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Research Article

Estimating carrying capacity of quagga mussels (*Dreissena rostriformis bugensis*) in a natural system: A case study of the Boulder Basin of Lake Mead, Nevada-Arizona

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Editor's note:
This paper was prepared by participants attending the workshop entitled "Quagga Mussels in the Western United States – Monitoring and Management" held in San Diego, California, USA on 1-5 March 2010. The workshop was organized within the framework of the National Shellfisheries Association, American Fisheries Society (Fish Culture Section) and World Aquaculture Society's Triennial Conference. The main objective of this workshop was to exchange and share information on invasive quagga mussels among agencies. The data presented in this special issue provide critical baseline information on quagga mussel monitoring and management at the early stages of introduction in the western United States.

Abstract

Estimation of carrying capacity for bivalves is generally carried out for mussel culture systems wherein maximizing mussel numbers requires the consideration of both ecological and economic endpoints. We adapted an existing culture-system model to estimate potential carrying capacity of an invasive species, the quagga mussel (*Dreissena rostriformis bugensis*) in the Boulder Basin of Lake Mead, Nevada. We parameterized the model using both field measurements and known quantities previously published in the literature. To make this model most useful to ecologists and managers, we provide a detailed description and derivation, as well as an example calculation for the model. The model is based on mean Chlorophyll *a* concentrations in the Boulder Basin of Lake Mead, and the number of quagga mussels needed to filter a given reduction in food particles from the water column. Estimates ranged from a total of 1.51×10^{12} mussels with a net reduction of 50% of food particles to 1.02×10^{13} mussels when the net reduction was at the threshold level of survival (0.017 µg/L). Limitations to the model and potential environmental and ecological considerations are discussed.

Key words: Carrying capacity, *Dreissena rostriformis bugensis*, Incze Model, Lake Mead, quagga mussel

Introduction

Dreissenid mussels inhabit a variety of freshwater systems throughout the United States and Europe. Two representative species of this family, the zebra mussel (*Dreissena polymorpha* Pallas, 1771) and the quagga mussel (*Dreissena rostriformis bugensis* Andrusov, 1897), are of particular interest to invasive species ecologists owing to their rapid spread and their negative economic impact related to damage on water intake pipes and electrical generation plants (Britton et al. 2010); further, the potential extinction of native mussel species after invasions by zebra mussels and quagga mussels is of particular concern (Ricciardi et al. 1998).

Both species have similar geographic ranges and life-history strategies, but differ in the timing of their invasions in Europe and the United States (Mills et al. 1996; Baldwin et al. 2002; Orlova et al. 2005). Quagga mussels, first described in the 1890s in the Ukraine, are a particularly aggressive invader. They were documented to spread at least 500 km northward in the Ukraine between 1964 and 1989, and since 1996 have inhabited nearly all estuaries in the eastern and southern regions of the Ukraine by outcompeting the zebra mussel in that region (Mills et al. 1996). Similar rapid spread has been documented in the United States, with dreissenids first appearing in the late 1980s in the Great Lakes region and then spreading (presumably by recreational boats) to the western

U.S. Quagga mussels reached Lake Mead by 2007; they are now found in the western states of Nevada, Arizona, Colorado, California, Texas, and Utah (Britton et al. 2010).

Because of the rapid spread of quagga mussels and their potential negative impacts on the systems in which they invade, there is an interest in estimating the potential carrying capacity of this species. This requires the identification of possible ecological and/or environmental factors that may serve as limiting factors for the survival of quagga mussels, and then subsequently developing a carrying capacity model utilizing these limiting factors as input variables. Lake Mead provides favorable environmental conditions [i.e., warm water, high calcium concentrations, hard substrates, suitable pH and sufficient dissolved oxygen (Table 1)]. Limiting factors for quagga mussels are few; in fact, in Lake Mead, only one potential limiting factor exists; namely, Chlorophyll *a*, in phytoplankton, which serves as the primary food source for dreissenid species (Table 1) (Baker et al. 1998; Baldwin et al. 2002).

To that end, the intent of this case study was to utilize data from the literature and data collected from the Boulder Basin of Lake Mead, Nevada, in order to estimate quagga mussel carrying capacity. We adapted a mussel culture model (described in detail below) that utilizes food concentration as the primary input variable for this task. We provide carrying capacity estimates under a variety of scenarios, and also provide a worked calculation example for those wishing to utilize this or a similar approach for their own data.

Methods

Study location

Lake Mead, the largest reservoir in the United States in terms of volume (36.7×10^9 m^3), is a 66,000 ha-deep reservoir on the lower Colorado River, Nevada-Arizona (Figure 1) (LaBounty and Burns 2005). Boulder Basin, the most down-stream basin of Lake Mead, is where quagga mussels were originally identified and is thought to be the location where the introduction of the mussels occurred. Therefore, Boulder Basin was the focus of this case study (Figure 1).

Model framework

There are currently no known models that have been used for estimating carrying capacity of quagga mussels in a natural system. The primary purpose of this study, then, was to adapt an existing mussel culture model that requires minimal parameterization as an initial step in the potential development of a more comprehensive estimation approach. To that end, the suspended-culture model developed by Incze et al. (1981; hereafter the "Incze Model") was used in the current study.

The Incze Model was developed to estimate bivalve carrying capacity in mussel cultivation systems. The model is based on the geometry of the cultivation system, water flow-through, and the removal of suspended particles in the water. It assumes that there is a homogeneous representation of suspended particles in the water column and that water flow is both normal and laminar to the mussels in the system. This model can be envisioned as a set of "tiers" or conglomerations of mussels. As water, and the suspended particles that it contains, flow through the tiers in the system, particles get removed because they are consumed by the mussels as a food source. The removal of food particles as water flows through these tiers is the basis for estimating carrying capacity, as food is often a limiting source in mussel cultivation systems (Figure 2).

Incze Model derivation

As illustrated in Figure 2, food particles flowing through the tier system are assumed to be removed by the mussels in a given tier, resulting in a net reduction of available food particles at each subsequent tier; this net reduction continues until the available food particles fall below the minimum threshold needed to support the biological requirements of the mussels.

Assume that n_1 food particles enter the system initially, and that n_2 food particles remain after passing through the first tier; the difference of n_1 and n_2 would represent the food particles remaining in the tier system and therefore available to the next tier. To generalize, assume that n_i ($i = 1, 2, \ldots k$) particles enter a tier and n_j ($i<j$) particles exit a tier, illustrated thus:

$(n_i - n_j)$ = the total number of food particles filtered by mussels in a given tier

$\therefore$

$(n_1 - n_2)$ = the number of food particles filtered by tier 1

$(n_2 - n_3)$ = the number of food particles filtered by tier 2

$\vdots$

$(n_k - n_{k+1})$ = the number of food particles filtered by tier k

Table 1. Ecological and environmental variables that serve as potential limiting factors for the survival of dreissenid mussels.

Variable	Tolerance Limit*	Boulder Basin**
Calcium Concentration (mg/L)	< 12	69.1-87.0
Temperature (◦C)	> 30	< 28
Salinity (psu)	> 5	< 1
pH	< 6.5	8
Oxygen Saturation (%)	< 25	> 40
Turbidity (Secchi depth; m)	< 0.1	> 3.3
Chlorophyll *a* (µg/L)	< 2.5 *or* > 25	0.9-5.0

*From Spidle et al.1995; McMahon 1996; Mills et al. 1996; Jones and Ricciardi 2005.
** From LaBounty and Bourns 2005; Whittier et al. 2008.

Figure 1. Area map of Lake Mead National Recreation Area, Nevada-Arizona with Boulder Basin encircled.

Functionally, tier k+1 represents the supremum (i.e., maximal tier number) of the system, as insufficient particles remain in the system subsequent to this tier to support mussels. The key to determining the maximum number of tiers that a system can support requires the consideration of a relationship between the food particles initially entering a system (n_1) and the food particles available in the last viable tier (n_k). This is accomplished by representing the n_j^{th} particle concentration as a function of the n_1 particles entering through the first tier.

Let N = the volume of water (in L/hr) entering through the first tier; V = the flow rate of water (in m/hr) entering through the first tier; and A = area (in m^2) of the system (i.e., the product of system width and height); hence, $N = V \times A \times 10^3$. If it is assumed that seston is homogenously distributed in the water column, then N will be reduced by the amount of food particles filtered

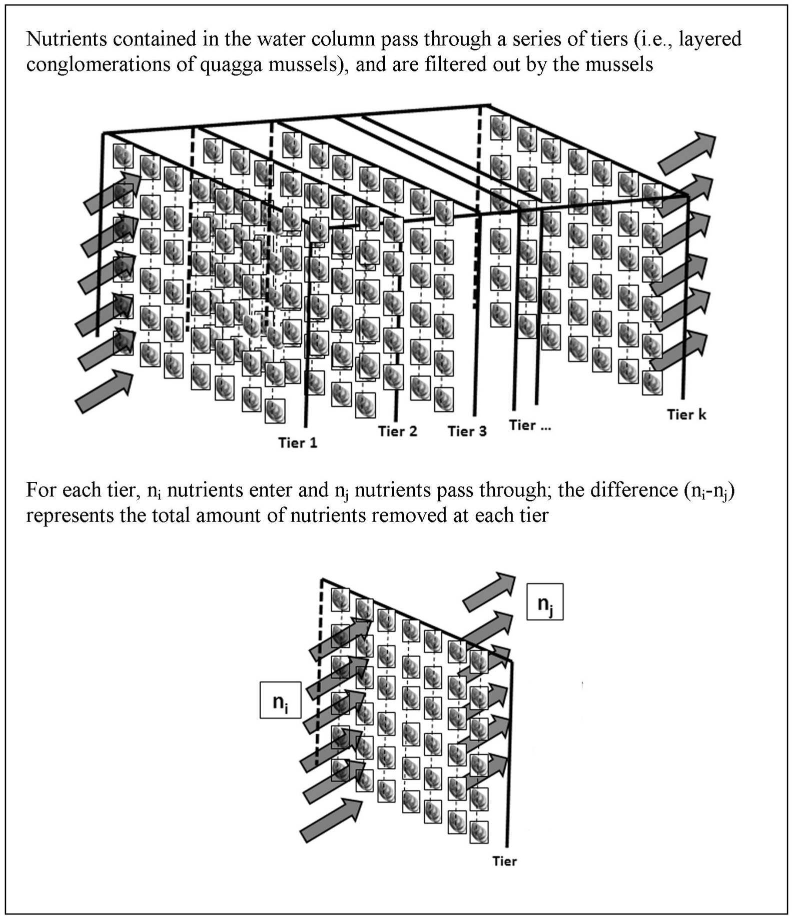

Figure 2. Graphical representation of the tier system model used to estimate carrying capacity for Boulder Basin in Lake Mead, Nevada-Arizona.

by mussels at each tier, and therefore the n_j^{th} particle concentration will simply be the product of n_1 and the fractional reduction of N, such that:

$$n_2 = n_1 \times \frac{(\text{N - food particles filtered})}{\text{N}}$$

$$n_3 = n_2 \times \frac{(\text{N - food particles filtered})}{\text{N}} = n_1 \times \left[\frac{(\text{N - food particles filtered})}{\text{N}}\right]^2$$

$$\vdots$$

$$n_k = n_1 \times \left[\frac{(\text{N - food particles filtered})}{\text{N}}\right]^{k-1}$$

$$\therefore$$

$$\frac{n_k}{n_1} = \left[\frac{(\text{N - food particles filtered})}{\text{N}}\right]^{k-1}$$

The number of food particles filtered can be represented as the product of the clearance rate of the mussels (CR; in L/hr) and the number of mussels (M). Solving the equation above for k yields:

$$k = \frac{\ln\left(\frac{n_k}{n_1}\right)}{\ln\left(\frac{\text{N - CR} \times \text{M}}{\text{N}}\right)} + 1.$$

Hence, this function provides the maximum number of viable tiers, and the product of k and the number of mussels per tier provides an estimate of carrying capacity.

Model parameterization

In the Boulder Basin of Lake Mead, artificial ABS plastic pipes (20 cm sections of 6 cm pipe) were lowered to different depths. They developed an average of 5,079 adult and juvenile mussels/pipe two years after being suspended in the water (Wen Baldwin and Wai Hing Wong, unpublished data). These pipes were used to represent tiers in this system model. The estimated filtration rate of 52 L/hr/tier was assumed to be equivalent to that observed in Lake Erie as reported by Baldwin et al. (2002). Measurements of Chlorophyll *a* taken from Boulder Basin ranged from 0.9-3.1 µg/L (Wong et al. in press); the mean of the measurements, 1.72 µg/L, was used as the initial available concentration (i.e., n_1) in the system. Finally, field measurements of flow rate differed by depths; flow in the Boulder Basin results from inflow from the Las Vegas Wash in the northwest to the Colorado River to the south of the Basin. The mean flow rate of 329.76 m/hr was used for 0-10 m depth, 111.24 m/hr was used for 10-20 m depth, and 123.48 m/hr was used for 20-30m depth (P. Roefer, personal communication). Meuting (2009) suggests that colonization below 30 m in Boulder Basin was quite slow in her substrate study; therefore, we limited our estimates to the first 30 m depth.

Results

As an illustrative example of calculations, please see Figure 3. The methodology shown in this figure was used to populate Table 2, which shows estimates for the decile depths shown above and across a range of ecological scenarios. Estimates ranged from a total of 1.51×10^{12} mussels with a net reduction of 50% of food particles to 1.02×10^{13} mussels when the net reduction was at the threshold level of survival (0.017 µg/L).

Discussion

Based on our maximum estimate of quagga mussel carrying capacity for study area (Table 2), and extrapolating across the estimated subsurface area of Boulder Basin (112 km^2; Twichell et al. 1999), nearly 100,000 adult mussels/m^2 are expected. Given the exceedingly large subsurface area of the lake (388 km^2, Twichell et al. 1999) and the ready food availability as evidenced by the Chlorophyll *a* levels, it is not surprising that carrying capacity estimates can reach such high numbers. What is unknown in this system, however, is how factors extraneous to this model may impact the actual carrying capacity.

Seasonality, for example, is not accounted for by this model, and this may potentially lead to changes in seston concentration, flow rate, and mussel density at different depths (LaBounty and Burns 2005; Chen et al. 2011). Additionally, water temperatures may be too great during the summer months to support quagga mussels at shallow depths given that survivability at warmer temperatures is diminished (Spidle et al. 1995). Moore et al. (2009) have found only a few mussels in the shallow areas (< 6.1 m) compared to deep areas (12.2 m and 18.3 m). What is less known, and a potential demonstrable factor in reducing the carrying capacity of Lake Mead, is the impact that ever-lowering water levels will have on this species. Water budget models by Barnett and Pierce (2008), for example, suggest that in the next seven years there is a 50% probability that Lake Mead levels will lower enough to reach the minimum power pool level. Even if their model prediction is not correct, reduction of water levels will impact the total available surfaces to which quaggas adhere, will reduce inflow rate, and may decrease seston availability; all of these factors can greatly impact the carrying capacity of the Lake.

Regardless of these potential environmental factors, the carrying capacity of the quagga mussel in Lake Mead, and the resulting environmental damage posed by them will continue to be problematic for the foreseeable future. Removal of available nutrients by the mussels potentially could have negative impacts on existing species in the lake, similar to the ecological impacts the zebra mussels have had on native fauna; biofouling may also lead to reduction of other bivalves (Ricciardi et al. 1998), such as the Asian clams (*Corbicula fluminea* Müller, 1774) in Lake Mead. Further, there may be similar impacts on water clarity and decline in the natural benthic community such as those seen in other areas with established, invasive dreissenids (Dermott and Kerec 1995). Though there are obvious environmental risks of having invasive quagga mussels in the ecosystem, there do not appear to be direct human health risks. Most risks are economic in nature (e.g., clogging of pipes, turbines, and filtration systems for power generation plants) (Britton et al. 2010). Time will tell just how detrimental this species is to Lake Mead ecosystem.

What is less clear when estimating the carrying capacity of quagga mussels in the Boulder Basin of Lake Mead, however, is the

Figure 3. Example calculation of carrying capacity for the 1-10m range with 50% reduction in Chlorophyll *a* for Boulder Basin in Lake Mead, Nevada. This calculation method was used to populate Table 2.

$$n_1 = 1.72\,\mu g/L$$

$$n_k = \frac{1}{2} n_1 = 0.86\,\mu g/L$$

$$M = 5079 \text{ mussels/tier}$$

$$CR = \frac{52 \text{ L/hr/tier}}{5079 \text{ mussels/tier}} = (0.0102 \times M) \text{ L/hr}$$

$$N = 329.76 \text{m/hr} \times 4{,}000 \text{m} \times 10 \text{m} \times 10^3 = 1.319 \times 10^{10} \text{ L/hr}$$

$$k = 1 + \frac{\ln\left(\frac{n_k}{n_1}\right)}{\ln\left(\frac{N - CR \times M}{N}\right)} = 1 + \frac{\ln\left(\frac{0.86}{1.72}\right)}{\ln\left(\frac{1.319 \times 10^{10} - 0.0102 \times 5079}{1.319 \times 10^{10}}\right)} = 1.74 \times 10^8 \text{ tiers}$$

$$\therefore$$

$$1.74 \times 10^8 \text{ tiers} \times 5079 \text{ mussels/tier} = 8.81 \times 10^{11} \text{ mussels}$$

Table 2. Estimates of carrying capacity at four Chlorophyll *a* concentrations for quagga mussels in the Boulder Basin of Lake Mead, Nevada. Chlorophyll *a* concentrations represent reductions from the beginning value of 1.72 µg/L calculated from field data in Boulder Basin (0.86 µg/L = 50% reduction; 0.17 µg/L = 90% reduction; 0.05 = 97% reduction; and 0.017 = 99% reduction, which also represents the lower threshold necessary for survival (Baldwin et al. 2002)).

Depth (m)	Chlorophyll *a* Concentration (µg/L)			
	0.86	0.17	0.05	0.017
0-10	8.81×10^{11}	2.98×10^{12}	4.56×10^{12}	5.96×10^{12}
10-20	2.97×10^{11}	1.00×10^{12}	1.54×10^{12}	2.01×10^{12}
20-30	3.30×10^{11}	1.11×10^{12}	1.71×10^{12}	2.23×10^{12}
Total	1.51×10^{12}	5.09×10^{12}	7.81×10^{12}	1.02×10^{13}

appropriateness of the Incze Model in this context. This model has been used by other researchers (Sara and Mazzola 2004), and was included in a review of available models by Smaal et al. (1998). It does appear to have good features that make it a useful tool for field ecologists and managers, particularly in that it is easy to parameterize and is a simple process to obtain estimates using basic calculations. Further, it is based on one of three minimum requirements listed by Smaal et al. (1998) for estimating carrying capacity of bivalves, namely it is based on transport dynamics. Further research may include sediment dynamics and separate models for organism vs. population level process, the other two key features of carrying capacity estimators suggested by Smaal et al. (1998). The use of other culture-based models may prove to be important for this purpose. Box model simulations have been used extensively in this context (Grant et al. 2005, 2007, 2008; Filgueira and Grant 2009), and would likely be ideal for future modeling exercises (such as validation of the present model) for estimating quagga mussel carrying capacity

Conclusions

Estimation of carrying capacity of organisms in their natural environment is key to understanding population dynamics and the potential impacts that a species will have on the environment and the native fauna. Based on mean Chlorophyll *a* concentrations in the Boulder Basin of Lake Mead, and the number of quagga mussels needed to filter a given reduction in food particles from the water column, the developed model estimates that the carrying capacity of adult mussels in this system can reach 1.02×10^{13} mussels when the net reduction is at the threshold level of survival (0.017 µg/L). Validation of the present model can be more useful for future modeling exercises.

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