

# The influence of two differently sized dams on mussel assemblages and growth

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**Abstract** Dams have been shown to impact freshwater mussels. We examined how mussels respond to differently sized dams (18 vs. 4 m) on the St. Croix River and its tributary, the Sunrise River. We hypothesized that: mussel density and growth rate would be greater downstream of the smaller dam due to the relatively greater food subsidies and temperature effects of the reservoir above it; and the effects of the small dam would moderate downstream as the localized impacts of the dam were reduced. We quantitatively sampled mussels upstream and downstream of the dams. For a common species, *Actinonaias ligamentina*, we ascertained growth rates by measuring successive growth rings. The highest mussel richness and diversity were upstream and downstream of the large dam. Higher mussel density was found immediately below the small dam but

declined downstream. *A. ligamentina* downstream of the small dam grew faster and were larger than individuals in other reaches. Food availability and temperature appeared to influence mussel density and growth rate for *A. ligamentina* downstream of the small dam. This study provides information that may help managers decide whether to remove small dams or to maintain them because of the unique mussel habitats below these structures.

**Keywords** Freshwater mussel · Unionid · Dam · Growth · Community density · Species diversity · *Actinonaias ligamentina*

## Introduction

For millennia, human development has relied on the ability to control the magnitude and timing of water movement. By constructing dams and reservoirs, societies have augmented the supply of water during droughts, reduced flood hazards, irrigated farmlands, produced hydropower, and provided recreational opportunities (Poff & Hart, 2002; Arthington et al., 2010). Yet the peak of this construction, along with its subsequent impacts, has only occurred within the past century (Ignatius & Stallins, 2011).

The massive proliferation of dams has fundamentally transformed the riverine landscape of North America. By changing the flow regime, dams significantly alter the physical structure of rivers. Free-

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flowing ecosystems turn into isolated segments of riverine habitat, restricting the ability of certain organisms to access suitable dwelling areas (Galbraith & Vaughn, 2011; Ignatius & Stallins, 2011). In turn, reduced connectivity and degradation of habitat can become a density-independent source of mortality (Gregory et al., 2002). Other challenges dams pose to organisms include exposure to novel environmental conditions, changes in the type and intensity of biotic interactions, a reduction in genetic diversity, and an accompanying influx of exotic plants and animals (Ignatius & Stallins, 2011). In addition to the direct effects of dams on aquatic organisms, there are also a variety of indirect effects. For example, as sediment traps, dams can influence nutrient retention by reducing velocity and increasing the residence time of water (Gregory et al., 2002; Stanley & Doyle, 2002) and can change the natural variation of stream temperature (Lessard & Hayes, 2003). However, dam size and mode of operation greatly influences the various impacts dams have on the physical and biological structure of stream systems, thus making attempts to extrapolate dam effects beyond site level analyses problematic. The site-specific nature of many dam impacts underscores the importance of the continued examination of a range of dams in a variety of riverine systems.

Freshwater mussels, widely recognized for their ecosystem engineering capabilities, account for nearly 50–90% of benthic biomass in North American river systems (Vaughn & Hakenkamp, 2001; Gutierrez et al., 2003; Vaughn et al., 2008). They influence nutrient availability in the water column through their prodigious filter-feeding capacity (Vaughn et al., 2004; Newton et al., 2011), affect sediment structure by producing feces and pseudofeces, and provide habitat for benthic algae and macroinvertebrates (Vaughn & Spooner, 2006). However, the effects of systemic habitat destruction, namely through riverine fragmentation, have caused a marked decline in freshwater mussel populations (Master et al., 2000; Strayer, 2008; Haag, 2012). Further, existing mussel populations often remain isolated from sources of recolonization, thus increasing their vulnerability to extinction (Sethi et al., 2004; Haag, 2012). An important factor in determining the downstream impact of a dam on mussel assemblages is distance. Vaughn & Taylor (1999) found that mussel assemblages “recovered” from the impact of a dam, but only

if there was sufficient distance before the next impoundment. As conditions alter from riverine just below the dam to lentic in the next downstream reservoir, mussel species composition often changes with abundance and diversity declining.

The effects of large dams on aquatic organisms have been well documented, but few studies have examined effects of ubiquitous small, surface-release or low-head dams (overflow or spillway structures) (Gangloff et al., 2011). This is mainly due to the fact that >90% are privately owned or occur on smaller, more difficult to access streams (Singer & Gangloff, 2011). Existing research has highlighted the negative impacts of dams on mussels, including interruptions to the natural flow regime, altered sediment cycles and restrictions in host fish distributions (Sethi et al., 2004). At the same time, other studies suggest that some invertebrates in reaches downstream from lake-outlets and low-head dams may benefit from lentic-derived food or temperature subsidies (Gangloff et al., 2011). Indeed, some tailwater reaches in rivers impounded by small dams support dense mussel beds with abundances comparable to free-flowing rivers (Haag, 2012). In addition to influencing mussel density, the heat and food resource supplements immediately below the dam may enhance growth conditions for mussels (Singer & Gangloff, 2011). Since mussel size is correlated with reproductive output (Haag, 2012), with larger females producing more and higher quality glochidia than smaller conspecifics, increased growth rates can benefit mussel populations (Singer & Gangloff, 2011).

Dam removal is increasingly being used in stream restoration projects as a means to enhance habitat connectivity and ecosystem function; however, habitat- and assemblage-level effects of small dams on stream mollusk assemblages are poorly documented (Gangloff et al., 2011). Sediment movement and geomorphic adjustments associated with uncontrolled dam removals may have negative consequences for downstream mollusk populations (Sethi et al., 2004). The rapid aging of small dams, as well as the costs of maintaining relicts belonging to an outdated infrastructure, suggest that dam removal will continue at a brisk pace for the foreseeable future (Poff & Hart, 2002). Doyle & Shields (2012) describe the economic and policy forces that tend to favor dam removal. Yet many small dams and their reservoirs have existed for decades, suggesting that by now, river channels have

adjusted to altered hydrologic and sediment transport regimes; thus, dam removal itself could represent a geomorphic disturbance to a quasi-adjusted riverine system (Doyle et al., 2003). Considering not only that mussels influence several critical ecosystem processes (e.g., transferring nutrients from the water column to the benthic environment, and their shells providing habitat for various organisms) but also their current state of endangerment, dam removal may prove too risky to undertake, given the possibility of wiping out downstream mussel populations.

The purpose of this study was to describe how mussel assemblages and growth of a common mussel in this system [*Actinonaias ligamentina* (Lamarck, 1819)] responded to the presence of dams on two rivers. We hypothesized that: (1) mussel density and growth rate would be greater downstream of the smaller dam on the tributary stream compared to the larger dam on the St. Croix due to the relatively greater food subsidies and temperature effects of the reservoir above the smaller dam, and (2) the effects of the small dam would moderate downstream as the localized impacts of the small dam were reduced.

## Methods

### Study area

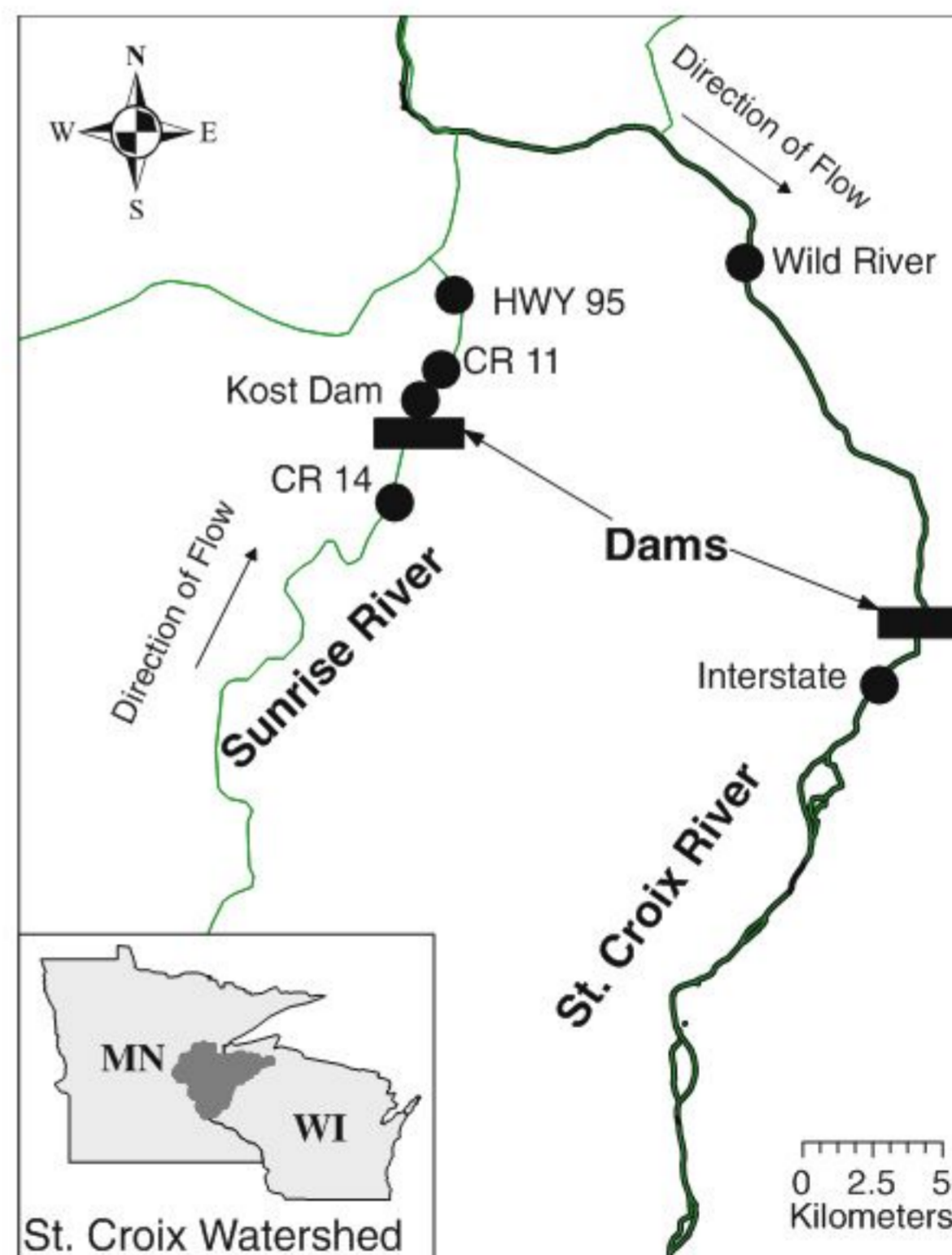
The St. Croix River is a national Wild and Scenic River with its headwaters in northwestern Wisconsin and flows 200 km south to its confluence with the Mississippi River in east central Minnesota (Fig. 1). It drains a watershed of  $\sim 20,000$  km<sup>2</sup> (Fago & Hatch, 1993) and passes through two ecoregions the Northern Lakes and Forests (NLF) ecoregion in the north and the North Central Hardwood Forests (NCHF) ecoregion in the south (Niemela et al., 2005). There are two existing dams on the mainstem (remnants of older logging dams also exist), with the 18 m high hydroelectric dam at Taylor's Falls, MN and St. Croix Falls, WI being the largest. The St. Croix River is home to 41 species of mussels including four federally endangered species (Hornbach, 2001; USFWS, 2012). The lower St. Croix River holds some of the most dense and diverse mussel assemblages in Minnesota and Wisconsin (Sietman, 2003).

The Sunrise River is a major tributary, generally flowing north-northwest before converging with the St.

Croix River (Fig. 1). A catchment area of  $\sim 259$  km<sup>2</sup> drains into the Sunrise River (Waters, 1977). The main branch (South Fork) of the Sunrise is  $\sim 40$  km long with a width ranging from 5 to 25 m. There are three intact dams along this reach with the largest being Kost Dam, a former low-head ( $\sim 4$  m) hydroelectric dam. The Sunrise River is home to 21 mussel species (Davis & Miller, 1996). The mussel assemblage downstream of Kost Dam is unusually dense compared to other low-head dams and unimpounded streams in Minnesota (pers. comm. Bernard Sietman & Mike Davis, Minnesota Department of Natural Resources).

### Mussel sampling

We sampled mussels at four locations in the Sunrise River in 2012 and two locations in the St. Croix River, one in 2010 and one in 2011. In addition at one site in the Sunrise River (Kost Dam) we sampled mussels in 1998, 2004, and 2010. For the Sunrise River sampling in 2012 we chose one site upstream of Kost Dam and



**Fig. 1** Map of the study area showing the two river systems, the St. Croix River and its tributary the Sunrise River. Circles depict sampling sites and rectangles represent the location of dams

three sites downstream of the dam (Fig. 1). We used a Garmin® model 60CSx GPS system to map a 100 m river reach at each location and used ArcMap® 10.0, to select 25 random points each reach for sampling 0.25 m<sup>2</sup> quadrats. In the St. Croix River [2010 at the downstream site (Interstate) and 2011 at the upstream site (Wild River)] as well as at the Kost Dam site on the Sunrise River in 1998, 2004, and 2010 we used a different method to choose sampling locations. We took 120, 100, and 40 quadrats at Interstate, Wild River and Kost Dam, respectively, half being taken within 10 m of shore with the remaining midstream. A fuller description of the sampling methodology used in 1998, 2004, and 2010 is detailed in Hornbach & Deneka (1996). For all quadrats taken in this study, divers removed approximately the top 10 cm of substrate, including mussels, placing it in a 20-l bucket. The sediment was passed through a series of five sieves with openings of 91.9, 50, 11.8, 5.9, and 0.5 mm, respectively. Care was taken to collect juvenile mussels attached to the sieves or to objects by their byssal threads. Mussels collected were identified and their length (maximum anterior–posterior dimension) was measured with a digital caliper to the nearest 0.1 mm. Mussel nomenclature follows Turgeon et al. (1998). Analyses of variance were used to examine differences in mussel density on log-transformed data. All statistical analyses were carried out with JMP Pro 9.0.2® (SAS Institute, Cary, NC).

#### *Actinonaias ligamentina* growth

We used external shell measurements to assess the growth of *A. ligamentina*, the numerically dominant species at three of four sites in the Sunrise River and a co-dominant at the Interstate and Wild River sites on the St. Croix River. We measured the anterior to posterior length of presumptive annuli with a digital caliper to the nearest 0.1 mm. Studies by Sansom et al. (2013) on aging *A. ligamentina* at Wild River and Interstate showed that external ring counts consistently underestimated internal ring counts (thin sections of shells) by 4 years. Internal ring counts have been used widely to estimate mussel age (Haag & Commens-Carson, 2008). Despite differences in internal and external age estimates, growth appraisals were consistent between the two methods (Sansom et al., 2013). In this study, the erosion of the umbo of the shells of many individuals made age determination impossible.

Because our external measurements of growth do not accurately assess age, we used Ford–Walford plots [ $L_{t+1} = L_{\infty} (1 - e^{-K}) + L_t e^{-K}$  (Anthony et al., 2001)] to estimate parameters of the von Bertalanffy model of growth [ $L_t = L_{\infty}(1 - e^{-K(t-t_0)})$  where  $L_t$  is length (mm) at time  $t$  (age),  $L_{\infty}$  is length (mm) at time infinity (the predicted mean maximum length for the population),  $K$  is a growth constant that describes the rate at which  $L_{\infty}$  is attained,  $t$  is age (years) and  $t_0$  is the time at which length = 0 (Haag & Rypel, 2011)]. Since there can be an interaction between  $K$  and  $L_{\infty}$  it is often difficult to interpret these values. In this study an analysis of covariance with  $L_{t+1}$  as the dependent variable, location as the independent variable and  $L_t$  as a covariable allows for the examination of the differences among locations in  $K$  and  $L_{\infty}$ . We also examined the growth interval between adjacent external rings and examined whether these growth intervals differed among populations, while adjusting for the size of the organism (the starting length of the external ring for each growth interval) using analysis of covariance.

#### Habitat factors

Previous studies suggest that some invertebrates in reaches downstream from lake-outlets and low-head dams may benefit from lentic-derived food or temperature subsidies (Gangloff et al., 2011). For the period June 8–October 12, 2012 the water temperature was logged every 15 min at the four Sunrise River sites using StarOddi® temperature loggers. Loggers were lost at the Sunrise River CR 11 site. At the downstream St. Croix River site (Interstate), 15 min water temperature data were obtained from the USGS gaging site (USGS gage 05340500). In 2009 water temperature was logged every 15 min with iBCod® temperature loggers at both St. Croix River sites. Degree days for growth were calculated based on Snyder (2005) using minimum and maximum temperatures for growth of 10 and 30°C, respectively. Spooner & Vaughn (2008) indicate that *A. ligamentina* is a thermally sensitive species with temperatures >25°C leading to metabolic stress. At temperatures <15°C, metabolic activities were low.

Because food availability varies seasonally and with discharge, we measured sediment organic matter as a proxy for long-term organic input available for mussel consumption. Taylor & Roff (1982) indicated

that the nature of allochthonous inputs and physical features, such as water velocity, were important in determining the character of benthic particulate organic matter. Benstead et al. (2009) describe the complex interactions between sediment organic matter storage, organic matter input to streams and nutrient enrichment. They conclude that the storage of organic matter in stream sediments is related to both organic matter inputs and heterotrophic processing of these sediments. Thus, we measured benthic organic matter by taking 10 cm deep sediment cores from each quadrat where mussels were sampled and using weight loss on ignition (500°C) as a measure of organic matter.

## Results

### Mussel assemblages

The mussel assemblage at Kost Dam had the highest density (>4.5 times the next most dense site CR 11—Table 1) of the four Sunrise River sites and the two St. Croix River sites (ANOVA  $F_{5,314} = 12.8$ ,  $P < 0.0001$  for total density and  $F_{5,314} = 35.9$ ,  $P < 0.0001$  for *A. ligamentina*). The mussel assemblage at the downstream St. Croix site (Interstate) had the greatest species richness and diversity with *Truncilla truncata*, *A. ligamentina*, and *Pleurobema sintoxia* being the most common species, accounting for about 40% of the mussels. Another four species, *Cyclonaias tuberculata*, *Elliptio dilatata*, *Fusconaia flava* and *Quadrula pustulosa*, account for another 26% of the assemblage (Table 1). At the upstream St. Croix site (Wild River) *Actinonaias ligamentina* is a co-dominant (along with *E. dilatata* and *Q. pustulosa*). The assemblage at Kost Dam is most similar to those sites downstream in the Sunrise, with *A. ligamentina* numerically dominating all sites. The mussel assemblage at the upstream Sunrise River site (CR 14) is most unlike the other five sites in this study, being dominated by *Amblema plicata*. The two St. Croix River sites had higher species richness and diversity indices than any of the Sunrise River sites (Table 1). Within the Sunrise River the Kost Dam site had the highest species richness, but the upstream site (CR 14) had the highest species diversity because the population was not as dominated by a single species as the other Sunrise River sites.

The total mussel density at the Kost Dam site declined 43% during the period from 1998 to 2012 but this decline was not statistically significant (repeated measures ANOVA,  $F_{2,9} = 1.86$ ,  $P = 0.2$ ) (Fig. 2). The density of the dominant species, *A. ligamentina*, declined by 22% and this decline was also not statistically significant (repeated measures ANOVA,  $F_{2,9} = 0.37$ ,  $P = 0.7$ ).

The shell-length frequency diagrams of *A. ligamentina* showed a skewed distribution of mussels toward large size classes throughout this 1998–2010 period (Fig. 3). A contingency analysis (grouping mussels into four shell-length classifications—0–80, 80–100, 100–120, and >120 mm) showed significant differences in the shell-length distributions, ( $\chi^2 = 65.4$ , 6 df,  $P < 0.0001$ ) with a decrease in the proportion of smaller mussels (<80 mm) from 14% of the population in 1998 to 5% of the population in 2010 and a concomitant increase in the 100–120 mm size class from 37 to 53% of the population.

### *Actinonaias ligamentina* growth

*Actinonaias ligamentina* shell-length frequency diagrams for the St. Croix River sites [downstream (Interstate) from 2010, upstream (Wild River) from 2011] and Sunrise River sites (2012) indicate that not only are *A. ligamentina* more dense at Kost Dam, but the population also consists of larger individuals [those > 100 mm—contingency analysis on the four shell-length classifications described in the paragraph above— $\chi^2 = 132$ , 15 df,  $P < 0.0001$ ; (Fig. 4)] than other sites in the Sunrise or St. Croix Rivers. Interestingly, only the downstream St. Croix site shows a significant number of smaller individuals in the population.

Table 2 shows the growth constant ( $K$ ) and the predicted maximum length of *A. ligamentina* ( $L_{\infty}$ ) from the von Bertalanffy model of growth as obtained from Ford–Walford plots. Kost Dam had the highest predicted maximum length while Wild River had the highest growth constant.

Because of interaction between  $K$  and  $L_{\infty}$ , it is often difficult to interpret these values. However, an analysis of covariance of the Ford–Walford plots with  $L_{t+1}$  as the dependent variable, location as the independent variable and  $L_t$  as the covariable shows  $L_{t+1}$  is significantly influenced by  $L_t$ , location and their interaction ( $F_{1,2746} = 79,720$ ,  $F_{4,2746} = 105$  and

**Table 1** Percent composition of the mussel assemblage, mussel density, and assemblage richness and diversity in the Sunrise and St. Croix Rivers, MN

Species	Sunrise River—2012				St. Croix River	
	CR 14 (%)	Kost Dam (%)	CR 11 (%)	HWY95 (%)	Wild River (%)	Interstate (%)
<i>Actinonaias ligamentina</i> (Lamarck, 1819)	1.5	72.1	66.1	82.4	26.9	13.1
<i>Alasmidonta marginata</i> (Say, 1818)	1.5	0.2				0.5
<i>Amblyma plicata</i> (Say, 1817)	47.7	3.6	9.3	5.9	0.9	3.0
<i>Cyclonaias tuberculata</i> (Rafinesque, 1820)					4.9	5.4
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)						3.8
<i>Elliptio dilatata</i> (Rafinesque, 1820)	7.7	1.7	5.8	2.9	27.2	4.9
<i>Epioblasma triquetra</i> (Rafinesque, 1820)						4.1
<i>Fusconaia flava</i> (Rafinesque, 1820)	6.2				4.3	6.3
<i>Lampsilis cardium</i> Rafinesque, 1820	1.5	3.9	1.7	5.9	1.5	3.5
<i>Lampsilis higginsii</i> (Lea, 1857)						0.3
<i>Lampsilis siliquoidea</i> (Barnes, 1823)	18.5	2.8	0.8		2.4	
<i>Lasmigona complanata</i> (Barnes, 1823)		0.4			0.4	
<i>Lasmigona costata</i> (Rafinesque, 1820)	3.8	8.6	6.8	2.9	1.2	0.5
<i>Leptodea fragilis</i> (Rafinesque, 1820)		0.9	0.8		1.2	2.2
<i>Ligumia recta</i> (Lamarck, 1819)		0.9	4.2		0.4	0.5
<i>Obliquaria reflexa</i> Rafinesque, 1820					0.4	3.0
<i>Obovaria olivaria</i> (Rafinesque, 1820)					5.5	3.5
<i>Pleurobema sintoxia</i> (Rafinesque, 1820)	4.6	0.4	2.5		2.4	12.0
<i>Potamilus alatus</i> (Say, 1817)		0.6	0.8		3.6	1.1
<i>Quadrula fragosa</i> (Conrad, 1836)						0.5
<i>Quadrula metanevra</i> (Rafinesque, 1820)						3.5
<i>Quadrula pustulosa</i> (Lea, 1831)		1.4			15.6	9.8
<i>Strophitus undulatus</i> (Say, 1817)	7.7	0.6			0.9	
<i>Toxolasma parvus</i> (Barnes, 1823)		0.2				
<i>Tritogonia verrucosa</i> (Rafinesque, 1820)						2.5
<i>Truncilla truncata</i> Rafinesque, 1820		1.9	1.7		0.9	15.8
Mean mussel density (number/m <sup>2</sup> ) [SD]	10.4 [10.5] <sup>b,c</sup>	86.4 [84.9] <sup>a</sup>	18.9 [11.9] <sup>a,b</sup>	5.4 [10.7] <sup>c</sup>	13.1 [16.8] <sup>b</sup>	12.3 [10.7] <sup>b</sup>
Mean <i>A. ligamentina</i> density (number/m <sup>2</sup> ) [SD]	0.16 [0.8] <sup>b</sup>	61.9 [69.1] <sup>a</sup>	12.5 [9.0] <sup>a</sup>	4.5 [9.6] <sup>b</sup>	3.5 [6.9] <sup>b</sup>	1.6 [3.5] <sup>b</sup>
Species richness (number of species)	10	16	11	5	18	22
Species diversity (Shannon index)	1.7	1.2	1.3	0.7	2.1	2.7

Different letters denote significant differences

$F_{4,2746} = 19$ , respectively; all  $P < 0.0001$ ) with  $L_{t+1}$  being significantly greatest at the mean  $L_t$  at Kost Dam, followed by the upstream St. Croix site (Wild River), the two sites farthest downstream on the Sunrise (HWY 95 and CR 11) and the downstream St. Croix site (Interstate).

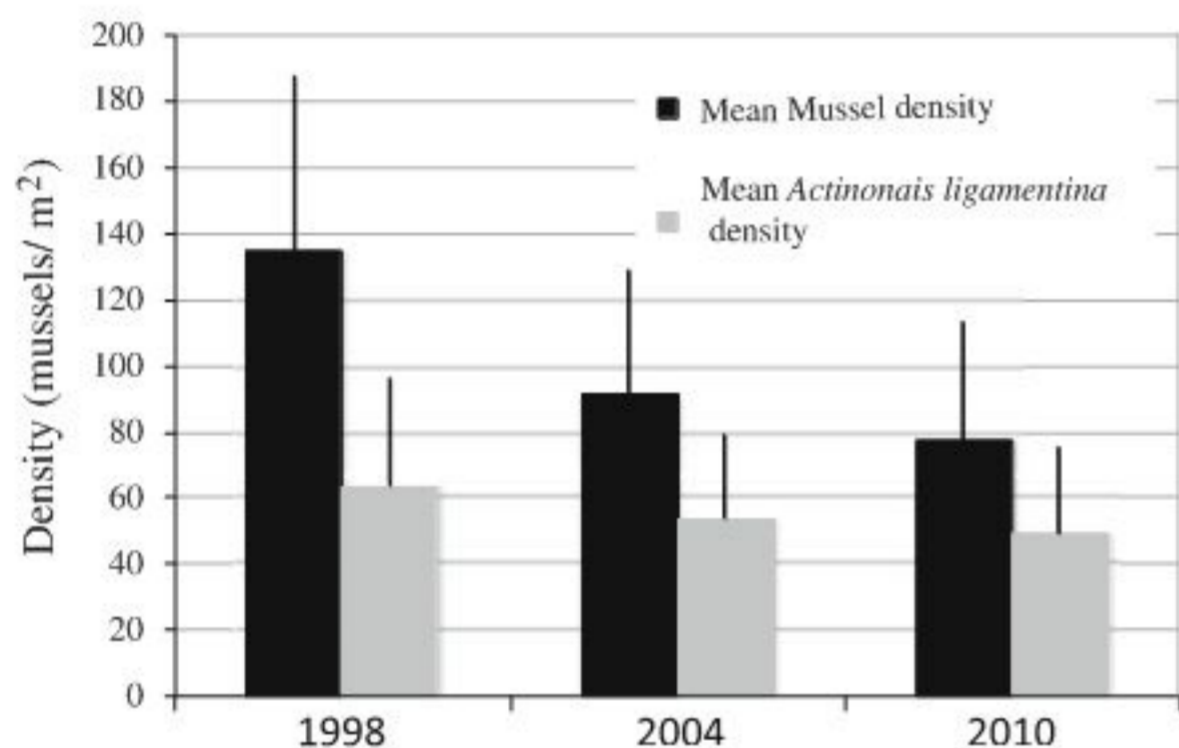
Another way to assess differences in shell growth is to calculate the growth interval between adjacent

external rings and to examine whether these growth intervals differ among populations, while adjusting for the size of the organism (the starting length of the external ring for each growth interval). Figure 5 shows that growth rates decline with increasing length. An analysis of covariance, with the natural log of the growth interval as the dependent variable, location as the independent variable and starting length at the

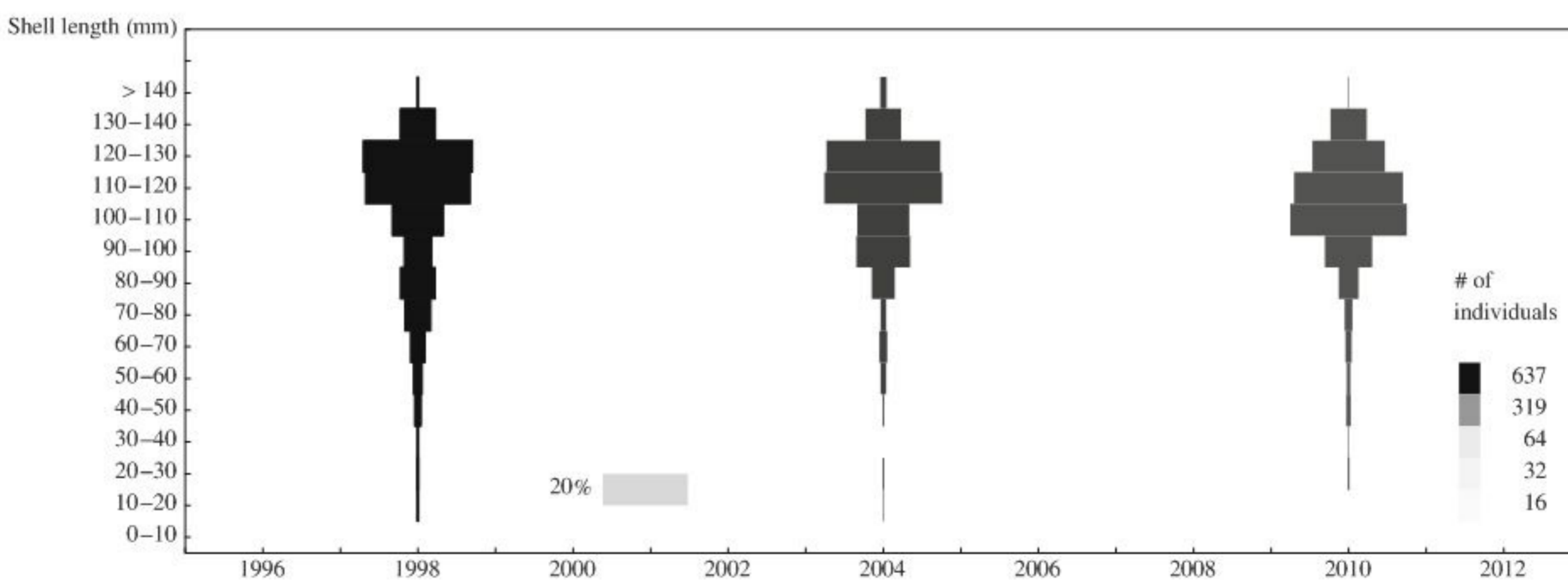
beginning of the growth interval as the covariable, showed a significant impact of location, the length at the beginning of the growth interval and their interaction on growth rate ( $F_{4,27} = 95$ ,  $F_{1,27} = 2765$ , and  $F_{1,27} = 35$ , respectively; all  $P < 0.0001$ ). The least squares mean, a growth rate based on the ANCOVA (growth rate at the average shell length), is significantly highest (Tukey comparison) at Kost Dam with the lowest growth rate at the next downstream site on the Sunrise (CR 11) (Table 2).

Habitat factors

The number of growing degree days (GDD—no growth below 10°C or above 30°C) is shown in Table 2. We have some data from 2009 for the St.



**Fig. 2** Total mussel density and density of *Actinonaias ligamentina* at Kost Dam, 1998–2010. Error bars are 1 SD



**Fig. 3** Shell-length frequency diagrams at the Kost Dam site. The horizontal bars represent 10 mm shell-length classes. The length of the bars is proportional to the percent of the population

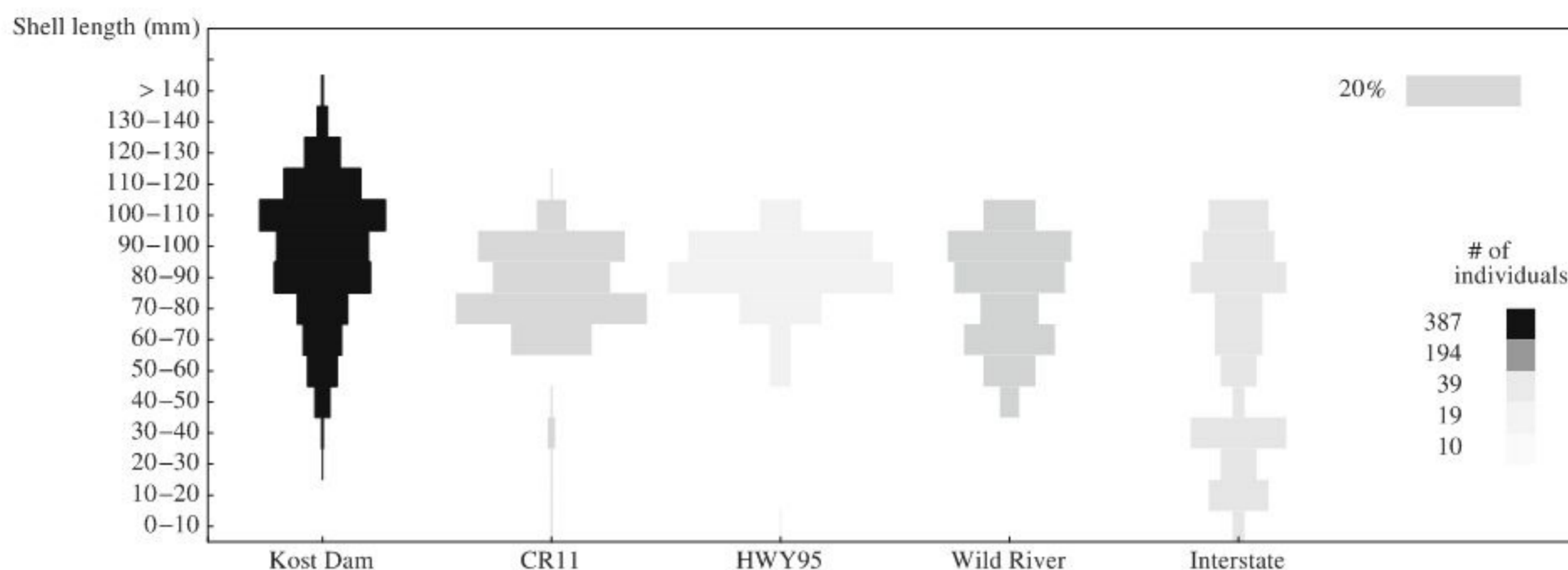
Croix sites for a similar (but shorter) period of time, June 6–September 16, 2009. The GDDs were 1152 and 1247 for upstream (Wild River) and downstream (Interstate) sites, respectively.

An analysis of variance on arcsine square root transformed sediment organic matter showed there were significant differences among sites ( $F_{5,13} = 9.64$ ,  $P < 0.0001$ ). A Tukey multiple comparison showed that the Kost Dam site had significantly higher amounts of sediment organic matter than the other sites (Table 2).

Discussion

Dams may have negative or positive impacts on downstream mussel assemblages. Negative impacts of dams on mussels include changes in water quality (temperature and oxygen availability), the change in the reservoir from a lotic to lentic environment and the interruption of fish migration (e.g., Layzer et al., 1993; Williams et al., 1993; McMurray et al., 1999; Watters, 1999). However, Haag (2012) indicates that the tailwaters below some dams can be sites of high mussel richness if these reaches retained relatively natural temperature and oxygen regimes and where sediments remain composed of mixed sand and gravel. In our study, dam tailwater sites exhibited habitat qualities similar to those previously associated with high mussel richness as described by Haag (2012). Thus, our finding that the greatest mussel species richness in both the

that each shell-length category represents. The gray-scale of the bar is proportional to the number of mussels that each category represents



**Fig. 4** Shell-length frequency diagrams for *Actinonaias ligamentina* (2010 for Interstate, 2011 for Wild River and 2012 for the three sites from the Sunrise River). The horizontal bars represent 10 mm shell-length classes. The length of the bars is

proportional to the percent of the population that each shell-length category represents. The gray-scale of the bar is proportional to the number of mussels that each category represents

**Table 2** Variable values from the von Bertalanffy growth model and the least squares mean of the growth rate for *Actinonaias ligamentina*. Growing Degree Days June 8–October 12, 2012 and percent sediment organic matter

Location	Growth constant— $K$	$L(\infty)$	Least squares mean of $\ln[\text{growth rate}]$ [SE]	Growing degree days	% Sediment organic matter (SD)
CR 14	–	–	–	1,410	0.63 <sup>a</sup> (0.21)
Kost Dam	0.14	137.61	2.21 <sup>a</sup> [0.01]	1,443	1.03 <sup>b</sup> (0.54)
CR 11	0.18	104.01	1.83 <sup>d</sup> [0.02]		0.58 <sup>a</sup> (0.27)
HWY 95	0.14	118.38	1.94 <sup>b</sup> [0.02]	1,332	0.57 <sup>a</sup> (0.24)
Wild River	0.21	101.30	1.92 <sup>b,c</sup> [0.02]		0.44 <sup>a</sup> (0.10)
Interstate	0.13	120.31	1.88 <sup>c,d</sup> [0.02]	1,463	0.63 <sup>a</sup> (0.25)

Different letters denote significant differences

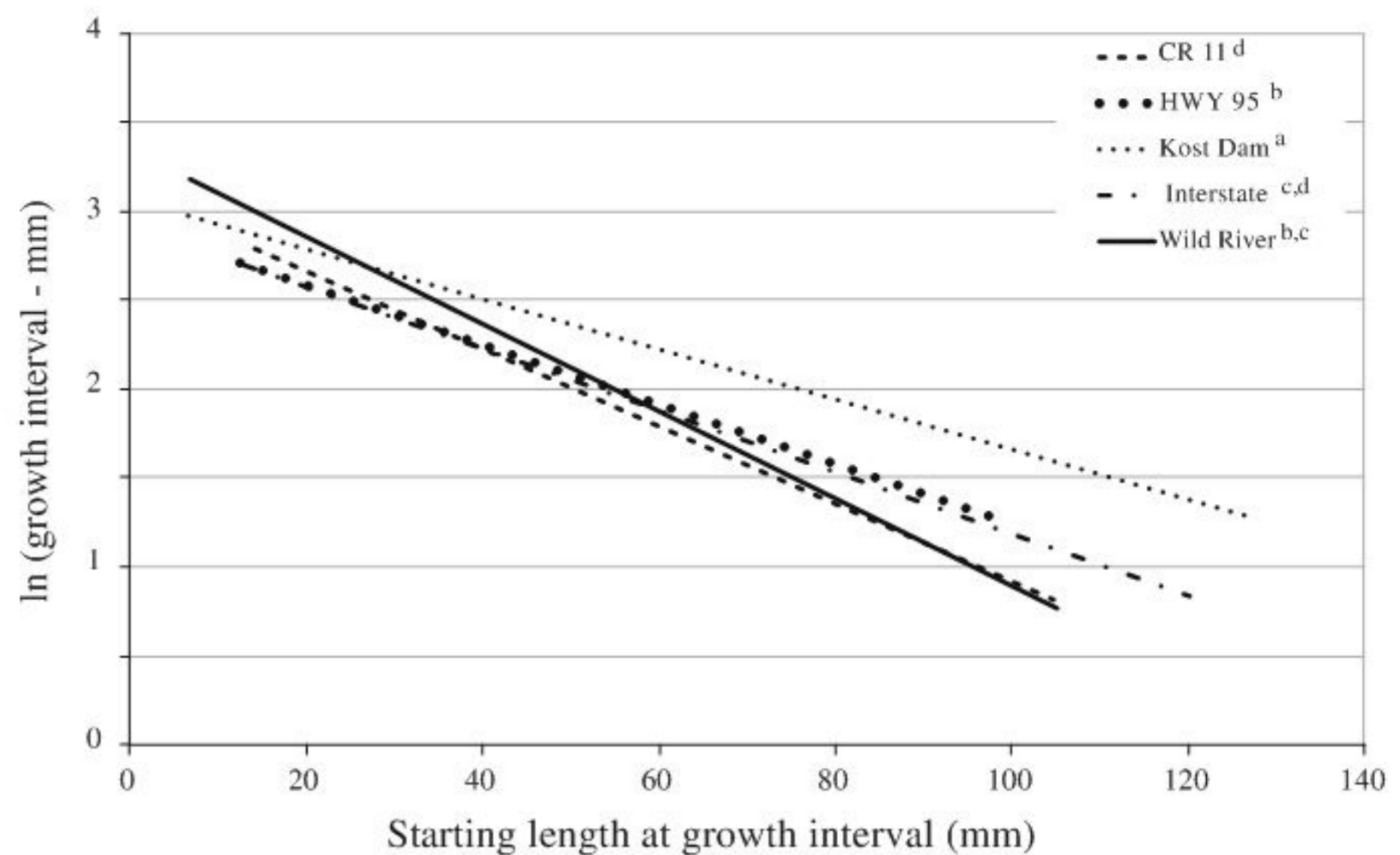
Sunrise and St. Croix Rivers is located directly below dams is not unprecedented. Of course, there are many factors other than the presence of dams that may affect mussel richness. For example, mussel richness generally increases with increasing watershed size (Strayer & Jirka, 1997) and may be related to fish host richness (Watters, 1992). More recently, Daniel & Brown (2013) showed that mussel richness increased with stream order but fish richness did not. Forty-one species of mussels have been found in the St. Croix River (Hornbach, 2001), while only 21 species are found in the Sunrise River (Davis & Miller, 1996) and thus the difference in richness between the rivers may be due to the difference in watershed size.

Kost Dam, the low-head dam on the Sunrise River, influenced the downstream mussel assemblage in a variety of ways. As hypothesized mussel density was

highest below this dam. Both total mussel density and the density of the dominant species (*A. ligamentina*) declined quickly downstream to levels similar to sites upstream of the dam (CR 14) and in the mainstem of the St. Croix River (Wild River and Interstate). Singer & Gangloff (2011) also found higher densities of the dominant species (*Elliptio arca*) below a small mill dam compared to upstream or downstream sites, although their densities of *E. arca* were much lower than *A. ligamentina* below Kost Dam in our study (8 vs. 61.9 mussels/m<sup>2</sup>, respectively). While Gangloff et al. (2011) initially hypothesized that high mussel densities downstream from some dams might result from fish aggregations, another study by the same research group found no evidence that dams aggregate fish hosts or otherwise alter downstream fish communities (Helms et al., 2011).



**Fig. 5** Change in *Actinonaias ligamentina* growth rates (natural log of the growth interval) with size (shell length) among locations in the Sunrise and St. Croix Rivers. Names of sites with the same letter represent growth rates for the average sized mussels that are not significantly different



The long-term stability of highly dense mussel populations below small dams has rarely been documented. Both total mussel density and *A. ligamentina* density appear to have largely declined from 1998 to 2010 (44% for overall mussel density and 22% for *A. ligamentina*). The shell-length distribution of *A. ligamentina* shows that recruitment, while occurring, seems to be low at this location over the period. Vaughn et al. (2007) found that *A. ligamentina* influenced the body condition of other mussel species in their study and they hypothesized that *Actinonaias* may be affecting food resource procurement by other mussel species, either through higher consumption, interference, or both. *Actinonaias* had higher algal filtration rates than the other species in their study (including *A. plicata* and *Lampsilis cardium* the second and third most abundant species at Kost Dam), and may be depleting food resources. *A. ligamentina* is a co-dominant at Interstate downstream of the dam on the St. Croix River and thus is found at much lower density. At Interstate there is clear evidence of recruitment, suggesting that the factors limiting recruitment at Kost Dam are not in evidence here. Vaughn & Hakenkamp (2001) describe conflicting evidence concerning the role of resource limitation in structuring bivalve communities. They state that bivalve control of primary production is most likely when their biomass is large relative to the water volume and where hydrologic residence time is long. The lower flow in the Sunrise River compared to the St. Croix River suggests a longer hydrologic residence

time and this combined with the unusually high mussel density and high filtering rates of *A. ligamentina* may help to explain the differences in recruitment of juveniles at Kost Dam. Vaughn et al. (2007) showed that at densities of 32 *A. ligamentina*/m<sup>2</sup>, not only did *A. ligamentina* influence the body condition of other species but also reduced its own body condition. Since the average mussel density at the Kost Dam site greatly exceeded this value, there is the possibility that decreased condition of *A. ligamentina* could lead to reduced reproductive output.

While the high density of mussels may have reduced their condition, the size of *A. ligamentina* below Kost Dam is greater than at other sites. The larger size could be due to greater longevity, greater growth rates, or both. We did not assess internal growth rings and since there is controversy over the use of external growth rings to ascertain age (Haag & Commens-Carson, 2008), we cannot state with complete confidence that the differences in sizes are not related to longevity differences. However, in two of our populations (Wild River and Interstate), Sansom et al. (2013) showed that ages obtained from internal and external examination of shells while different, were correlated. More importantly, growth rates determined from external examination were similar to those obtained from internal measurements.

Maximum predicted shell length ( $L_{\infty}$ ) is greatest (137.6 mm) for the Kost Dam population of *A. ligamentina* and this predicted value is near that of individuals actually collected at Kost Dam. However,

the growth constant ( $K$ ) is not the greatest at Kost Dam; rather it is greatest upstream of the dam on the St. Croix River at Wild River. Our values are similar to those reported by Haag & Rypel (2011) for seven populations in central North America ( $K = 0.077$ – $0.173$  and  $L_{\infty} = 107.8$ – $161.3$  mm). Since  $K$  and  $L_{\infty}$  are correlated in the von Bertalanffy model high values of  $K$  combined with a low value of  $L_{\infty}$  can give nearly the same fit to data as low values of  $K$  and high values of  $L_{\infty}$  (De Graaf & Prein, 2005). Because of these limitations with the von Bertalanffy model we assessed the differences in growth rates for *A. ligamentina* by examining the relationship between growth increments between external growth lines and the size of the mussel at the beginning of the growth period. Mussels greater than about 30 mm in length from the Kost Dam site had higher growth rates than mussels from other sites. Thus, though we cannot rule out the influence of disparities in mussel longevity among sites, differences in growth rates are, at least in part, responsible for the larger size of the mussels at the Kost Dam site.

Singer & Gangloff (2011) also found that growth rates of the dominant species in a small river in Alabama (*Elliptio arca*) were greatest below a mill dam. They suggested that both increased temperatures below the dam (leading to a longer time for growth each year) and enhanced food resources were responsible for enhanced growth rates. In our study, there is a greater number of GDD at Kost Dam when compared to the downstream (HWY 95) site on the Sunrise River as would be expected with higher growth rates at this site. However, there are a greater number of GDD at Interstate than at the Kost Dam site even though the growth rates for *A. ligamentina* are lower at this location. One reason for this apparent discrepancy may be the greater number of days with maximum temperatures greater than 25°C at Interstate. Maximum temperatures exceed 25°C for 40% of the days at Interstate while all of the other sites had fewer than 25% of their days with temperatures exceeding 25°C. Spooner & Vaughn (2008) showed filtration rates for *A. ligamentina* peaked at 25°C and thus temperatures higher than this could lead to reduced growth in this species. Sansom et al. (2013) indicated that in 2007 the hydroelectric dam switched from operating on a peaking schedule to run-of-the-river/partial peaking. Growth patterns between the Wild River site upstream of the dam and the Interstate site downstream of the

dam were similar both before and after the change in operation. At the Interstate site, however, older mussels had higher growth rates after the change in operation than the same sized mussels collected before the change. During the 6 year period before the change to run-of-the-river operation 54.4% of the days had maximum water temperatures exceeding 25°C while after the change only 45.6% of the days exceeded 25°C, potentially accounting for some of the increased growth rates. More research is needed to better understand the “optimal” temperature for growth in various species of mussels.

The degree to which enhanced food resources below small dams increase mussel growth is difficult to ascertain. As discussed by Vaughn et al. (2008), unionid mussels play an important role in aquatic systems removing nutrients and organic matter from the water column and transferring these to sediments. Spooner & Vaughn (2006) found that sediment organic matter was higher in areas surrounding *A. ligamentina* than *A. plicata*. They attributed the difference to bioturbation by *A. ligamentina* because of its greater activity level. In this study we found sediment organic matter to be highest at the Kost Dam site, but not significantly different among other sites. Given the high mussel density at Kost Dam, this finding is not surprising. However, this large amount of sediment organic matter may be indicative of a significant amount of food available to the mussel assemblage downstream of Kost Dam. As Singer & Gangloff (2011) point out reservoirs above small dams are known to increase particulate organic matter in the water column which leads to increased density of a variety of filter-feeding invertebrates.

Haag (2012) suggests that a far-reaching method of restoring mussel diversity is to remove dams. He points out that this method is not likely to be adopted on a large-scale basis given its contentious nature and the negative short-term effects that dam removal can have on mussel populations. He suggests the restoration of tailwaters would provide improved mussel habitat. Haag (2012) also points out that the removal of small dams may be especially problematic since they may have allowed the survival of numerous species from other watershed scale impacts. Gangloff et al. (2011) showed that intact small dams were associated with greater mussel density when compared to breached or relict dams, although relict dams were associated with greater species richness. They suggest

that intact dams provide some benefits and that at least in the short-term, restoration projects focus on breached dams that have both low mussel density and richness. A study by Heise et al. (2013) showed that the removal of a small hydroelectric dam (5 m high) had no significant effect on mussel density, growth or survivorship over a 4-year period. They suggested that the impacts of dam removal, if appropriately planned with attention to timing and the method of removal, might have minimal impacts on downstream mussel assemblages.

In our study, the presence of a small dam was associated with high mussel density and richness and enhanced growth of at least one species. It appears as if the local conditions in the reservoir above the dam provide enhanced food resources and a beneficial thermal environment for the mussel assemblage immediately below the dam. These impacts were localized in nature with sites just a few km downstream not influenced. Thus, the question is whether this site is actually anomalous and that the other sites on this river are more typical of “natural” conditions. It also allows us to pose the question whether a range of habitats, including those below small dams, need to be protected to support a variety of mussel habitats. Studies that examine the effects of surrounding land use are needed to better understand these confounding impacts on river systems before wise management decisions can be made about the removal of various types of dams.

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