (± SE)	<i>P</i> mg m <sup>-2</sup> (± SE)
Mean	189.84 (145.19, 234.49)	68.63 (52.47, 84.79)	1.56 (1.19,1.92)	0.56 (0.43,0.70)
-1 SE	120.18 (91.91, 148.44)	43.45 (33.21, 53.68)	0.99 (0.75,1.22)	0.36 (0.27,0.44)

+1 SE	259.11 (198.17, 320.05)	93.67 (71.61,115.73)	2.12 (1.62,2.62)	0.77 (0.59,0.95)
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Estimated O<sub>2</sub> Consumption Rates for *Corbicula* in the Jordan River

Table 63 contains estimated O<sub>2</sub> consumption and CO<sub>2</sub> respiration rates for *Corbicula* in the river based on Hakenkamp and Palmer (1999) rates.

Table 63. Estimated O<sub>2</sub> consumption and CO<sub>2</sub> respiration rates (mg m<sup>-2</sup> hr<sup>-1</sup>) by *Corbicula* in run habitat sections of the Jordan River downstream CVWRF to 900 South.

<i>Corbicula</i> Density (m <sup>-2</sup> ) <sup>a</sup>	<i>Corbicula</i> Dry Weight (g m <sup>-2</sup> ) <sup>b</sup>	O <sub>2</sub> consumption (mg m <sup>-2</sup> hr <sup>-1</sup> ) <sup>b</sup>	CO <sub>2</sub> respiration (mg m <sup>-2</sup> hr <sup>-1</sup> ) <sup>c</sup>
Median = 650	0.52	1.01	0.85
Mean (± SE) = 1,436 (910, 1962)	1.15 (0.73, 1.57)	2.01 (1.34, 2.67)	1.70 (1.14, 2.27)
75 <sup>th</sup> = 1,223	0.98	1.74	1.45
95 <sup>th</sup> = 3,700	2.96	4.87	4.14
99 <sup>th</sup> = 12,400	9.92	15.86	13.48

<sup>a</sup>Jordan River *Corbicula* density estimates downstream of CVWRF in non-pools (from Richards 2017)(see Table 59 for more descriptive stats on density estimates).

<sup>b</sup>Based on Hakenkamp and Palmer (1999) *Corbicula* dry weight estimates and regression model: oxygen consumed = 0.19 + (1.58 X *Corbicula* dry weight (g)).

<sup>c</sup>Based on Bott (2007) Respiratory Quotient: 1 mol CO<sub>2</sub> respired/1 mol O<sub>2</sub> consumed = 0.85

Based on these estimates of high O<sub>2</sub> consumption rates and CO<sub>2</sub> respiration rates, it is obvious that *Corbicula* contributes strongly to total metabolism in the water column and streambed sediments in the Jordan River. Because every 1 mole of oxygen consumed by *Corbicula* is roughly equivalent to the release of 1 mole of carbon in the form of carbon dioxide (Respiratory Quotient = 0.85; e.g., Bott 1996), the high respiration rate found for *Corbicula* reflects significant utilization of organic matter resources (Hakenkamp and Palmer 1999). These CO<sub>2</sub> respiration rates combined with the as of yet unmeasured amount of sequestering of C into their shells, and results from Hakenkamp and Palmer (1999), clearly shows that *Corbicula* is likely the single most important species in the Jordan River with respect to carbon dynamics and stream metabolism.

Total O<sub>2</sub> consumption rates in the Jordan River obviously need to include *Corbicula* consumption rates but also need to account for other sources (i.e. decomposition of dead phytoplankton, microbes, plant and animal matter, and benthic algae, etc). This report has shown that *Corbicula* can remove vast amounts of small POM including phytoplankton and zooplankton and microbes from the water column and OM from the sediments, which otherwise would have contributed significantly to O<sub>2</sub> demand in the Jordan River. In addition, *Corbicula* reduces turbidity by consuming vast amounts of suspended solids in the water column, which allows more light to reach the benthos, which in turn allows photosynthetic benthic algae to grow and respire O<sub>2</sub> during daylight hours. The net result would be that the proportion of the total O<sub>2</sub> demand in the river contributed by *Corbicula* O<sub>2</sub> consumption rates would be substantially lower. However, as stated earlier, the benefit of *Corbicula* on reducing hypoxia depends on a reduction in the flux of organic detritus to benthic sediments that creates biochemical oxygen demand (BOD) through heterotrophic respiration and decomposition of organic material (Konrad 2013).

#### Estimated Ammonium and Phosphorus Excretion Rates in the Jordan River

Newell et al. (2005) reported average ammonium excretion rates of *Corbicula*:

$$\cong 6.0 \mu\text{mol NH}_4^+ \text{ g}^{-1} \text{ DW h}^{-1} \text{ (DW = dry tissue weight)}$$

and phosphorus excretion rates:

$$\cong 1.2 \mu\text{mol P g}^{-1} \text{ DW h}^{-1} \text{ (DW = dry tissue weight)}$$

Table 64. contains *Corbicula* ammonium and phosphorus excretion rates based on these values.

Table 64. Estimated average ammonium (NH<sub>4</sub><sup>+</sup>) and phosphorus (P) excretion rates of *Corbicula* in the mid-Jordan River

Density (m <sup>-2</sup> ) <sup>a</sup>	Dry weight (g m <sup>-2</sup> ) <sup>b</sup>	NH <sub>4</sub> <sup>+</sup> excretion (μmol m <sup>-2</sup> day <sup>-1</sup> ) <sup>b</sup>	P excretion (μmol m <sup>-2</sup> day <sup>-1</sup> ) <sup>b</sup>
Median = 650	0.52	75	15
Mean (± SE) = 1,436 (910,1962)	1.15 (0.73 1.57)	165 (105, 226)	33 (21, 45)
75 <sup>th</sup> = 1,223	0.98	141	28
95 <sup>th</sup> = 3,700	2.96	426	85

99 <sup>th</sup> = 12,400	9.92	1,426	286
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### Estimated Sediment Organic Matter Consumption Rates in Jordan River

Table 65 contains estimated *Corbicula* organic matter rates in the Jordan River based on these values.

Table 65. Estimated organic matter (OM) consumption rates (mass unit area<sup>-1</sup> day<sup>-1</sup>) by *Corbicula* pedal feeding in the Jordan River.

Density <sup>1</sup>	g m <sup>-2</sup> day <sup>-1</sup>	kg km <sup>-1</sup> day <sup>-1</sup>	metric tons km <sup>-1</sup> year <sup>-1</sup>
Mean	7	72	26
(± SE)	(6, 10)	(46, 986)	(17, 36)
Median	3	33	12
75th	6	61	22
95th	19	185	68
Maximum	62	6,200	226

Boltovskoy et al. (1995) estimated *Corbicula* densities between 450 and 4500 m<sup>-2</sup> (mean 2000 m<sup>-2</sup>) and 66 to 673 mg C m<sup>-2</sup> h<sup>-1</sup> (mean: 289 mg C m<sup>-2</sup> h<sup>-1</sup>) required for respiration only, which translates to approximately 16 to 162 (mean 69) g C m<sup>-2</sup> day<sup>-1</sup>.

### Carbon Consumption and Fixation Rates of *Corbicula* in the Jordan River

Aldridge and McMahon (1978) showed that *Corbicula* had shell production rates of 18–400 g shells m<sup>-2</sup> year<sup>-1</sup> and that dense populations of *Corbicula* are capable of producing large amounts >10 kg shells m<sup>-2</sup> year<sup>-1</sup> (Stayer and Malcom 2007). Baker (2010) estimated that *Corbicula* shells were approximately 12% carbon by weight (Baker 2010). This suggests that average densities in the Jordan River, *Corbicula* are capable of sequestering ≈ 1 kg C m<sup>-2</sup> year<sup>-1</sup>. This could equate to ≈ 10 metric tons C km<sup>-1</sup> year<sup>-1</sup> in some sections of the Jordan River.

### *Potamopyrgus* in the Jordan River

Hall et al. (2003) estimated production, excretion, and egestion rates for *Potamopyrgus* in a highly productive stream at snail densities 500,000 m<sup>-2</sup>. Densities of *Potamopyrgus* in the Jordan River are within this range and the Jordan River is likely much more productive than the river

examined by Hall et al. (2003). Therefore, the estimates made by Hall et al. (2003) are probably similar for the Jordan River. Assuming these values are reasonably accurate, then *Potamopyrgus* in the Jordan River can have production rates  $\approx 1500 \text{ mg AFDM m}^{-2} \text{ day}^{-1}$ ; excretion rate  $\approx 8 \text{ mg N m}^{-2} \text{ day}^{-1}$ ; and egestion rates  $\approx 200 \text{ mg N m}^{-2} \text{ day}^{-1}$ . At these high rates, *Potamopyrgus* is most certainly co-dominating nitrogen and carbon cycles with *Corbicula* in the Jordan River and likely with other ecosystem functions, including those that affect water quality. Much more research is needed on nutrient and carbon rates and other ecosystem effects of *Potamopyrgus* to the river.

### *Corbicula* and *Potamopyrgus* in the Jordan River

Individually, *Corbicula* and *Potamopyrgus* have major ecosystem effects in the Jordan River as shown throughout this report. However, both co-occur in the river with potentially synergistic effects. For example, as illustrated in Figure 67, *Corbicula* filter feed (ingest) vast amounts of POM, nutrients, bacteria, etc. from the water column, which decreases turbidity, increases light penetration, and transform nutrients (TN and TP) into more biologically available forms (e.g.  $\text{NH}_4$  and  $\text{PO}_4$ ). The increased light penetration can allow benthic photosynthetic algae, SAV, and epiphytes on SAV to prosper, which *Potamopyrgus* readily grazes (doesn't graze SAV). The effects of grazing are to stimulate algae and epiphyte production by reducing standing stock and increasing readily used nutrients via snail excretion. Reduction of epiphyte biomass also allows SAV to increase production. Increased primary-autotrophic production mitigated by *Corbicula* and *Potamopyrgus* in combination, accelerates nutrient cycling in the river.

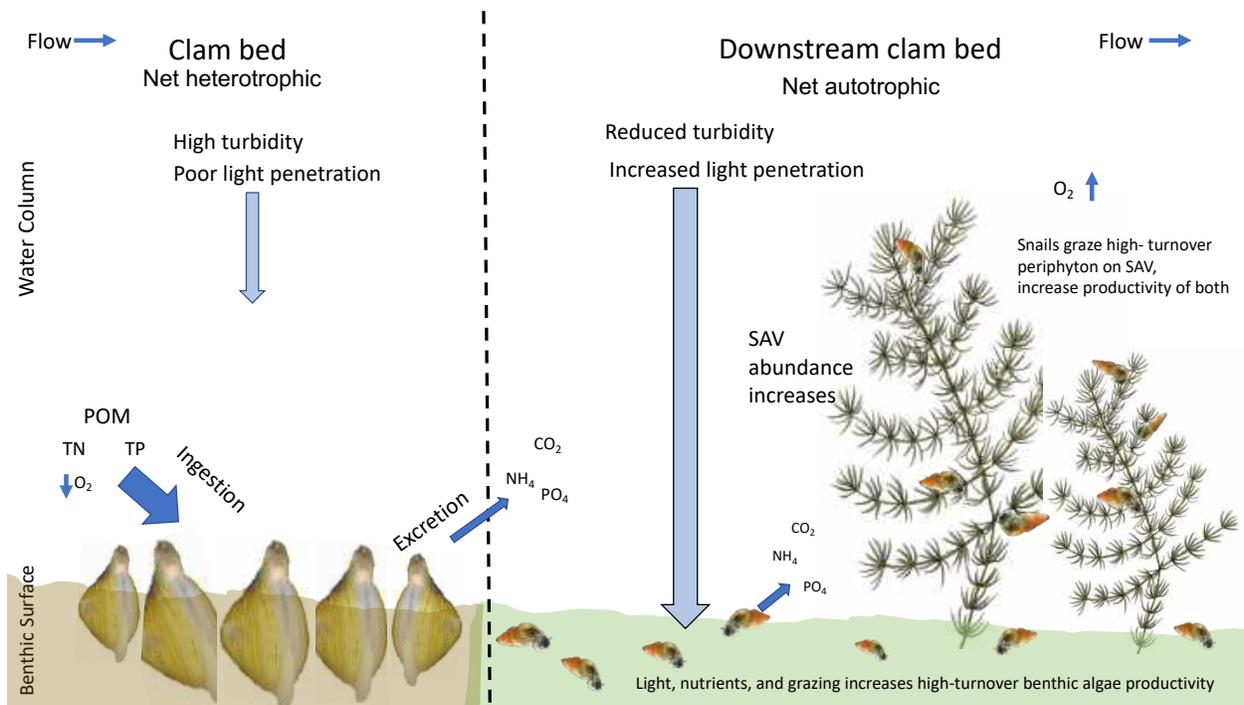


Figure 67. Potential synergistic effects of *Corbicula* and *Potamopyrgus* on nutrient cycling in the Jordan River. See text above for description.

Figure 67 is but one example of the potential synergistic effects of *Corbicula* and *Potamopyrgus* on the Jordan River's ecosystem. Much more research is needed to determine the interaction effects between these snails and clams and the Jordan River ecosystem.

## Discussion and Conclusion

Results from this report clearly show that the invasive 'good luck clam' *Corbicula fluminea* and the New Zealand mudsnail, *Potamopyrgus antipodarum* co-dominate ecosystem functions in the Jordan River with pathways that have been well described in the literature. These snails and clams can mitigate improved water quality in the Jordan River, free of monetary expenditures. Contrary to the current Jordan River paradigm; microbial assemblages do not govern ecosystem functioning in the Jordan River. It is both *Corbicula* and *Potamopyrgus* that co-regulate the community structure of aerobic and anaerobic microbes. The effects of the snails and clams on the Jordan River's metabolism, nutrient cycling, cyanoHABS, etc. should now be well apparent to researchers and managers and when taken into account, explain the vast majority of unexplained variability and discrepancies reported in past research. *Corbicula* and *Potamopyrgus* are here to stay in the Jordan River and for better or worse, are now integral components of what is considered by restoration and conservation ecologists to be a 'novel ecosystem'. A novel ecosystem is the establishment of an ecosystem that differs in composition and/or function from the past system and is an almost inevitable consequence of changing species distributions and environmental alteration through climate and land use change (Root and Schneider 2006; Harris et al. 2006; Hobbs et al. 2009). The novel Jordan River ecosystem is now dependent on the services of two once invasive species but who are now residents to maintain and improve its current ecological state and provide resilience to anthropogenic nutrient inputs; the grazer, *Potamopyrgus* and the filter-feeding, benthic-feeding, pseudofeces-forming bivalve, *Corbicula*.

## Recommendations

1. Conduct field research to verify and update estimated values calculated for Jordan River from literature and presented in this report. Specifically, estimate densities of *Corbicula* and *Potamopyrgus* in sections not surveyed by OreoHelix Consulting and The Wasatch Front Water Quality Council. Conduct in situ experiments using the most up to date methods for estimating: carbon, nitrogen, and phosphorous filtering and consumption rates, excretion rates, and carbon fixation rates, etc. (see Same and Olenin 2005; . Relate these findings to water chemistry values in the Jordan River and determine the effects of the clam and snail. Update all Jordan River reports with this new information. Inform researchers and managers.
2. The Clean Water Act explicitly provides for the protection and propagation of our nation's fish and shellfish, of which *Corbicula* and *Potamopyrgus* obviously are the latter. UDWQ does not differentiate between native and invasive species in their monitoring or protection and is thus responsible for the snails and clams continued

persistence and viability. However, *Corbicula* or *Potamopyrgus* could be having trade-off between positive and negative impacts (e.g. O<sub>2</sub> depletion, lower N:P) in the Jordan River when their densities reach a certain, as of yet determined level. An possible solution would be to harvest *Corbicula*, either recreationally or commercially at a yet to be determined rate, as they do in many places in the world. However, these clams may be considered unsafe for consumption because of toxic substances in their tissues (e.g. metals, *E. coli*). If toxicants are a problem in the Jordan River then it stands to reason that a major impairment in the Jordan River is not nutrients (*Corbicula* and *Potamopyrgus* take care of this) but toxic substances, including *E. coli*, which should be considered a management priority by water quality managers.

3. Consider aquaculture use of *Corbicula* in Jordan River to reduce nutrient inputs from POTWs. Nutrient trading schemes are being considered between municipal waste water treatment facilities and the extra market value of nutrient removal offered by bivalve aquaculturalists in Chesapeake Bay and monitored by EPA. (Newell 2004). *Corbicula* harvesting would also be a measurable contribution to reducing CO<sub>2</sub> emissions and the effects global climate change.

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## Literature Cited

- Aldridge D.W. & McMahon R.F. (1978) Growth, fecundity, and bioenergetics in a natural population of the Asiatic freshwater clam, *Corbicula manilensis* Philippi, from north central Texas. *Journal of Molluscan Studies*, 44, 49–70.
- Alonso, A. and P. Castro-Diez. 2012. The exotic aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca): state of the art of a worldwide invasion. *Aquat. Sci.* 74: 375-383.
- Arango, C. P., Riley, L. A. , Tank, J. L., and R. O.Hall. 2009. Herbivory by an invasive snail increases nitrogen fixation in a nitrogen-limited stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 2009, 66(8): 1309-1317, <https://doi.org/10.1139/F09-079>.
- Asmus RM Asmus H 1991 Mussel beds, limiting or promoting phytoplankton? *J Exp Mar Biol Ecol* 148: 215-232

- Baker, P. and S. Baker. 2010. Carbon fixation by hard clam aquaculture in Florida. Florida Sea Grant College Program. PD-09-10. <http://shellfish.ifas.ufl.edu/projects/shellfish-farm-environment/carbon-fixation/>.
- Beaver, J. R., Crisman, T. L., and R. J. Brock. 1991. Grazing effects of an exotic bivalve (*Corbicula fluminea*) on hypereutrophic lake water. *Lake and Reservoir Management*. 7(1): 45-51.
- Boltovskoy, D., Izaguirre, Ir. And N. Correa. 1995. Feeding selectivity of *Corbicula fluminea* (Bivalvia) on natural phytoplankton. *Hydrobiologia*. 312: 171-182.
- Bott, T.L. 2007. Primary productivity and community respiration. In: Hauer FR, Lamberti GA (eds) *Methods in stream ecology*. Academic Press, San Diego, page 668.
- Bowler, P. A. 1991. The rapid spread of the freshwater hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the Middle Snake River, southern Idaho. *Proceedings of the Desert Fishes Council*. 21: 173-182.
- Bowler, P.A. 2001. Photophobic reactions in Hydrobiid snails from the Owens Valley, California, and the first record of the New Zealand Mudsail, *Potamopyrgus antipodarum* (Gray, 1843) from the Owens River. *Proceedings of the Desert Fishes Council* 32: 51-52
- Buttner, J. K. . 1986. Biology of *Corbicula* in catfish rearing ponds. In: *Proceedings of the Second International Corbicula Symposium*, JC Britton (Ed). American Malacological Union, Hattiesburg. *Am Malacol Bull* 2 (Special ed.) pp 211-218.
- Cleland JD (1988) Ecological and physiological considerations of deposit-feeding in freshwater bivalve, *Corbicula fluminea*. Masters Thesis, University of Texas, Arlington.
- Cohen, R. R. H., Dresler, P.V., Phillips, E. J.P. and R. L. Cory. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol. Oceanogr.* 29(1):170-180.
- Cross, W. F., Rosi-Marshall, E. J., Behn, K. E. et al. 2010. Invasion and production of New Zealand mud snails in the Colorado River, Glen Canyon. *Biol. Invasions*. 12: 3033-3043.
- Dame RF Spurrier JD Wolaver TG 1989 Carbon, nitrogen and phosphorus processing by an oyster reef. *Mar Ecol Prog Ser* 54: 249-256
- Dame RF Dankers N Prins TC Jongsma H Smaal AC 1991a The influence of mussel beds on nutrients in the western Wadden Sea and eastern Scheldt estuaries. *Estuaries* 14: 130-138

- Fulford, R. S., Breitburg, D. L., Newell, R. I. E., Kemp, W.M., and M. Luckenbach. 2007. Effects of oyster population restoration strategies on phytoplankton biomass in Chesapeake Bay: a flexible modeling approach. *Marine Ecology Progress Series*. 336: 43-61.
- Hall, Tank, J. L., and M. F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Front. Ecol. Environ.* 1(8): 407-411.
- Hall, R. O., Dybdahl, M. F., and M. C. VanderLoop. 2006. Extremely high secondary production of introduced snails in rivers. *Ecological Applications*. 16(3): 1121-1131.
- Hakenkamp, C.C. and M. A. Palmer 1999. Introduced bivalves in freshwater ecosystems: the impact of *Corbicula* on organic matter dynamics in a sandy stream. *Oecologia*. 119: 445-451.
- Harris, J.A. et al. (2006) Ecological restoration and global climate change. *Rest. Ecol.* 14, 170–176.
- Henriksen K Kemp WM 1988 Nitrification in estuarine and coastal marine sediments. In: Nitrogen Cycling in Coastal Marine Environments. TH Blackburn J Sorensen (Eds). Wiley and Sons, Chichester, England, pp 205-249
- Hobbs, R. J. , Higgs, E., and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution*. doi:10.1016/j.tree.2009.05.012.
- Huang, S.C., Jeng, S., and H. L. Hsieh. 2005. The function of filter-feeding bivalves in aquatic ecosystems: using Tapeng Bay as an example. *Journal of the Fisheries Society of Taiwan*. 32(1): 17.
- Isom BG (1986) Historical review of Asiatic clam (*Corbicula*) invasion and biofouling of waters and industries in the Americas. In: Britton JC (ed) Proceedings of the Second International *Corbicula* Symposium (American Malacological Bulletin special edition 2). American Malacological Union, Hattiesburg, pp 1±6
- Konrad, C. P. year. 2013. Approaches for evaluating the effects of bivalve filter feeding on nutrient dynamics in Puget Sound, Washington. USGS. Scientific Investigations Report 2013–5237.
- Kristensen E 1988 Benthic fauna and biogeochemical processes in marine sediments, microbial activities and fluxes. In: Nitrogen Cycling in Coastal Marine Environments. TH Blackburn and J Sorensen (Eds). Wiley and Sons, Chichester, England, p 275-299
- Krom MD Berner RA 1981 The diagenesis of phosphorus in a nearshore marine sediment. *Geochim Cosmo Acta* 45: 207-216

- Lauritsen, D. D. 1986. Filter-feeding in *Corbicula fluminea* and its effect upon seston removal. J. N. Am. Benthological Society. 5:165-172.
- Lauritsen, D. D., and S.C. Mozley. 1989. Nutrient excretion by the Asiatic clam *Corbicula fluminea*. J. North. Amer. Benthol. Soc. 8:134-139.
- Leff, Laura G.; Burch, Jarrett L.; and McArthur, J. Vaun .1990. Spatial Distribution, Seston Removal, and Potential Competitive Interactions of the Bivalves *Corbicula Fluminea* and *Elliptio Complanata*, in a Coastal Plain Stream. Freshwater Biology 24(2), 409-416. doi: 10.1111/j.1365-2427.1990.tb00720.x Retrieved from <https://digitalcommons.kent.edu/bscipubs/50>
- Magni P Montani S Takada C Tsutsumi H 2000 Temporal scaling and relevance of bivalve nutrient excretion on a tidal flat of the Seto Inland Sea, Japan. Mar Ecol Prog Ser 198: 139-155
- McMahon, R.F. and A.E. Bogan. 2001 Mollusca: Bivalvia. In: Ecology and Classification of North American Freshwater Invertebrates, 2nd Edition, JH Thorp AP Covich (Eds.), Academic Press, Inc., pp 331-430.
- McMahon R.F. 2002. - Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. Can. J. Fish. Aquat. Sci., 59, 1235-1244.
- Moore, J. W., Herbst, D. B., Heady, W. N. and S. M. Carlson. 2012. Stream community and ecosystem responses to the boom and bust of an invading snail. Biol. Invasions. DOI 10.1007/s10530-012-0240-y.
- Newell RIE (1988) Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? In: Lynch MP, Krome EC (eds) Understanding the estuary: advances in Chesapeake Bay research. Chesapeake Research Consortium, Gloucester Point, VA, p 536–546
- Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J Shellfish Res 23:51–61
- Newell RIE, Koch EW (2004) Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries 27:793–806
- Newell RIE, Langdon CJ (1996) Mechanisms and physiology of larval and adult feeding. In: Kennedy VS, Newell RIE, Eble AF (eds) The eastern oyster *Crassostrea virginica*. Maryland Sea Grant College, College Park, MD, p 185–230

- Newell RIE, Ott J (1998) Macrobenthic communities and eutrophication. In: Malone TC, Malej A, Harding LW, Smodlaka N, Turner RE (eds) Ecosystems at the land–sea 60 margin: drainage basin to coastal sea. *Coast Estuar Stud* 55: 265–293
- Newell RIE, Fisher TR, Holyoke RR, Cornwell JC (2005) Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. In: Dame R, Olenin S (eds) The comparative roles of suspension feeders in ecosystems. NATO Science Series: IV Earth and Environmental Sciences, Vol 47. Springer, Netherlands, p 93–120
- Newell, R. I. E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *Journal of Shellfish Research*. 23(1): 51-61.
- Phelps, H. I. 1994. The Asiatic Clam (*Corbicula fluminea*) invasion and system -level ecological change in the Potomac River estuary near Washington, D.C. *Estuaries*. 17(3):614-621.
- Poff, NL, Palmer MA, Angermeier PL, Vadas Jr RL, Hakenkamp CC, Bely A, Arensburger P, Martin AP (1993) The size structure of a metazoan community in a Piedmont stream. *Oecologia* 95:202±209
- Prokopovich, N. P. 1969. Deposition of clastic sediments by clams. *J. Sediment. Petrol.* 30:891-901.
- Reid, R.G.B, McMahon RF Foighil DO Finnigan R 1992 Anterior inhalant currents and pedal feeding in bivalves. *Veliger* 35: 93-104
- Richards, D. C. 2017a. Lower Mill Creek and Mid-Jordan River Native Mussel Survey 2017: As it pertains to the Central Valley Water Reclamation Facility Discharge. Report to: Wasatch Front Water Quality Council. Salt Lake City, UT.
- Richards, D. C. 2017b. Native Unionoida Surveys, Distribution, and Metapopulation Dynamics in the Jordan River-Utah Lake Drainage, UT. Report to: Wasatch Front Water Quality Council. Salt Lake City, UT. OreoHelix Consulting, Vineyard, UT. Version 1.5 May, 26, 2017. Available at: <http://wfwqc.org/wp-content/uploads/2017/04/Native-Unionoida-Surveys-and-Metapopulation-Dynamics-in-the-Jordan-River-Utah-Lake-drainage-UT-Version-1.5-compressed.pdf>. With supporting documentation at: <http://wfwqc.org/wp-content/uploads/2017/10/Appendix-8-Native-Mussels-Spreadsheet-FINAL-read-only.xlsx>.
- Richards, D. C., L. D. Cazier, and G. T. Lester. 2001. Spatial distribution of three snail species, including the invader *Potamopyrgus antipodarum*, in a freshwater spring. *Western North American Naturalist*.61: 375-380

- Richards, D. C., T. Arrington, S. Sing, and B. L. Kerans. In revision. Competition and coexistence between an invasive aquatic snail and its threatened native congener. American Malacological Society Bulletin.
- Richards, D. C. and T. Arrington. In review. Spatial and environmental relationships of three snail taxa in a freshwater spring: with estimates of their abundance. Journal North American Benthological Society.
- Richards, D. C., C. M. Falter, G. T. Lester, and R. Myers. In revision. Mollusk survey of Hells Canyon reservoirs and free flowing Snake River, Idaho and Oregon, USA: with focus on rare and listed taxa, including a newly described *Taylorconcha* sp. American Malacological Society Bulletin.
- Richards, D. C., P. O'Connell, and D. C. Shinn. In preparation. Growth Rates of the threatened Bliss Rapids Snail, *Taylorconcha serpenticola* and the invasive New Zealand mudsnail *Potamopyrgus antipodarum* at six temperatures.
- Richards, D. C. 2010. Mollusk diversity and estimated predation rates by gastropod shell borehole drillers on *Turritella* spp. at Playa Grande, Las Baulas National Park, Costa Rica. American Malacological Society Newsletter. Vol. 41. No. 2. Pg 5-7.
- Richards, D. C. and T. Arrington. 2008. Evaluation of Threatened Bliss Rapids Snail, *Taylorconcha serpenticola* susceptibility to exposure: potential impact of 'load following' from hydroelectric facilities. American Malacological Society Bulletin.
- Richards, D. C. In review. Some life history studies of the threatened Bliss Rapids snail and invasive New Zealand mudsnail. Western North American Naturalist.
- Richards, D. C. and D. C. Shinn. 2004. Intraspecific competition and development of size structure in the invasive snail, *Potamopyrgus antipodarum*. American Malacological Society Bulletin. 19. 1.2.
- Richards, D. C., P. O'Connell, and D. C. Shinn. 2004. Simple control method for the New Zealand mudsnail, *Potamopyrgus antipodarum*. Journal North American Fisheries Management. 24:114-117.
- Richards, D. C., L. D. Cazier, and G. T. Lester. 2001. Spatial distribution of three snail species, including the invader *Potamopyrgus antipodarum*, in a freshwater spring. Western North American Naturalist. 61: 375-380.
- Risgaard-Petersen N Rysgaard S Nielsen LP Revsbech NP 1994 Diurnal variation of denitrification and nitrification in sediments colonized by benthic microphytes. Limnol Oceanogr 39: 573-579

- Root, T.L. and Schneider, S.H. (2006) Conservation and climate change: the challenges ahead. *Conserv. Biol.* 20, 706-708.
- Seitzinger SP 1988 Denitrification in freshwater and coastal marine ecosystems, ecological and geochemical significance. *Limnol Oceanogr* 33: 702-724
- Shannon, J. P., E. P. Benenati, H. Kloeppel, and D. C. Richards. 2003. Monitoring the aquatic food base in the Colorado River, Arizona during June and October 2002. Annual Report. Grand Canyon Monitoring and Research Center. USGS. Cooperative Agreement-02WRAG0028.
- Sousa, R., Antunes, C., and L. Guilhermino. 2008. Ecology of the invasive clam *Corbicula fluminea* (Muller, 1774) in aquatic ecosystems: an overview. *Ann. Limnol.-Int. J. Lim.* 44(2): 85-94.
- Strayer D.L., Cole J.J., Likens G.E. & Buso D.C. (1981) Biomass and annual production of the freshwater mussel *Elliptio complanata* in an oligotrophic softwater lake. *Freshwater Biology*, 11, 435-440.
- Strayer, D. L. and H. M. Malcom. 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. *Freshwater Biology*. 52: 1611-1617.
- Vincent, Vaillancourt & Lafontaine, 1981
- Vincent B. & Lafontaine N. (1984) Cycle de developpement, croissance et production de *Sphaerium striatinum* (Bivalvia: Pisidiidae) dans le Saint-Laurent (Quebec). *Canadian Journal of Zoology*, 62, 2418-2424.
- Way, C.M., Hornbach, D. J., Miller, Way, C. A. , Payne, B. S., and A. C. Miller. 1990. Dynamics of filter-feeding in *Corbicula fluminea* (Bivalvia: Corbiculidae). *Can. J. Zool.* 68: 115-120.

## 1 Appendices

*Appendix 36. Summary of approaches for assessing the effects of bivalve filter feeding on nutrient dynamics. From Konrad 2013.*

Approach	Key data requirements	Typical temporal scale	Temporal scaling	Typical spatial resolution	Spatial scaling
1. Nutrient mass balance	Mass of bivalve harvested in area of interest	Life-span of bivalve	Can be scaled down to a "typical" year by calculating mean annual nutrient uptake	Area of bivalve bed harvested	Can be scaled over larger areas where bivalve densities are known and growth rates are comparable
2. Spatially aggregated model based on clearance rates	Filter feeding rates representative of area of interest	Synoptic—same as period used to calculate filtration rate	Can be scaled over longer periods by adjusting filtration rate to account for temporal variability in seston, temperature, metabolic demand of bivalve, etc.	Same as area used to calculate filtration rate	Can be scaled over larger areas by adjusting filtration rate for variability in seston, temperature, bivalve density, etc.
3. Spatially aggregated biophysical indicators	Rates of primary production, filter feeding, and mixing for area of interest	Seasonal—same as period used to calculate rates in key data requirements	Can be scaled over time by adjusting rates to account for temporal variability	Area of estuary where rates (key data requirements) are relatively homogeneous	Scaling over larger areas requires rates appropriate for the area
4. Biophysical model in a spatial framework	Spatially distributed rates of primary production, filter feeding, and mixing	Seasonal—same as period used to calculate rates in key data requirements	Can be scaled over time by adjusting rates to account for temporal variability	Area of estuary where rates (key data requirements) are relatively homogeneous	Scaling over larger areas requires appropriate spatial distributions of rates and parameters
5. Biogeochemistry in a low trophic level model	Rates of primary production (as function of nutrient concentrations) and filter feeding by bivalve, dissolved nutrient flux from bivalve (soluble and solid) and from sediment diagenesis, denitrification, rates of other filter feeders and associated nutrient fluxes to sediment and water column	Seasonal—same as period used to calculate rates in key data requirements	Can be scaled over time by adjusting rates to account for temporal variability	Area of estuary where rates (key data requirements) are relatively homogeneous	Scaling over larger areas requires appropriate spatial distributions of rates and parameters
6. Spatially aggregated, bioenergetics model with full trophic dynamics	Spatially distributed rates of primary production, filter feeding, higher level predation, and decomposition	Seasonal—same as period used to calculate rates in key data requirements	Can be scaled over time by adjusting rates to account for temporal variability	Area of estuary where rates (key data requirements) are relatively homogeneous	Scaling over larger areas requires appropriate spatial distributions of rates and parameters
7. Spatially explicit ecosystem model	Spatially distributed rates of all significant biological and physical processes (may be a subset of all those listed for other approaches)	Seasonal—same as period used to calculate rates in key data requirements	Can be scaled over time by adjusting rates to account for temporal variability	Area of estuary where rates (key data requirements) are relatively homogeneous	Scaling over larger areas requires appropriate spatial distributions of rates and parameters

*Appendix 37. Effects of inorganic suspended matter on mussel population viability in the Utah lake/Jordan river drainage: a preliminary literature review.*

Version 1.2

***Effects of Inorganic Suspended Matter on Mussel Population Viability in the Utah Lake/Jordan River Drainage: A Preliminary Literature Review***

Addendum

To:

Richards (2016) “Recalculation of Ammonia Criteria for Central Valley Water Reclamation Facility’s Discharge into Mill Creek, Salt Lake County, UT based on Native Unionoida Surveys and Metapopulation Dynamics”

and

Richards (2016) “Recalculation of Ammonia Criteria for Timpanogos Special Service District and the Cities of Orem and Provo Water Reclamation Facilities Discharge into Utah Lake based on Native Unionoida Surveys and Metapopulation Dynamics”

Submitted to:

Jordan River Farmington bay Water Quality Council

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## Introduction

Detailed analyses of native mussel population surveys and viability in the Utah Lake/Jordan River drainage were presented to the Jordan River Farmington Bay Water Quality Council in several reports including, Richards (2016) “*Recalculation of Ammonia Criteria for Central Valley Water Reclamation Facility’s Discharge into Mill Creek, Salt Lake County, UT based on Native Unionoida Surveys and Metapopulation Dynamics*” and Richards (2016) “*Recalculation of Ammonia Criteria for Timpanogos Special Service District and the Cities of Orem and Provo Water Reclamation Facilities Discharge into Utah Lake based on Native Unionoida Surveys and Metapopulation Dynamics*”. Because of the large number and combination of stressors and factors examined in these reports that were considered responsible for the near extinction of the two once abundant native mussel taxa in this drainage, *Margaritifera falcata* and *Anodonta nuttalliana/californiensis*, only a limited discussion on the effects of suspended inorganic matter (SIM) on their viability was included. A brief literature review on the importance of SIM to native mussel population viability in Utah Lake/Jordan River drainage follows.

## Literature Review

High concentrations of inorganic solids (sand, silt, clay, etc.) often originate from erosion related to agriculture, forestry, and urbanization, and can alter feeding patterns, substrate composition, and food web dynamics (Waters 1995). Concentrations of suspended inorganic matter (SIM)(e.g. suspended inorganic solids) are well known to affect mussel respiration, growth, parasite infestation and reproduction (Box and Mossa 1999, Robinson et al. 1984, Alexander 1994, Rosewarne et al 2013, and Tokumon et al. 2016). These effects subsequently can reduce native mussel population viability and increase extinction risk.

Feeding is strongly impeded for many filter feeding bivalves due to high levels of SIM (Robinson et al. 1984, Jorgensen 1996, Lei et al. 1996, Cheung and Shin 2005, Velasco and Navarro 2005, and Tokumon et al. 2016). The reasons for negative effects of SIM on mussel feeding are numerous and can include decreases in the proportion of organic material (i.e. food) in suspension, which can then result in much higher energy expenditures in sorting out and eliminating energetically unprofitable particles (Jorgensen 1990, Velasco and Navarro 2005, Safi and Hayden 2010). Tokumon et al. (2016) suggested that water pumping activity of the invasive bivalve, *Limnoperna fortunei* (Family Mytilidea) did not differ noticeably at different SIM concentrations, but at low sediment loads the production of pseudofaeces was moderate whereas at high concentrations mussels expelled mucus-embedded strings of material at noticeably higher rates. This indicates that the ability of mussels to sort and ingest organic particles from total suspended solids can be reduced severely by SIM (Robinson et al. 1984, Berg et al 1996, Baker et al 1998).

Gascho Landis et al. (2013) showed that total suspended solids (TSS) interfered with fertilization and caused reproductive failure of *Ligumia subrostrata* (Family Unionidae). They found that clearance rates dropped abruptly and remained uniformly low at a threshold level of total suspended solids  $> 8 \text{ mg l}^{-1}$ . Gascho Landis et al. (2013) proposed that “reduced clearance rates could decrease the chance of females encountering suspended sperm during filter feeding, or an increase in pseudofeces production could bind sperm in mucus and lead to its egestion before fertilization”. They also concluded that “interruption of fertilization coincident with high TSS (total suspended solids) is a potential mechanism to explain the lack of mussel recruitment in many locations”.

TSS can have profound effects on reproduction. In the Gascho Landis et al. (2013) study, the percentage of brooding *Ligumia subrostrata* females decreased sharply with increasing TSS and complete reproductive failure occurred in hypereutrophic ponds with TSS  $> 20 \text{ mg l}^{-1}$ . They found that the proportion of females that became gravid during the experiment was strongly related to TSS best characterized by an exponential decline. At the lowest mean TSS, the majority of females were gravid, but this percentage declined rapidly with increasing mean TSS. No gravid unionid females were found at TSS  $> 20 \text{ mg l}^{-1}$  (Gascho Landis et al. 2013). Gascho Landis et al. (2013) also reported that *L. subrostrata* mussels were largely extirpated from lakes with the shallowest Secchi depths (hyper- eutrophic lakes), possibly indicating a threshold above which increased nutrients and resultant organic solids have a negative effect.

In other studies, decreased clearance rates (the volume of water cleared of particles per unit time) for 3 unionid species subjected to intermittent exposure to extremely high levels of suspended sediment was proposed as a cause of decreased growth or starvation (Aldridge et al. 1987). Recruitment strength of *Margaritifera margaritifera*, the European version of *M. falcata* was negatively related to turbidity and deposited sediment, but the mechanism for this relationship was unclear (Osterling et al. 2010). Others have also shown that unionid filter feeding is often disrupted at levels  $> 20 \text{ mg l}^{-1}$  (Hornbach et al. 1984, Way et al. 1990).

Even relatively pollution tolerant invasive Asian clams (*Corbicula* sp.) and fingernail clams (Sphaerium) initiated pseudofeces production at 17 to 20 mg l<sup>-1</sup> TSS (Fuji 1979, Hornbach et al. 1984, Way et al. 1990). Invasive Zebra mussels (*Dreissena polymorpha*) can initiate pseudofeces production at 27 mg l<sup>-1</sup> (Lei et al. 1996, Schneider et al. 1998) and TSS loads dominated by inorganic particles can decrease their growth rates (Osterling et al. 2007).

#### SIM and Native Mussel Viability in the Utah Lake/Jordan River Drainage

Total suspended solids in Utah Lake and Jordan River proper, although relatively low compared to many other waters in the world (Meybeck 2003), have levels that are likely detrimental to native mussel viability. By itself, high levels of TSS could explain the absence of *Margaritifera falcata* and the near extirpation of *Anodonta nuttalliana/californiensis* from this drainage. Combined with the other factors reported in the Richards 2016 reports; the likelihood of recolonization of either taxon in the drainage is near zero.

Jordan River Farmington Bay Water Quality Council researchers reported TSS levels of 56.3 mg l<sup>-1</sup> (VSS = 11.7 mg l<sup>-1</sup>) in Utah Lake at its outlet into the Jordan River. Background TSS levels are typically between 23 and 38 mg l<sup>-1</sup> (VSS about 5 mg l<sup>-1</sup>) downstream in the Jordan River. These TSS levels are well within and above the known ranges that have been shown to severely affect mussel reproduction (see Literature Review above). High levels of TSS in Beer Creek that supports one of the last remaining *Anodonta nuttalliana/californiensis* populations could also partially explain why no apparent reproduction has been observed. TSS will likely continue to negatively affect remaining native mussel viability and their recolonization potential in the Utah Lake/Jordan River drainage until TSS levels are drastically reduced from sources such as erosion related to agriculture, forestry, industrialization, and urbanization.

#### Literature Cited

- Aldridge, D. W., Payne, B. S., A. C. Miller. 1987. The effects of intermittent exposure to suspended solids and turbulence on 3 species of freshwater mussels. *Environmental Pollution* 45:17–28.
- Alexander, J. E., Thorp, J. H. and R. D. Fell. 1994. Turbidity and temperature effects on oxygen consumption in the Zebra Mussel (*Dreissena polymorpha*). *Canadian Journal of Fisheries and Aquatic Sciences*. 51: 179-184.
- Baker, S. M. Levinton, J. S. , Kurdziel, J. P. and S. E. Shumway. 1998. Selective feeding and biodeposition by zebra mussels and their relation to changes in phytoplankton composition and seston load. *Journal of Shellfish Research*. 17: 1207-1213.
- Berg, D. J., Fisher, S. W. and P. F. Landrum. 1996. Clearance and processing of algal particles by zebra mussels (*Dreissena polymorpha*). *Journal of Great Lakes Research*. 22: 779-788.
- Box, J.B. and J. Mossa. 1999. Sediment, land use, and freshwater mussels: prospects and problems. *Journal of the North American Benthological Society*, 18, 99–117.
- Cheung, S. and P. Shin. 2005. Size effects of suspended particles on gill damage in green-lipped mussel. *Marine Pollution Bulletin*. 51: 801-810.
- Fuji, A. 1979. Phosphorous budget in a natural population of *Corbicula japonica* Prime in a poikilohaline lagoon, Zyusan-Ko. *Bulletin of the Faculty of Fisheries Hokkaido University* 30:34–49.
- Gascho Landis, A. M. Haag, W. R. and J. A. Stoeckel. 2013. High suspended solids as a factor in reproductive failure of a freshwater mussel. *Freshwater Science*. 32: 70-81.

- Hornback, D. J. , Way, C. M. Wissing, T. E., and A. J. Burky. 1984. Effects of particle concentration and season on the filtration rates of the freshwater clam, *Sphaerium striatinum* Lamarck (Bivalvia, Pisidiidae). *Hydrobiologia*. 108:83–96.
- Jorgensen, C. B. 1990. Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen and Olsen. Fredensborg. Denmark.
- Jorgensen, C. B. 1996. Bivalve filter feeding revisited. *Marine Ecology Progress Series*. 142: 287-302.
- Lei, J., Payne, B. S. and S. Y. Wang. 1996. Filtration dynamics of the Zebra Mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Sciences*. 53: 29-37.
- Meybeck, M., Laroche, L., Durr, H. H., and J. P. M. Syvitski. 2003. Global variability of daily total suspended solids and their fluxes in rivers. *Global and Planetary Change*. 39:65-93.
- Osterling, E. M. Bergman, E. , Greenberg, L. A., Baldwin, B. S., and E. L. Mills. 2007. Turbidity-mediated interactions between invasive filter-feeding mussels and native bioturbating mayflies. *Freshwater Biology* 52:1602–1610.
- Robinson, W. E., Wehling, W.E., and M. P. Morse. 1984. The effect of suspended clay on feeding and digestive efficiency of the surf clam, *Spisula solidissima* (Dilwyn). *Journal of Experimental Marine Biology and Ecology*, 14: 1-12.
- Rosewarne, P. J., Svendsen, J. C., Mortimer, R. J. G. and A. M. Dunn. 2013. Muddied waters: suspended sediment impacts on gill structure and aerobic scope in an endangered native and an invasive freshwater crayfish. *Hydrobiologia*. 722: 61-74.

- Safi, K. A., and B. Hayden. 2010. Differential grazing on natural planktonic populations by the mussel *Perna canaliculus*. *Aquatic Biology*. 11: 113-125.
- Schneider, D. W., Madon, S. p., Stoeckel, J. A., and R. E. Sparks. 1998. Seston quality controls zebra mussel (*Dreissena polymorpha*) energetics in turbid rivers. *Oecologia* (Berlin). 117:331–341.
- Tokumon, R. , Cataldo, D., and D. Boltovskoy. 2016. Effects of suspended inorganic matter on filtration and grazing rates of the invasive mussel *Limnoperna fortunei* (Bivalvia: Mytiloidea). *Journal of Molluscan Studies*. 82: 201-204.
- Velasco, L. A. and J. M. Navarro. 2005. Feeding physiology of two bivalves under laboratory and field conditions in response to variable food concentrations. *Marine Ecology Progress Series*. 201: 115-124.
- Way, C. M., Hornbach, D. J., Payne, B. S., and A. C. Miller. 1990. Dynamics of filter feeding in *Corbicula fluminea* (Bivalvia, Corbiculidae). *Canadian Journal of Zoology* 68:115–120.
- Waters, T. F. 1995. *Sediment in streams: sources, biological effects, and control*. American Fisheries Society, Bethesda, Maryland.