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Abundance and size of quagga mussels (Dreissena bugensis) veligers in Lake Mead, Nevada-Arizona

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VELIGERS OF INVASIVE QUAGGA MUSSELS (*DREISSENA ROSTRIFORMIS BUGENSIS,* ANDRUSOV 1897) IN LAKE MEAD, NEVADA–ARIZONA

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ABSTRACT The planktonic veligers of the invasive quagga mussel were present year-round from April 2008 to March 2009 in Lake Mead, with high abundance from September to October (>20 veligers/L), whereas the percentage of competent veligers, in terms of the ability to settle, peaked from November 2008 to January 2009 (>60%). The results from this experiment are useful in understanding the life history and population dynamics of quagga mussels in the lower Colorado River Basin.

KEY WORDS: invasive species, quagga mussel, veliger, *Dreissena rostriformis bugensis*, Lake Mead

INTRODUCTION

Two dreissenid mussels were introduced into the Laurentian Great Lakes of North America during the 1980s: the zebra mussel (*Dreissena polymorpha* Pallas 1771) and the quagga mussel *Dreissena rostriformis bugensis* (Hebert et al. 1989, May & Marsden 1992, Mills et al. 1993, Nalepa & Schloesser 1993, Carlton 2008). Later, these invasive mussels spread east to the Hudson River and to the south along the Mississippi River and other ecosystems on the east side of the 100th Meridian (100° W longitude). Before its discovery in the Boulder Basin of Lake Mead (Nevada, USA) on January 6, 2007, the quagga mussel was primarily restricted to the Great Lakes region and the Mississippi River near St. Louis (Missouri, USA). The presence of quagga mussels in Lake Mead, the largest reservoir in the United States in terms of volume (36.7×10^9 m^3) (LaBounty & Burns 2005), was the first known introduction of a dreissenid species in the western United States. In addition, this was the first time that a large ecosystem was infested by quagga mussels without previous infestation by zebra mussels (LaBounty & Roefer 2007). Quagga mussels have since colonized the lower Colorado River, as well as lakes and reservoirs in Arizona, California, Colorado, and Utah. The zebra/quagga mussel has become arguably the most serious nonindigenous biofouling pest introduced into North American freshwater systems (LaBounty & Roefer 2007). The presence of dreissenid mussels has led to severe ecological, recreational, and economic impacts in the Great Lakes and other systems in the eastern United States. In the arid southwest, mussel impacts may be even more severe because the 27 million people in California, Arizona, and Nevada are completely reliant on the lower Colorado River. For example, the Metropolitan Water District of Southern California expects to spend between $10 million and $15 million a year to address quagga mussel infestations in its 390-km Colorado River aqueduct and reservoir system (Fonseca 2009). To improve monitoring and management of quagga mussels, the ecology and biology of the quagga mussel must be researched in depth.

Similar to marine bivalve molluscs, quagga mussels have 2 life-forms: planktonic and benthic. After external fertilization between a mature egg and a sperm in the water column, embryological development occurs as a single cell divides by mitosis. There are 3 major stages in the life cycle of quagga mussel: larval veliger, juvenile, and adult stages (Ackerman et al. 1994). The larvae are planktonic free-swimming veligers, and the juvenile and adult stages are mostly motile individuals attaching to substrates with their proteinaceous byssal threads. Usually, the planktonic larval stage is further divided into 4 stages: trochophore, straight-hinged veliger (or D-shaped veliger), umbonal veliger (or veliconcha), and pediveliger. During the pediveliger period, they swim with the velum, crawl by means of a foot, and secrete byssal threads to settle on a substrate. The amount of time required for a fertilized gamete to become a fully developed juvenile can range from 8–240 days, and is dependent on many environmental factors, such as temperature, food quality and quantity, and available substrates (Nichols 1996). Most veligers settle on appropriate substrates 18–90 days after fertilization (Ackerman et al. 1994, Crosier & Molloy 2001). After metamorphosis, pediveligers become juveniles.

The vast majority of zebra and quagga mussel life history information is from the Great Lakes region. Garton & Hagg (1993) found that, in the shallow western basin of Lake Erie, there were 2 veliger abundance peaks in late July and late August of 1989, whereas there was only 1 peak in late July 1990. No veligers were present in the water from October to April, and the peak density of veligers in western Lake Erie was usually more than 200 veligers/L (Garton & Hagg 1993). Compared with the Great Lakes, Lake Mead is significantly different in water quality, salinity, temperature, and several other characteristics. Specifically, the average water temperature is much higher in the lower Colorado River than in the Great Lakes region. For example, the lowest recorded temperature in Lake Mead is about 12°C (LaBounty & Burns 2005). Therefore, the life and behavior of quagga mussels in the arid southwest may be different from that in other ecosystems in North America and Europe (Mackie & Schloesser 1996). The goal of this study was to investigate the abundance and size of quagga mussel veligers in the Boulder Basin of Lake Mead to elucidate further their life history and population dynamics in the lower Colorado River.

MATERIALS AND METHODS

Each month from August 2008 to March 2009, a vertical plankton tow (mesh size, 64 μm; diameter, 15 cm) was conducted to collect veliger samples in the open water of Boulder Basin, Lake Mead. The location was marked by an emerged yellow buoy with "Government Property Restricted

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Access" written on the side. GPS coordinates of the yellow buoy were N 36.0537, W 114.75. The water depth during the experiment ranged from 60–63 m. Samples were collected by gently lowering the plankton net to the water at rate of approximately 1 m/sec (a steady and unhurried hand-over-hand motion), and the net was towed for a total of 60 m. Pulling too fast can cause a pressure wave in front of the net that pushes the water and plankton away from the mouth of the net, and thus does not sample effectively the desired volume of water. Usually, the minimum water volume collected was 1,000 L. After each tow, the net top to bottom from the outside was washed with distilled water to rinse veligers into the collection cup. The collection cup side screens were also washed from top to bottom and then emptied into a 500-mL Nalgene (U.S. Plastic Corp, Lima, OH) bottle. The collection cup was rinsed twice with small amounts of water and emptied into the same bottle. The bottle was labeled with the date and location. Sample bottles were kept on ice while in the field. After sampling was complete, the plankton net was decontaminated by being soaked in a 5-gallon bucket filled with white vinegar for about 45 min. The plankton net was thoroughly rinsed with clean water after each soaking. The sample was preserved using ethyl alcohol until it comprised 25% of the final sample volume. Samples were refrigerated until they were ready to be analyzed.

Quagga mussel veligers were processed and counted in the laboratory using a modified combination of the Standard Method (10,200 G) Zooplankton Counting Techniques (Eaton et al. 2005), the U.S. Army Corps of Engineers method for calculating *Dreissena* veliger densities (http://www.usace.army.mil/). In the laboratory, the sample was added to an Imhoff settling cone with a Venoset delivery system. The veligers were allowed to settle in the Imhoff cone for a minimum of 24 h. Successive aliquots of settled sample were transferred into a centrifuge tube (50 mL) until no sediment remained in the Imhoff cone. One milliliter of the well-mixed sample was "pipetted" and dispensed into a Sedgwick-Rafter counting cell. The coverslip was placed on the counting cell perpendicular to the long axis of the slide. The filled Sedgwick-Rafter cell was examined under a dissecting microscope fitted with a cross-polarized light (Carl Zeiss SteREO Discovery.V8, Toronto, Ontario, Canada), and the number of veligers was recorded with a click counter. The utilization of cross-polarized light aids in counting accuracy of veligers as a result of the birefringent crystalline structure of the calcite in the larval shell (Johnson 1995). One of the major limitations for using cross-polarized light is its inability to discriminate among various bivalve species that have planktonic larvae. In the 1980s, the Asian clam *Corbicula fluminea* was the only bivalve species and was a dominant benthic organism (100–200 mussels/m^2) in Lake Mead (Peck et al. 1987). However, in recent years, live clams are difficult to find (Wen Baldwin, pers. comm.). Therefore, the potential error of quagga mussel veliger count resulting from Asian clams is assumed to be negligible. Five 1-mL subsamples were repeated, and the mean of the 5 counts was calculated for each concentrated sample. The monthly veliger density was estimated further. The size of veligers in a random proportion of sample (usually more than 60 veligers) was measured with the AxioVision 4 Image Analysis Software setup for an AxioCam (Carl Zeiss Inc., Peabody, MA), which connects a computer to the stereomicroscope.

The size of a veliger in this article refers to the length measured perpendicular to the axis from the umbo or center of the hinge line to the opposing margin of the shell (Nichols & Black 1994). The mean size of all measured veligers and the percentage of pediveligers (most of them larger than 230 μm) were also calculated. Different developmental stages of veligers were identified based on the keys provided by Nichols and Black (1994). The protocol for sample collection and veliger enumeration was mainly developed by Bureau of Reclamation Technical Service Center in Denver, CO, and is used by the Lower Colorado Region Bureau of Reclamation Fisheries group for their monthly quagga mussel veliger sampling program. This has been recommended as a standard monitoring protocol for veliger monitoring in the lower Colorado River Basin (Wong et al. 2011).

RESULTS

Quagga mussel veligers were present continuously year-round (Fig. 1A). There were 2 peaks: one in June (9.5 veligers/L) and the other in September (28.6 veligers/L). In January, February, March, and April 2008, the abundance was low (1 veliger/L or less). The minimum and maximum sizes in each month from August 2008 to March 2009 were 77.8 and 344.6 μm, 84.7 and 329.3 μm, 88.7 and 328.5 μm, 101.8 and 327.7 μm, 92.7 and 355.6 μm, 86.1 and 312.7 μm, 92.9 and 307.2 μm, and 93.0 and 285.5 μm, respectively, with the mean size increasing from August to November 2008 and then decreasing from January to March 2009 (Fig. 1B). The highest percentage of pediveligers was noted

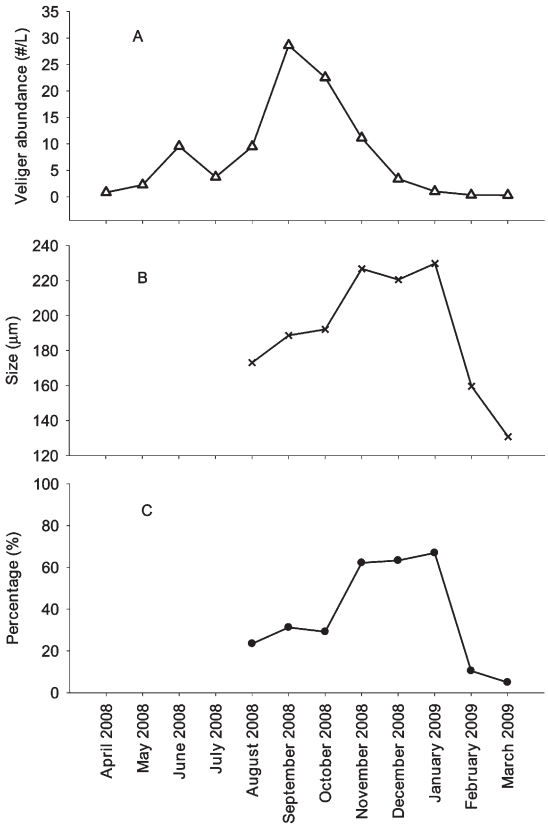

Figure 1. (A–C) Veliger abundance (A), mean size (B), and percentage of pediveligers of the total abundance (C) in the Boulder Basin of Lake Mead. Veliger abundance data from April to July 2008 were provided by Chris Holdren.

from November 2008 to January 2009 (>60%), and the lowest was from February to March 2009 (10% or fewer; Fig. 1C). From August to October 2008, the percentage of pediveligers was between 2% and 30%. Figure 2 provides more detailed information on size frequency for veligers collected from August 2008 to March 2009. Most veligers were umbonal veligers and pediveligers from August 2008 to January 2009, umbonal veligers in February 2009, and straight-hinged veligers in March 2009.

DISCUSSION

The planktonic veligers of the invasive quagga mussel were present year-round from April 2008 to March 2009 in the Boulder Basin of Lake Mead. Many environmental factors can affect the abundance of *Dreissena* planktonic veligers, such as food quantity and quality, temperature, waves, hydrodynamics, and so on. The veliger abundance in riverine and lacustrine systems are different; for example, some veligers found in one site can be produced by local adult populations whereas some can drift from upstream, which is dependent on the local flow regimes (Schneider et al. 2003).

In general, the presence of veligers and hence spawning was reported when water temperature was more than 12°C because dreissenid eggs cannot fully develop at temperatures less than 11°C, although spawning has been observed in dreissenid mussels at temperatures as low as 2.5°C (Garton & Hagg 1993 and references therein, Nichols 1996). Temperature is the primary factor explaining the timing of reproduction of *Dreissena*. The mean annual temperature ranges in the epilimnion, metalimnion, and hypolimnion of Boulder Basin of Lake Mead are between 12–27°C, 12–18°C, and 12–12.5°C, respectively (LaBounty & Burns 2005). Therefore, it is not surprising that veligers were

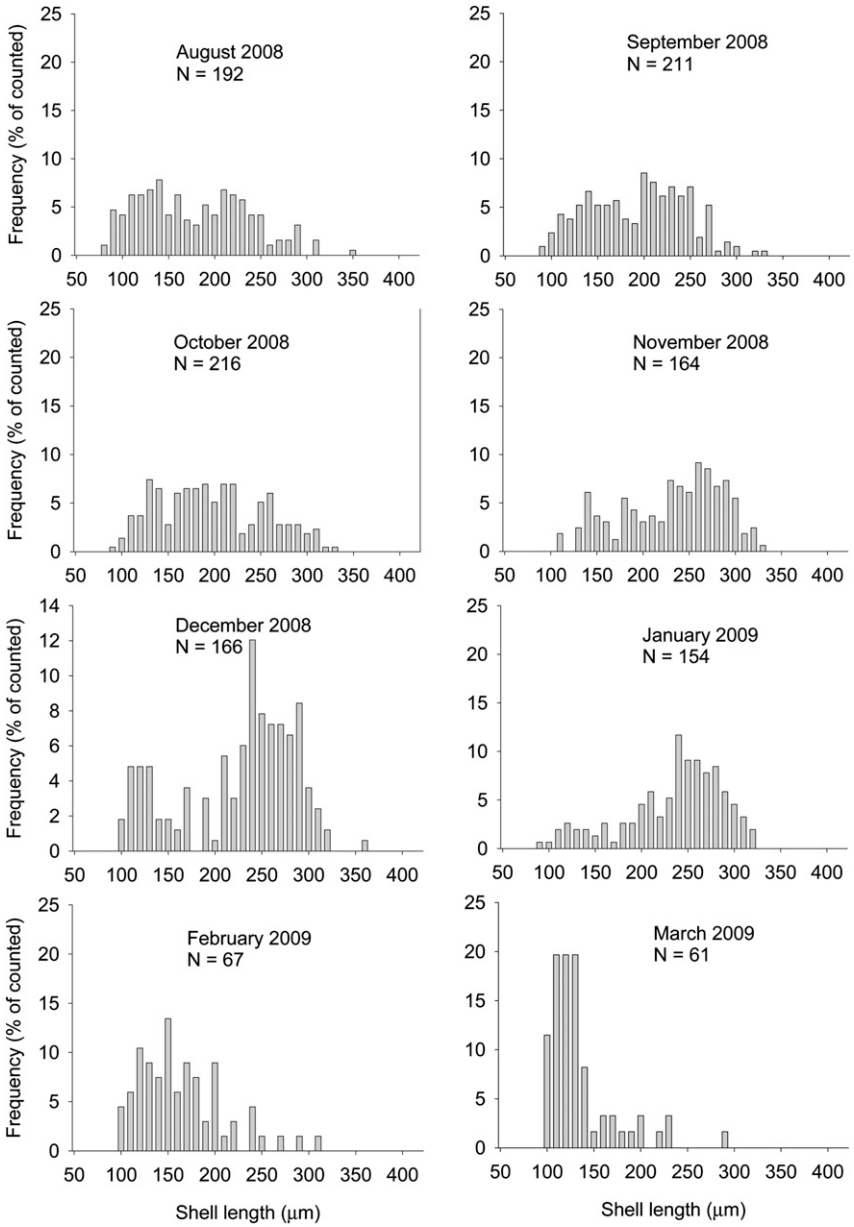

Figure 2. Frequency (measured as a percentage) of counted quagga mussel veligers with different sizes from August 2008 to March 2009.

detected throughout the year in the Boulder Basin as a result of the minimum Lake Mead water temperature being well above the lower temperature threshold for spawning. In areas where water temperatures do not decrease to less than 12°C, such as thermally heated reservoirs or laboratory conditions, larval production has been documented year-round (Nichols 1996). The temperature in January, February, and March 2009 at the epilimnion, metalimnion, and hypolimnion was about 13.2°C, 13.0°C, and 12.0°C, respectively. The disappearance of the 250-μm cohort and the growth of the 130–155-μm cohort from January to February 2009 may demonstrate that veligers can settle and develop in this reservoir in winter.

Independent experiments determined that quagga mussels settled on artificial substrates when temperatures were cold from January to April of (Mueting et al. 2010, Wen Baldwin and David Wong, unpubl. data), such as acrylonitrile butadiene styrene plastic, high-density polyethylene plastic, concrete underlayment board, aluminum, stainless steel, and fiberglass. The cohort with sizes around 110 μm (mostly straight-hinged or D-shaped veligers) from February to March 2009 showed that some adult mussels were able to reproduce in these cold months. It is reported that overwintering veligers found in the water column in Russia and North America (temperatures less than 5°C) are produced in the fall, and their development was delayed or very slow as a result of the colder temperatures (Nichols 1996 and references therein).

Lake Mead is a deep, complex ecosystem with complete stratification occurring about every other year in the outer Boulder Basin. Temperature profiles in the epilimnion, metalimnion, and hypolimnion are known to vary significantly (LaBounty & Burns 2005) (Figure 3). Based on temperature profiles, it was found that the veliger density had the highest correlation with water temperature profiles of the metalimnion ($R^2 = 0.87$, $P = 0.0002$; Fig. 3). Veliger density was less significantly correlated with temperature in the epilimnion ($R^2 = 0.67$, $P = 0.02$), and was poorly correlated with temperature in the hypolimnion ($R^2 = 0.45$, $P = 0.14$). The optimum temperature for larval development is 18°C (Sprung 1987). In the metalimnion, the temperature from July to November ranges from 17.8–21.0°C. The lower than optimal temperatures in the hypolimnion may force most veligers to live in the metalimnion and, to some extent, in the epilimnion.

In an independent study, it was found that very low settlement of juveniles in the hypolimnion occurred throughout a year-long period (Mueting et al. 2010). Therefore, most of the veligers observed in the current study might come from the metalimnion and some from the epilimnion, although this needs to be confirmed in further experiments by sampling veligers at different depths. If the aforementioned hypothesis is confirmed (i.e., most veligers are living in the metalimnion), temperature in this zone will be the key factor affecting veliger abundance in Lake Mead. When the temperature is 17.5°C or higher in this zone, the veligers can reach a density of 10 individual/L or more. It is reported that 17–18°C is the peak *Dreissena* spawning threshold where spawning activity is maximized (McMahon 1996). In the current study, when temperature in the metalimnion and epilimnion ranged from 17–22°C in June 2008, the veliger abundance peaked for the first time. When temperature in the metalimnion and epilimnion was between 21.2°C and 26.0°C in September, the second peak was observed (Fig. 3).

This bimodal pattern in veliger production is typical in many ecosystems reported in Europe, Russia, and North America; larval density is low at the beginning of appearance; requires 4–8 wk to reach the first of usually 2 peaks; and after the second

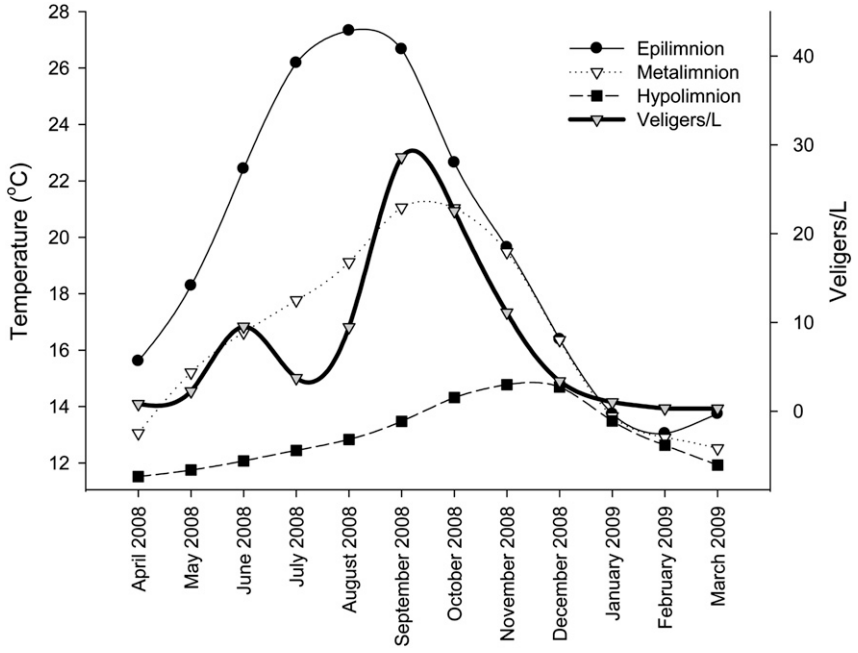

Figure 3. Temperature profile in the epilimnion and metalimnion, and veliger abundance during the experimental period. The temperature data were collected every 6 hours from March 27, 2008, to March 5, 2009 by the U.S. Geological Survey with a YSI 6600 multiparameter water quality probe at their Sentinel Island station. This station is only about 10 m away from the veliger sampling site. The mean monthly data for the epilimnion, metalimnion, and hypolimnion were calculated from the raw data, which were provided by Ronald Veley.

peak, veliger numbers gradually decline over time (Nichols 1996 and references therein). In the shallow western basin of Lake Erie, abundance of veligers had no correlation with water temperature and veligers were present throughout the summer when lake temperatures exceeded 18°C. There were no veligers found in the water from October to April, but the peak density of veligers in western Lake Erie is usually more than 200 veligers/L (Garton & Hagg 1993), which is much higher than the peak density in the current investigation (25 veligers/L).

A bimonthly substrate monitoring project on quagga mussel veligers showed that the settlement rates recorded from December 2008 to January 2009 and from October to November 2008 were 45,264 and 28,926 settled juveniles/m^2, respectively, whereas the settlement rates from August to September 2008 and from February to March 2009 were only 8,062 and 15,719 settled juveniles/m^2, respectively (Mueting et al. 2010). The time when higher settlement rates occurred corresponded to the period when higher percentages of pediveligers were observed in the current study (Fig. 1C). This confirms that settling rates are more dependent on maturational stages of larvae than simply on number of planktonic veligers in the water column (Garton & Hagg 1993, Ackerman et al. 1994). The higher percentage of pediveligers from November 2008 to January 2009 highlights that most veligers during this period were more competent in terms of the ability to settle.

Infestation on different kinds of infrastructures is mainly the result of larval settlement. Knowledge of the temporal presence of the competent pediveligers to settle on substrates, instead of the abundance of all veligers, is critical for implementing antifouling measures in a timely and efficient way. In Lake Mead, although high abundance of veligers was detected in June, September, and October 2008, the percentages of the competent pediveligers were the highest from November 2008 to January 2009. This information is critical for quagga mussel containment and prevention in the lower Colorado River Basin. For example, lake managers should pay more attention to boat disinfection from November to January of each year when the high percentages of veligers in water are more capable to settle successfully compared with other times of the year.

Based on the literature, it takes dreissenid veligers about a month to grow from fertilization to metamorphosis (Ackerman et al. 1994 and references therein). If this is true for quagga mussels in Lake Mead, monthly sampling used in the current study would not have identified the entire size spectrum of veligers. This might explain why only 1 straight-hinged veliger peak was found, and no trochophore peak was observed in our monthly sampling (Fig. 2). Furthermore, weekly sampling is recommended to monitor veliger abundance, because sampling at this frequency can track the peak density of veligers (Marsden 1992) and will not underestimate the maximum veliger counts. Therefore, to monitor better the abundance, size, and development of different stages of veligers in Lake Mead, continued investigations using weekly sampling frequency are needed. The difference in temperature in the epilimnion, metalimnion, and hypolimnion may also lead to differences in the life history of quagga mussels in Lake Mead (Fig. 3). The abundance and size of veligers, as well as the gonadal development of quagga mussel adults at different depths, need to be investigated in the near future to understand more completely the veliger population dynamics in this system.

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