

Research Article

Potential effects of invasive Dreissenid mussels on a pelagic freshwater ecosystem: using an ecosystem model to simulate mussel invasion in a sockeye lakePatricia Woodruff^{1,*}, Brett T. van Poorten^{1,2}, Carl J. Walters¹ and Villy Christensen¹¹Institute for the Oceans and Fisheries, University of British Columbia, 2202 Main Mall, Vancouver, BC, Canada²School of Resource and Environmental Management, Simon Fraser University, 8888 University Drive, Burnaby, BC, CanadaAuthor e-mails: p.woodruff@oceans.ubc.ca (PW), bvanpoor@sfu.ca (BTP), c.walters@oceans.ubc.ca (CJW), v.christensen@oceans.ubc.ca (VC)

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Received: 16 June 2020**Accepted:** 21 December 2020**Published:** 18 February 2021**Thematic editor:** Ian Duggan**Copyright:** © Woodruff et al.This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).**OPEN ACCESS****Abstract**

Dreissenid (zebra and quagga) mussels are spreading across North America and having an impact on freshwater ecosystems, through bottom-up impacts. Lakes in British Columbia are known to be at risk for mussel invasion due to favourable water chemistry and significant cross-border boat movements. This project uses Ecopath with Ecosim (EwE) to model a hypothetical mussel invasion into Shuswap Lake: one of the most popular lakes for recreation and one of the most productive sockeye lakes in the province. A model of the ecosystem was fit to available data and then projected forward to examine the effects from three different scenarios: no invasion, a base mussel invasion scenario resulting in a carrying capacity of 5 g·m⁻² and 15 g·m⁻² of zebra and quagga mussels, respectively, and a high density invasion scenario resulting in a combined carrying capacity of 40 g·m⁻² of Dreissenid mussels. The greatest ecosystem impacts resulted in declines in large piscivorous rainbow trout and lake trout, followed by non-anadromous kokanee salmon, with little effect observed on anadromous sockeye salmon. Two mechanisms limit the predicted impact of mussels in the study system: (1) paucity of shallow water habitat, limiting the scope for invasion; and (2) movements by fish in and out of the system. This second mechanism includes some resident species that rear for up to three years upstream of the lake, as well as anadromous species, which spend most of their life in the marine environment. While most of the effects are observed on recreationally important species, there is also the possibility of mussels spreading from this system into others within the same watershed, reiterating the importance of preventing the invasion and spread of Dreissenid mussels.

Key words: freshwater, aquatic invasions, invasive mussels, Ecopath with Ecosim, food web, ecosystem modelling

Introduction

Aquatic invasive species can impact whole freshwater ecosystems through a combination of competition and predation on various endemic species. Introductions of invasive ecosystem engineers, such as zebra mussels (*Dreissena polymorpha* Pallas, 1771) and quagga mussels (*D. bugensis* Andrusov, 1897), can result in a regime shift to an alternate stable state (Matsuzaki et al. 2009). Such invasive species represent a large risk to both native biodiversity and ecosystem function (Karatayev et al. 1997; Therriault

et al. 2013). Non-indigenous mussel species can affect water quality and have significant impacts on all major trophic levels (Higgins and Vander Zanden 2010; Therriault et al. 2013). These mussels have few natural predators, and generally provide poor nutritional value (French III 1993; Therriault et al. 2013). The presence of these mussels can result in an increase in toxic algal blooms and the fouling of boats, water structures (such as docks and pilings) and industrial water intakes. The biggest impact could be on native mussel species, which include some of the most at-risk groups in North America (Karatayev et al. 2002; Therriault et al. 2013).

Invasive mussel species transfer nutrients from the pelagic to the benthic zone, affecting pelagic phytoplankton, zooplankton, planktivorous fish and their predators. The result is a potential re-organization of the food web due to a loss of nutrients and increased competition for limited resources. The efficient filtration rate and high level of planktivory observed with Dreissenid mussels can lead to decreased productivity and changes in the plankton community structure (Allinger and Reavie 2013; Fishman et al. 2010; Kumar et al. 2016). The primary negative effects are seen with fish species that solely utilize zooplankton; fish that are able to feed on littoral zoobenthos can increase in numbers due to the shift in nutrient pathways (Therriault et al. 2013). Fish species that rely on zooplankton will decline if significant numbers of zebra and quagga mussels invade (Therriault et al. 2013). The presence of zebra mussels can also lead to an increase in abundance of littoral zone fishes, such as sunfish, black bass (*Centrarchidae*) and perch (*Percidae*) species (Therriault et al. 2013). These fish species have also been introduced well beyond their native range of eastern North America (McPhail 2007). One unexpected impact of mussels may thus be the facilitation of invasion for other invasive species (Strayer et al. 2004).

The two invasive Dreissenid species have different habitat preferences. Zebra mussels are found primarily on hard surfaces or aquatic plants, while quagga mussels can be found on hard and soft substratum (Higgins and Vander Zanden 2010; Therriault et al. 2013). Quagga mussels are found at higher densities than zebra mussels in cooler and deeper waters (Higgins and Vander Zanden 2010; Therriault et al. 2013). Quagga mussels take longer to reach their maximum population size; however, they can have much higher densities than zebra mussels and can also outcompete them by depleting food resources (Karatayev et al. 2015). Both mussel species require a Calcium concentration of at least 12 mg/L (Therriault et al. 2013), and their densities appear to be negatively correlated with high levels of nitrogen and phosphorus (Ramcharan et al. 1992).

There are currently no invasive mussels present in freshwater in the provinces and states of the Pacific Northwest, including British Columbia, although they have been detected on boats entering these jurisdictions (BC Ministry of Environment and Climate Change Strategy 2018). Overland dispersal through “hitchhiking” on recreational boats and equipment is

one of the primary methods of Dreissenid mussel colonization (Bossenbroek et al. 2007; Johnson et al. 2001), therefore, lakes with high recreational value are also at higher risk of invasion by these freshwater mussels (Kelly et al. 2013; Vander Zanden and Olden 2008; West et al. 2009). Past studies have examined different properties of freshwater systems, in order to determine the likelihood of colonization by invasive mussels (Bossenbroek et al. 2007; Jones and Ricciardi 2005; Ramcharan et al. 1992; Spidle et al. 1995; Therriault et al. 2013). Calcium concentration was identified as one of the primary factors that influences mussel survival (Ramcharan et al. 1992), along with temperature (Spidle et al. 1995), depth, and substrate size (Jones and Ricciardi 2005). However, different mussel species have different physiological limitation (Jones and Ricciardi 2005), and other factors can influence mussel survival in systems with lower calcium or finer sediments (Davis et al. 2015; Strayer and Malcom 2006).

Shuswap Lake in British Columbia is one of the largest lakes in the region, with multiple opportunities for anglers and multiple fish species to target. In fact, the strong recreational fishery is partially supported by a prey-base dependent on the annual influx of adult Pacific salmon (*Oncorhynchus* spp.) and their offspring. Shuswap Lake is at high risk of invasion by Dreissenid mussels: there is a very high probability of mussel survival due to the calcium concentration and temperature of the lake, with a resulting high risk to the environment (Therriault et al. 2013). In addition to just the lake itself, the tributaries to the lake represent some of the largest salmon runs in the Fraser River, and therefore the ecological, economic and cultural consequences of Dreissenid invasion may also be quite high (Therriault et al. 2013).

This research evaluates the potential impact of Dreissenid invasion on an entire lake ecosystem. We specifically build an ecosystem model of Shuswap Lake and predict impacts of invasion by both species based on multiple hypotheses of carrying capacity, derived from bathymetric characteristics of the lake. Through this analysis, we evaluate local impacts of invasion on all parts of the food web, with particular emphasis on salmon and trout fisheries.

Materials and methods

Model

Shuswap Lake is located in the Fraser River watershed in British Columbia, Canada (Figure 1). The Shuswap Lake ecosystem was simulated using Ecopath with Ecosim (EwE) software. EwE notably includes two sub-models: a static mass-balance model (Ecopath) (Christensen and Pauly 1992) which describes initial abundances, productivities and interactions of various components; and a dynamic model (Ecosim) (Christensen and Walters 2004), which simulates changes in all components over time. Ecopath is

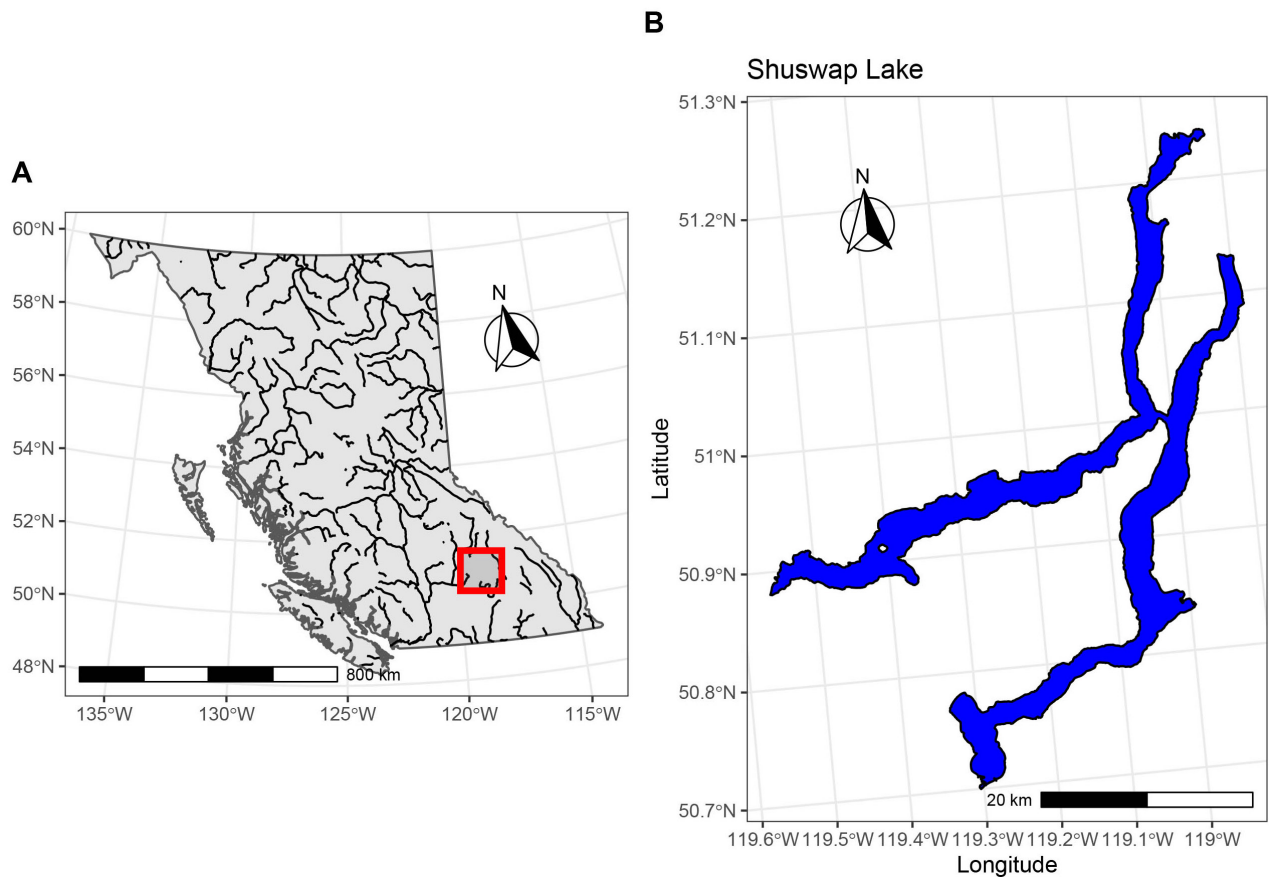


Figure 1. The location and map of Shuswap Lake within British Columbia, Canada.

parameterized using a combination of observations and literature values, while tuning due to density-dependent factors can be based on time-series of abundance available through population surveys. All available data was used to create a realistic representation of the Shuswap Lake ecosystem and its interactions, with the addition of invasive mussel species.

An EwE model was constructed for the Shuswap Lake ecosystem for the years 1975–2070. The starting year of 1975 was used to represent the initial state for Ecopath. The Ecopath model assumes mass balance and is constructed using two master equations: the first equation is for production:

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + M0_i \times B_i \quad (1)$$

where P_i is production of species i , Y_i is the fishery catch rate, $M2_i$ is the instantaneous predation rate, B_i is the biomass, E_i is the net migration rate, BA_i is the biomass accumulation rate, and $M0_i$ is the mortality rate from all other sources. The second equation is for energy balance:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (2)$$

The input parameters used for the Ecopath model of Shuswap Lake were biomass, P/B (production to biomass ratio), Q/B (consumption to biomass ratio), and the proportional diet composition of each consumer. The fish species included in the model were separated into different age stanzas in

Table 1. Functional groups and the Ecopath parameters used for the Shuswap Lake model.

Group name	Biomass (g·m ⁻²)	P/B or Z (year ⁻¹)	Q/B (year ⁻¹)
Lake trout 6+	0.200	0.200	0.662
Lake trout 3–5	0.0633	0.350	0.991
Lake trout 0–2	0.0248	0.700	1.884
Piscivorous rainbow trout 6+	0.100	0.800	2.100
Piscivorous rainbow trout 3–5	0.402	0.700	2.639
Piscivorous rainbow trout 0–2	0.444	1.00	4.819
Insectivorous rainbow trout 6+	0.00400	0.50	2.5
Insectivorous rainbow trout 3–5	0.00677	0.50	3.159
Insectivorous rainbow trout 0–2	0.00581	1.00	5.863
Sockeye moribund	0.00924	10.00	0.977
Sockeye spawners	0.01000	0.20	1.00
Sockeye 3+	0.151	2.00	1.115
Sockeye 2+	0.560	2.00	1.396
Sockeye 1+	1.004	1.70	2.048
Sockeye 0+	0.356	1.90	4.120
Kokanee spawners	0.0500	2.00	5.5
Kokanee 2+	0.121	1.20	6.356
Kokanee 1+	0.212	1.70	8.647
Kokanee 0	0.0979	1.90	16.05
Insects	3	10	40
Other zooplankton	10	11	120
<i>Epischura</i>	4	3	15
<i>Daphnia</i>	6	10	40
<i>Leptodiptomous</i>	4	3	15
Edible phytoplankton	30	113	
Stream food	0.400	10	40
Zebra mussels	1.00	1.00	12
Quagga mussels	2.00	0.50	5
Stream phytoplankton	0.400	113	
Detritus	100		
Ocean food	1000		

order to incorporate ontogenetic changes in diet; these were entered into the model as multi-stanza groups, and an estimate of total mortality (Z; equivalent to P/B) was used for the production component of each stanza.

Ecosim provides dynamic simulations for the model, where initial conditions are established through the Ecopath mass-balance solution. Estimates of P/B (production to biomass ratio; equal to instantaneous mortality at equilibrium) and Q/B (consumption to biomass ratio) were obtained from Thompson (1999) and tuned in order to balance the model. Diet composition was estimated from Thompson (1999). Parameter values for biomass, P/B and Q/B ratios are shown in Table 1; diet proportions for each functional group are shown in Tables 2-5. The time series of relative biomass estimates (based on the starting year of 1975) was included from 1975–2016.

Data

The Ecopath model included 16 functional groups: lake trout (*Salvelinus namaycush* Walbaum in Artedi, 1792), large (piscivorous) and small (insectivorous) rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792) populations, sockeye salmon (*O. nerka* Walbaum in Artedi, 1792), kokanee

Table 2. Diet matrix for lake trout and rainbow trout in Shuswap Lake. Numbers refer to the proportional contribution of prey (rows) to each stanza of lake trout, piscivorous and insectivorous rainbow trout (columns).

Prey/Predator	Lake trout			Piscivorous rainbow trout			Insectivorous rainbow trout		
	age 6+	age 3–5	age 0–2	age 6+	age 3–5	age 0–2	age 6+	age 3–5	age 0–2
Sockeye 1+	0.500	0.400		0.500	0.386				
Sockeye 0+		0.200			0.193	0.01			0.01
Kokanee 2+	0.300			0.300					
Kokanee 1+	0.200	0.200		0.200	0.253				
Kokanee 0+		0.200			0.108	0.001			0.001
Insects							0.100	0.100	
Other zooplankton			0.900		0.0602		0.900	0.900	
<i>Daphnia</i>			0.100						
Stream food						0.898			0.898

Table 3. Diet matrix for sockeye in Shuswap Lake. Numbers refer to the proportional contribution of prey (rows) to each stanza of sockeye (columns).

Prey/Predator	Sockeye moribund	Sockeye spawners	Sockeye 3+	Sockeye 2+	Sockeye 1+	Sockeye 0+
Other zooplankton					0.100	0.100
<i>Epischura</i>					0.100	0.100
<i>Daphnia</i>					0.700	0.700
<i>Leptodiptomous</i>					0.100	0.100
Ocean food	1.00	1.00	1.00	1.00		

Table 4. Diet matrix for kokanee in Shuswap Lake. Numbers refer to the proportional contribution of prey (rows) to each stanza of kokanee (columns).

Prey/Predator	Kokanee spawners	Kokanee 2+	Kokanee 1+	Kokanee 0+
Other zooplankton	0.150	0.150	0.100	0.100
<i>Epischura</i>	0.700	0.700	0.100	0.100
<i>Daphnia</i>	0.100	0.100	0.700	0.700
<i>Leptodiptomous</i>	0.050	0.050	0.100	0.100

Table 5. Diet matrix for insects, zooplankton and Dreissenid mussels in Shuswap Lake. Numbers refer to the proportional contribution of prey (rows) to predators (columns).

Prey/Predator	Insects	Other zooplankton	<i>Epischura</i>	<i>Daphnia</i>	<i>Leptodiptomous</i>	Zebra Mussels	Quagga Mussels
Other zooplankton					0.100	0.0125	0.0125
<i>Epischura</i>					0.050	0.0125	0.0125
<i>Daphnia</i>					0.100	0.0125	0.0125
<i>Leptodiptomous</i>						0.0125	0.0125
Edible phytoplankton		0.800	0.800	0.900	0.750	0.600	0.400
Stream phytoplankton	1.000					0.050	0.050
Detritus		0.200	0.200	0.100		0.300	0.500

salmon (nonanadromous freshwater sockeye salmon), insects, various zooplankton taxonomic groups, stream-based food and phytoplankton, edible phytoplankton in the lake, ocean food (used to support sockeye in the marine environment only), invasive zebra and quagga mussels (modeled as separate species), and detritus (Table 1). Data used directly for biomass calculations included zooplankton, kokanee, and sockeye. The sockeye escapement series is the longest time series available for this model; however, more recent data for other species has been included where available. Zooplankton were captured using a Wisconsin net with a 0.5 m throat diameter that was vertically hauled from a depth of 25 m. Sockeye and kokanee fry abundance indices were collected through fall

Table 6. Vulnerability matrix for lake trout and rainbow trout in Shuswap Lake. Numbers refer to the vulnerability of prey (rows) to each stanza of lake trout, piscivorous and insectivorous rainbow trout (columns).

Prey/Predator	Lake trout			Piscivorous rainbow trout			Insectivorous rainbow trout		
	age 6+	age 3–5	age 0–2	age 6+	age 3–5	age 0–2	age 6+	age 3–5	age 0–2
Sockeye 1+	2.0	2.0		2.0	2.0				
Sockeye 0+		10.0			10.0	2.0			2.0
Kokanee 2+	2.0			2.0					
Kokanee 1+	2.0	2.0		2.0	2.0				
Kokanee 0+		2.0			2.0	2.0			2.0
Insects							2.0	2.0	
Other zooplankton			2.0		2.0		2.0	2.0	
<i>Daphnia</i>			2.0						
Stream food						1.1			1.1

Table 7. Vulnerability matrix for sockeye salmon in Shuswap Lake. Numbers refer to the vulnerability of prey (rows) to each stanza of sockeye (columns).

Prey/Predator	Sockeye moribund	Sockeye spawners	Sockeye 3+	Sockeye 2+	Sockeye 1+	Sockeye 0+
Other zooplankton					3.0	3.0
<i>Epischura</i>					3.0	3.0
<i>Daphnia</i>					3.0	3.0
<i>Leptodiptomous</i>					3.0	3.0
Ocean food	2.0	2000	2000	2000		

Table 8. Vulnerability matrix for kokanee in Shuswap Lake. Numbers refer to the vulnerability of prey (rows) to each stanza of kokanee (columns).

Prey/Predator	Kokanee spawners	Kokanee 2+	Kokanee 1+	Kokanee 0+
Other zooplankton	2.0	2.0	2.0	2.0
<i>Epischura</i>	2.0	2.0	2.0	2.0
<i>Daphnia</i>	2.0	2.0	2.0	2.0
<i>Leptodiptomous</i>	2.0	2.0	2.0	2.0

Table 9. Vulnerability matrix for zooplankton groups in Shuswap Lake. Numbers refer to the vulnerability of prey (rows) to predators (columns).

Prey/Predator	Insects	Other zooplankton	<i>Epischura</i>	<i>Daphnia</i>	<i>Leptodiptomous</i>	Zebra mussels	Quagga mussels
Other zooplankton					2.0	2.0	2.0
<i>Epischura</i>					2.0	2.0	2.0
<i>Daphnia</i>					2.0	2.0	2.0
<i>Leptodiptomous</i>						2.0	2.0
Edible phytoplankton		2.0	2.0	2.0	2.0	80.0	80.0
Stream phytoplankton	2.0					2.0	2.0
Detritus		2.0	2.0	2.0		80.0	80.0

hydroacoustic and trawl surveys (D. Selbie, Fisheries and Oceans Canada, *pers. comm.*). Rainbow trout and lake trout data were modeled from tagging information and angler survey data (A. Morris, BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development, *pers.comm.*; Andrusak 2011). The estimated biomass was then divided by the habitat area in km² in order to obtain an estimate of pelagic density. Vulnerabilities for each prey group to each predator group were set to the values in Tables 6-9.

Maximum abundance of zebra and quagga mussels were limited by available depth habitat (data provided by Fisheries and Oceans Canada, Canadian Hydrographic Service) (Vanderploeg et al. 2010). The maximum

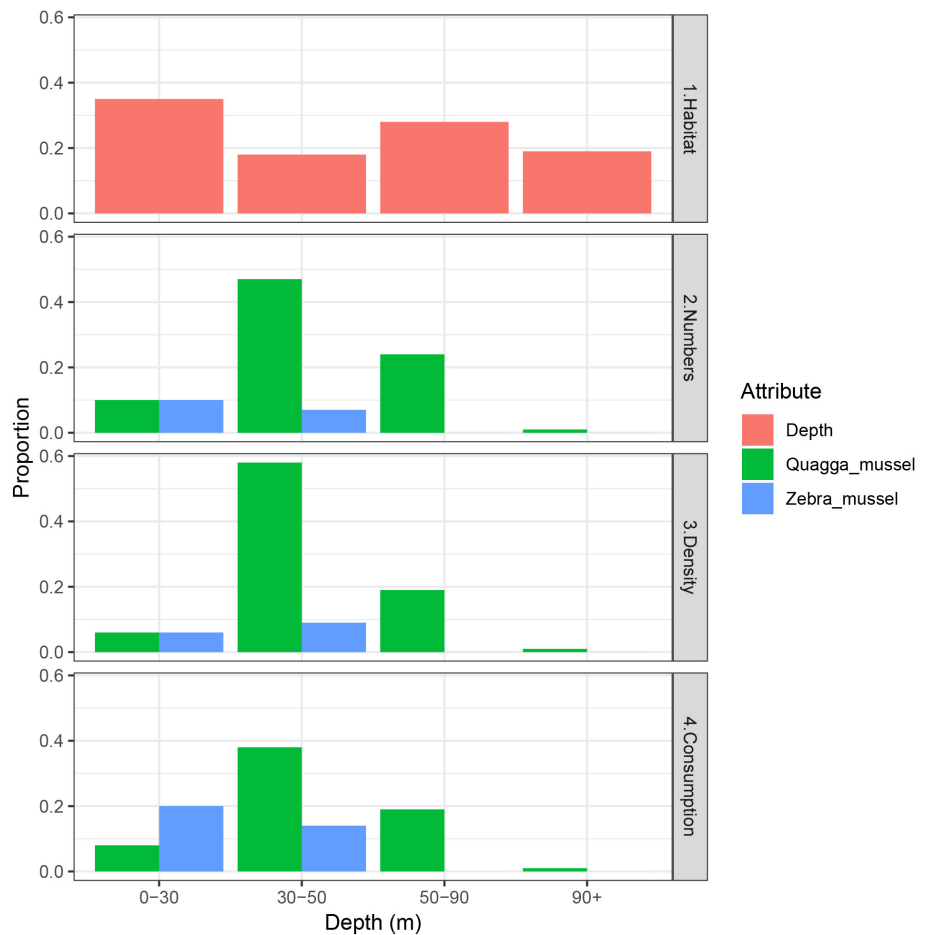


Figure 2. The proportion of habitat available at depth strata, and the proportion of mussels, mussel density, and mussel consumption by species for the different depth strata in Shuswap Lake.

mussel densities found at different depth strata were applied to the amount of habitat available at those depths in Shuswap Lake. Using information from Vanderploeg et al. (2010) and Nalepa et al. (2006), quagga mussel densities were $5 \text{ g}\cdot\text{m}^{-2}$ at $< 30 \text{ m}$, $45 \text{ g}\cdot\text{m}^{-2}$ at $30\text{--}50 \text{ m}$, $15 \text{ g}\cdot\text{m}^{-2}$ at $50\text{--}90 \text{ m}$ and $1 \text{ g}\cdot\text{m}^{-2}$ at $> 90 \text{ m}$, while zebra mussel densities were $5 \text{ g}\cdot\text{m}^{-2}$ at $< 30 \text{ m}$, $7 \text{ g}\cdot\text{m}^{-2}$ at $30\text{--}50 \text{ m}$, and $0 \text{ g}\cdot\text{m}^{-2}$ at both $50\text{--}90 \text{ m}$ and $> 90 \text{ m}$ (Figure 2; using dry weight). Approximately 35% of the lake was $< 30 \text{ m}$, 18% was $30\text{--}50 \text{ m}$, 28% of the lake was $50\text{--}90 \text{ m}$, and 19% of the lake was $> 90 \text{ m}$. For the purposes of Ecopath parameters, this translates to a maximum density of $5 \text{ g}\cdot\text{m}^{-2}$ and $15 \text{ g}\cdot\text{m}^{-2}$ for zebra and quagga mussels, respectively. This scenario was termed the base invasion scenario. A further scenario, termed the high density invasion scenario, doubled the maximum biomass of each species to evaluate uncertainty in this parameter.

Mussel invasion was modeled following the methods of Langseth et al. (2012): the biomass was set to the maximum biomass but initially suppressed by applying a high mortality, and then released by setting this artificial mortality to zero. Mussel biomass was then set (using the forced biomass function) in order to run three scenarios: one with no mussel invasion, one assuming the base invasion scenario, and one assuming the

high density invasion scenario. Because only habitable depth was used in calculating these biomass values, and these values were forced throughout the Ecosim simulations, we are implicitly incorporating a limitation to the maximum overall effect of mussel invasion on the lake's food-web. The transfer of nutrients from pelagic to benthic systems was simulated by mussels feeding primarily on phytoplankton and on zooplankton to a much lesser extent (Table 5). Mussels were assumed to only invade the lake itself; receiving streams used for spawning kokanee and sockeye and by rainbow trout for spawning and rearing were unaffected.

The positive effect of marine derived nutrients was included by simulating sockeye productivity as a mediating function on phytoplankton biomass the following year. When the model was fit to data, the cycle broke down as the model tried to find the average abundance over years, rather than specifically fitting to the typical cycle. Therefore, the model was not fit to the time series data due to the importance of including the four-year sockeye cycle (Supplementary material Figure S1); this cycle is a major determinant of the system dynamics. Fitting the model to the data also resulted in unrealistic vulnerability estimates and did not predict the wide variations observed in sockeye biomass. The vulnerabilities used in the model were low indicating the consumer groups generally were close to their carrying capacity. Low vulnerabilities also make the system more stable as there are considerable density-dependence effects, resulting in inter-species competition effects, which leads to the stability of the model. Higher vulnerabilities are used for groups that are far from their carrying capacity, e.g., for invasive species.

Results

Before the simulated invasion, the observed data showed a lot of variation over time. In general, zooplankton species showed an increasing trend in abundance, kokanee fry and spawners appeared to be declining, and the biomass of sockeye salmon, rainbow trout and lake trout were extremely variable.

The effect of the invasion by zebra and quagga mussels was observed in all species within the lake (Figures 3–6). Mussels were constrained in the amount of habitat that they could access, therefore, consumption of phytoplankton and zooplankton were limited. The greatest projected impact was found with the high density invasion scenario, with a combined mussel density of $40 \text{ g}\cdot\text{m}^{-2}$, with negative effects on species and age groups found within the lake. Increasing the biomass density of Dreissenid mussels had the most effect on *Leptodiptomous*, due to its reliance on both phytoplankton and zooplankton as food (Figure 3). Negative effects of mussels on zooplankton species were most pronounced in years that corresponded to low sockeye salmon returns (Figure 3). Kokanee fry and spawner biomass decreased with increasing mussel biomass (Figure 4).

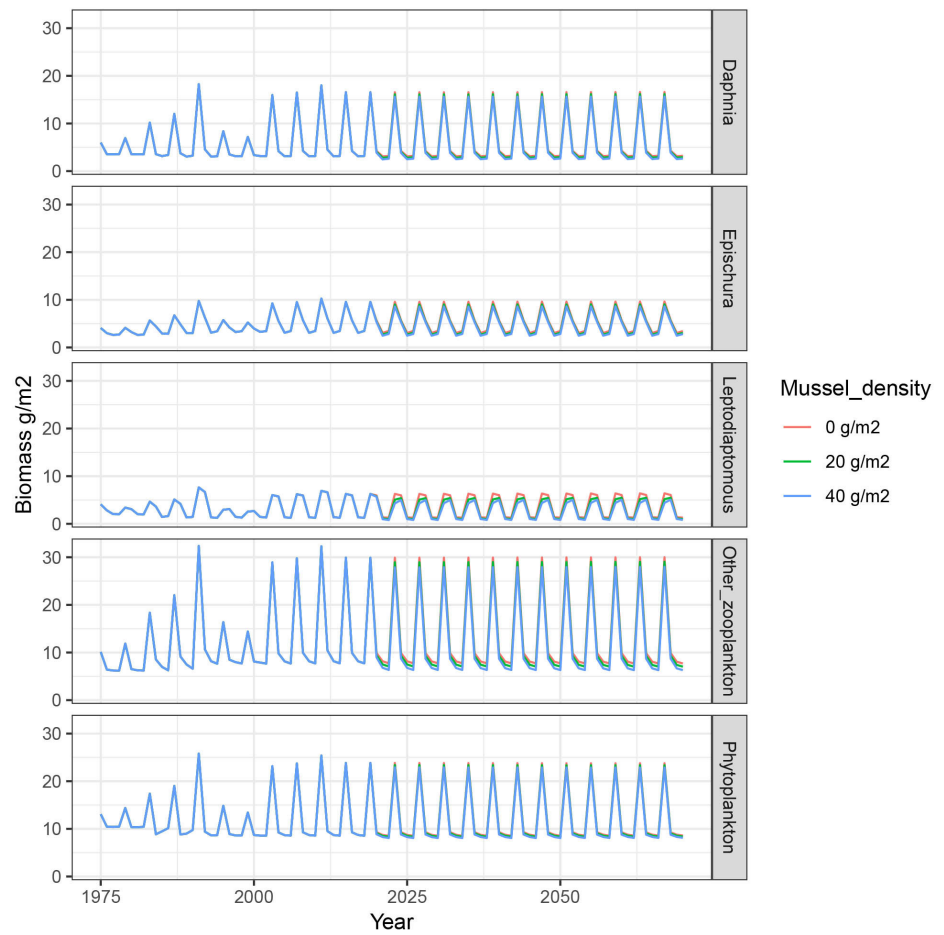


Figure 3. Modelled prediction of phytoplankton and zooplankton biomass without mussels (red); with mussels at a combined density of $20 \text{ g}\cdot\text{m}^{-2}$ (green); and with mussels at a combined density of $40 \text{ g}\cdot\text{m}^{-2}$ (blue).

Kokanee age 0 and age 1 showed higher predation mortality from rainbow trout following the invasion of Dreissenid mussels as kokanee increased their foraging time to account for reduced zooplankton prey availability.

The Dreissenid mussel invasion had a negligible impact on sockeye biomass (Figure 5). Predation mortality was predicted to increase for sockeye 0 and 1 age classes as shared predators compensate for a decrease in available kokanee prey; however, as the abundance of predators declines, so too does predation mortality on sockeye. Sockeye are in the ocean for much of their life and marine prey is predicted to be stable in the model, therefore there is minimal change in biomass with the addition of Dreissenid mussels, resulting in stable egg deposition and relatively stable population abundance compared with kokanee.

Both piscivorous rainbow trout and lake trout (Figure 6) declined with increasing mussel biomass; this decline occurred to a greater degree for lake trout. There was increased predation by lake trout and piscivorous rainbow trout on sockeye and decreased predation on kokanee following the onset of the invasion. Unlike lake trout, rainbow trout rear in streams for two years, providing a refuge from impacts due to Dreissenid mussels;

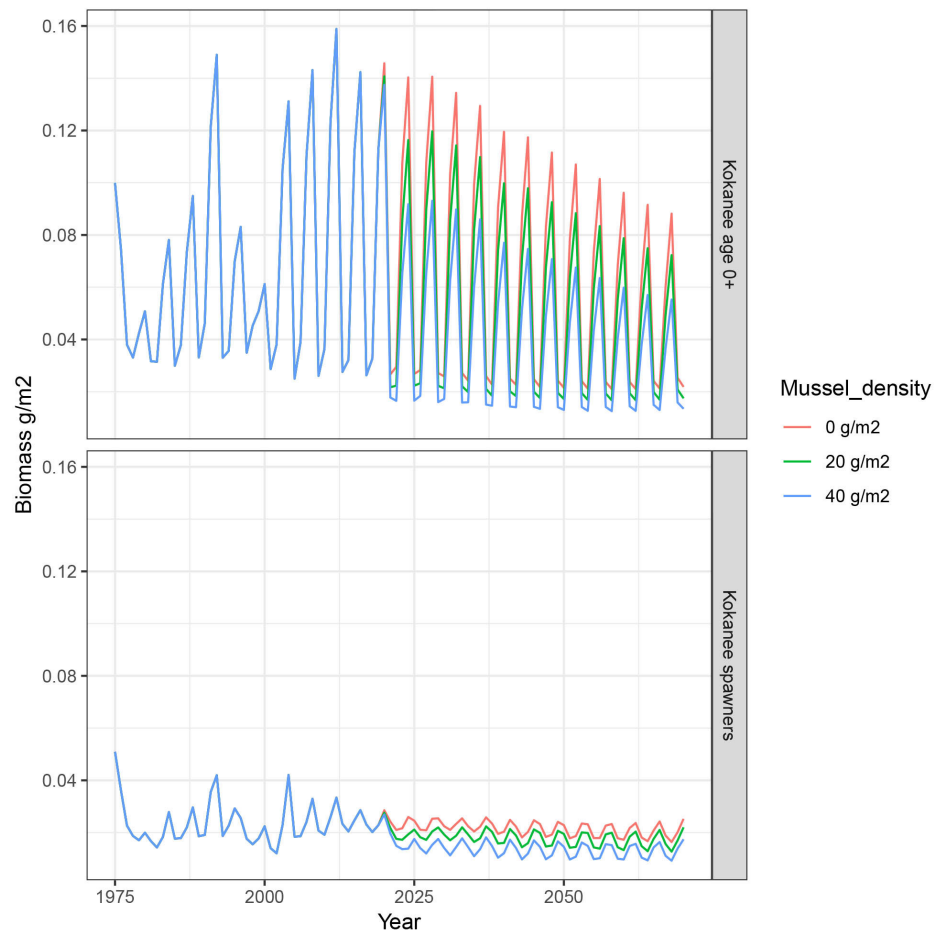


Figure 4. Modelled prediction of kokanee fry and spawner biomass without mussels (red); with mussels at a combined density of $20 \text{ g}\cdot\text{m}^{-2}$ (green); and with mussels at a combined density of $40 \text{ g}\cdot\text{m}^{-2}$ (blue).

therefore, rainbow trout were not as impacted in the base invasion scenario as lake trout following invasion.

Discussion

Dreissenid mussels have been demonstrated to have large impacts on many freshwater systems due to their high densities and high filtration rates. However, the bathymetry of Shuswap Lake, combined with a high influx of marine-derived nutrients, helps protect the aquatic ecosystem from some of the large system-wide impacts seen in other systems (Higgins and Vander Zanden 2010; Kumar et al. 2016; Strayer et al. 2004; Vanderploeg et al. 2010). Zebra mussels have a higher respiration rate, but are found at shallower depths and in warmer temperatures than quagga mussels, while quagga mussels are able to grow larger and prefer deeper and cooler waters (Stoeckmann 2003; Vanderploeg et al. 2010). Zebra mussels have been displaced by quagga mussels, even in warmer waters (Stoeckmann 2003; Vanderploeg et al. 2010). There is limited habitat available in Shuswap Lake at the preferred depths of 30–50 m (Figure 2), and the lower consumption rate of the more numerous quagga mussels results in a reduced effect on

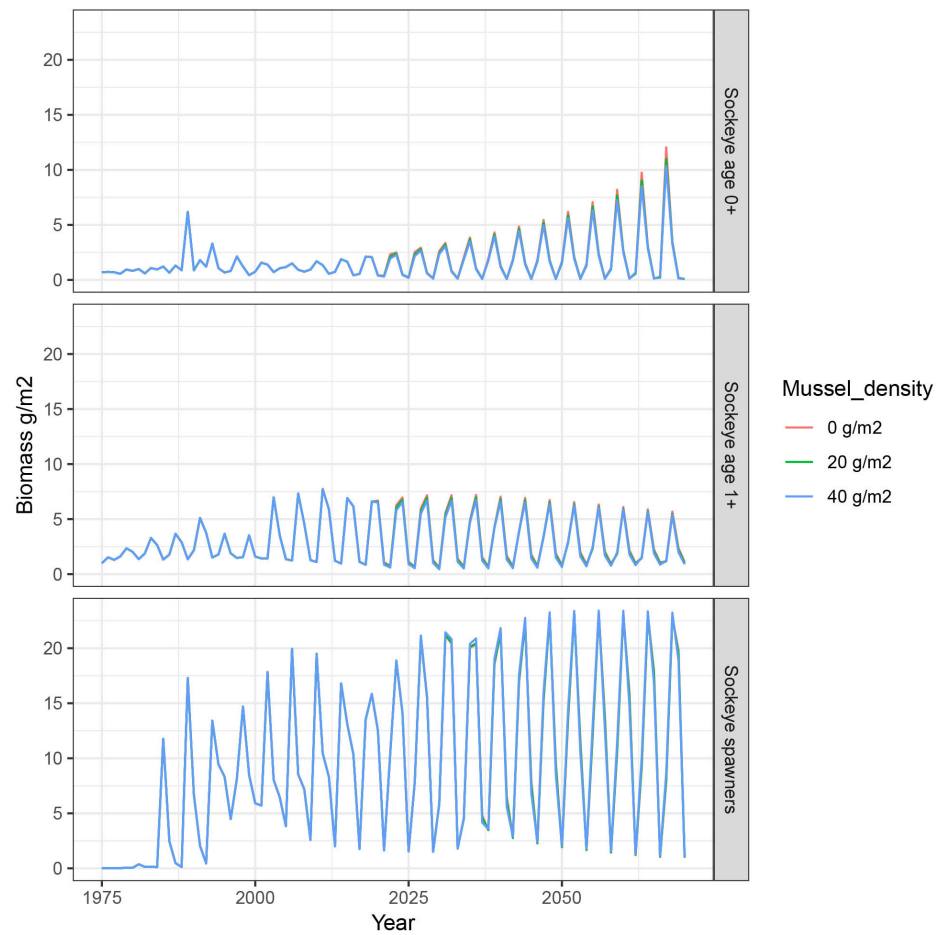


Figure 5. Modelled prediction of sockeye fry, age 1+ and spawner biomass without mussels (red); with mussels at a combined density of $20 \text{ g}\cdot\text{m}^{-2}$ (green); and with mussels at a combined density of $40 \text{ g}\cdot\text{m}^{-2}$ (blue).

phytoplankton and zooplankton. The effects of Dreissenid mussels appear to be limited on sockeye salmon, due in part to the introduction of marine-derived nutrients into the system, and the fact that this anadromous species spends approximately two years in the marine environment, and therefore is not solely reliant on the food sources within the lake. The increase in system productivity, due to marine-derived nutrients brought in by returning salmon spawners, improves the food supply for the nonanadromous kokanee salmon, although kokanee compete with sockeye for the same resources. Both piscivorous rainbow trout and lake trout are able to feed on the young sockeye; however, rainbow trout spawn and rear in streams, while lake trout spawn and rear in the lake. The streams provide a refuge for the young rainbow from any potential impacts of zebra mussels; if lake trout spawning sites are fouled with invasive mussels, there will be declines in egg deposition and increased damage to the eggs (Marsden and Chotkowski 2001). This model predicts that the longer fish remain in the lake, the more they will be affected, although the lack of suitable habitat at depth for invasive mussels and the addition of marine-derived nutrients alleviate some of the possible negative impacts.

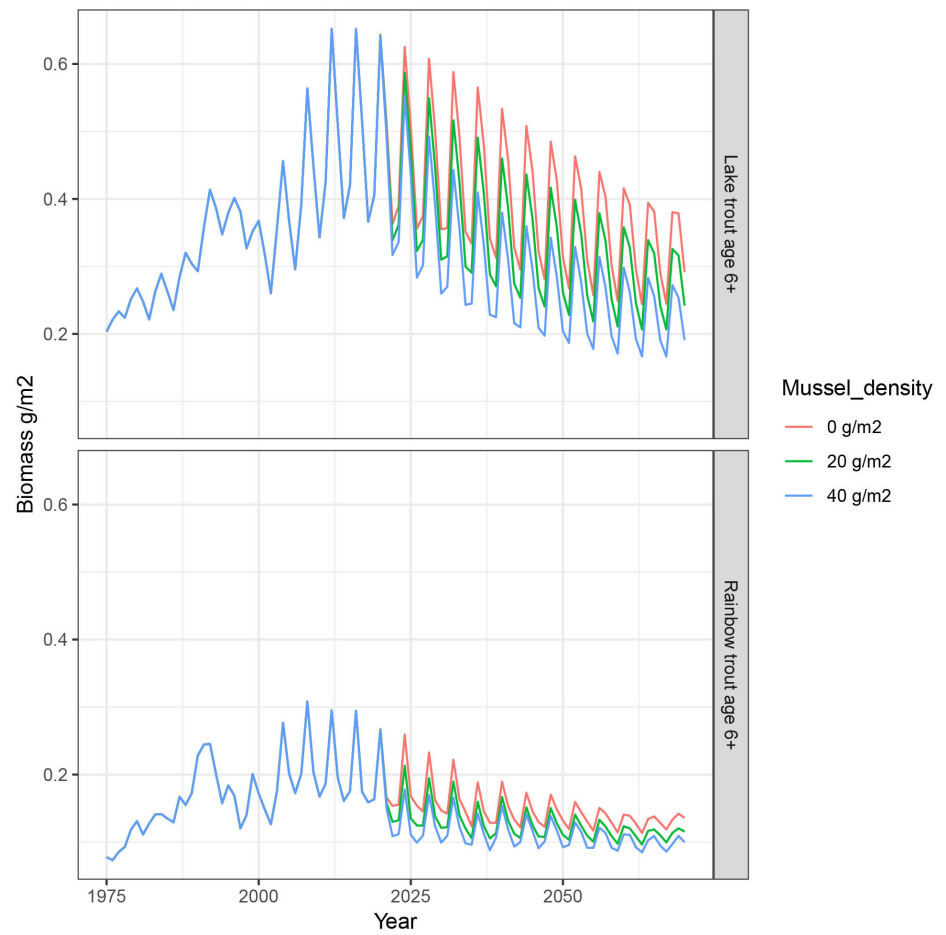


Figure 6. Modelled prediction of lake trout and rainbow trout biomass without mussels (red); with mussels at a combined density of 20 g·m⁻² (green); and with mussels at a combined density of 40 g·m⁻² (blue).

Depending on the size and depth of the lake, invasion of Dreissenid mussels may not show any significant effect on the phytoplankton and zooplankton abundances (Higgins and Vander Zanden 2010; Jaeger Miehl et al. 2009; Wong et al. 2010). Stratification can isolate the euphotic zone and offer a refugia from Dreissenid filter-feeding (Higgins and Vander Zanden 2010; Rowe et al. 2015). Climatic conditions and available nutrients can have more of an effect on overall phytoplankton abundance, although there can be localized effects of mussels (Barbiero et al. 2018; Rowe et al. 2017). Even with declines in phytoplankton, there may be little to no effect on zooplankton (Jaeger Miehl et al. 2009); smaller zooplankton species may be more affected than larger crustaceans (Karatayev et al. 2002). Effects of invasive mussels are generally predicted to be higher in shallow, non-stratified basins (MacIsaac et al. 1995). Shuswap Lake is a relatively deep and steep-sided lake: the low densities of invasive mussels in other systems that have been observed at depths below 90 m (Vanderploeg et al. 2010) limits the amount of colonization, and therefore the carrying capacity predicted for a system like Shuswap Lake. Observed zooplankton biomass variations were not necessarily correlated with ecosystem factors, as

climate, over-wintering conditions and timing of the spring bloom can all impact zooplankton abundance.

We explored two different mussel biomass carrying capacities to determine possible effects. Due to the amount of habitat at the different depth strata, a combined $20 \text{ g}\cdot\text{m}^{-2}$ was calculated to be the most likely biomass density for Dreissenid mussels in Shuswap Lake. A higher biomass density was also used to determine the tipping point of the ecosystem; any combined density greater than $40 \text{ g}\cdot\text{m}^{-2}$ resulted in a severe decline of phytoplankton and zooplankton species towards the end of the simulation, leading to declines in both planktivores and piscivores within the lake. The biomasses used here were much lower than reported in other studies (Kumar et al. 2016) but this reflects different constraints imposed on mussel biomass due to lake bathymetry, substrate availability and chemical composition of the water (Kao et al. 2014).

Even with increased mussel biomass, predatory fish species were predicted to decline but still persist in Shuswap Lake. This persistence appears to be due to the availability of sockeye salmon fry and yearlings as a food source, as well as the predicted low biomass of mussels, which explains the contrast to results found by Kumar et al. (2016). To some degree, sockeye maintained predatory species (rainbow trout and lake trout), which resulted in kokanee being both nutritionally stressed and subject to higher predation mortality. Planktivorous species, including fish, show the greatest declines following Dreissenid mussels invasion (Jaeger Miehl et al. 2009), which agreed to some degree with the results from this model. Although initial results in Karatayev et al. (1997) did not find documented evidence of an effect on planktivorous fish, later studies suggested that increased competition for food resources, combined with an increased predation risk due to greater water clarity, would have negative effects (Karatayev et al. 2015). Kao et al. (2014) found that nutrient levels had more of an effect on food webs than Dreissenid mussels, while Wong et al. (2010) found little impact by invasive mussels on the different zooplankton species in Lake Mead. The effect of invasive mussels is very dependent on conditions within each ecosystem (Strayer et al. 2014).

Previous studies indicate that an invasion of Dreissenid mussels has indirect impacts on pelagic fish (Jaeger Miehl et al. 2009; Riley et al. 2008). Lake trout and introduced Chinook salmon in the Laurentian Great Lakes were predicted to experience negative effects from nutritional stress, due to mussel-related declines in their forage fish prey (Roseman and Riley 2009). In the case of Shuswap Lake, kokanee (the forage fish) showed dramatic declines, followed by piscivorous rainbow trout and lake trout, while sockeye salmon showed minimal declines. Marine-derived nutrients, which sustained the sockeye stock and provided relatively stable recruitment of age-0 sockeye to the lake, helped sustain predators in this system, thereby increasing impacts to the kokanee stock. Influx of nutrients from an outside source

are believed to mitigate the effects of invasive mussels to some degree (Boegman et al. 2008; Kao et al. 2014), and the importance of marine-derived nutrients to Shuswap Lake demonstrates an important contrast from well-studied systems such as the Laurentian Great Lakes, which have no annual input of marine-derived nutrients from anadromous fish.

Due to the chemical composition of Shuswap Lake, and the recreational value and boat traffic to the lake, there is a substantial propagule pressure and risk of establishment (Therriault et al. 2013). Regionally, invasion in Shuswap Lake means a new node for invasion vectors to spread across waterbodies due to attachment to boats and equipment and transfer to other water bodies in the province (Muirhead and MacIsaac 2005). Additionally, Shuswap Lake is located approximately 500 km from the ocean, draining into the Thompson and Fraser Rivers. This connection within the Fraser watershed would lead to substantial downstream habitat for secondary invasions, likely leading to substantial changes to aquatic communities downstream. Anadromous fish such as sockeye salmon appear to be more resistant to the effects of the invasive mussels due to their ability to use the marine environment; this benefit may have less of an effect if marine survival becomes lower, due to warming temperatures (Kintisch 2015), competition (Batten et al. 2018) or increased predation (Walters et al. 2020).

Dreissenid invasions in North American aquatic systems have been characterized as one of the greatest ecological threats on the continent (Karatayev et al. 2015; Ludyanskiy et al. 1993). Our results indicate that impacts will be context-specific. While we predict noticeable impacts on non-anadromous fish species, impacts would be relatively unnoticed from other perspectives. Our case study is similar to other systems where observed impacts of invasion were relatively benign, due to the lakes being deeper and more stratified (Barbiero et al. 2018; Grigorovich et al. 2003; Higgins and Vander Zanden 2010). In Shuswap Lake, limited littoral habitat, large lake volume and mitigating nutrients from large sockeye salmon runs led to a relatively minor impact on the phytoplankton, zooplankton and anadromous sockeye salmon species. However, the real risk from invasion may be the establishment of a new regional source, which could result in new invasions in neighbouring systems (including further upstream) and downstream. This study demonstrates the different impacts that aquatic invasions can have throughout the freshwater food web, as well as the importance of differentiating regional risk from local consequences.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Observed (points) and model predictions of relative abundance for total sockeye salmon spawner returns, 1976–2018.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Woodruff_etal_SupplementaryFigure.pdf