Journal of Great Lakes Research 36 (2010) 50–59

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan

Henry A. Vanderploeg [a,*], James R. Liebig [a], Thomas F. Nalepa [a], Gary L. Fahnenstiel [b], Steven A. Pothoven [b]

[a] National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, 4840 S. State Road., Ann Arbor, MI 48108, USA
[b] Great Lakes Environmental Research Laboratory, Lake Michigan Field Station, 1431 Beach St., Muskegon, MI 49441, USA

ARTICLE INFO

Article history:
Received 14 September 2009
Accepted 21 April 2010

Communicated by Hunter Carrick

Index words:
Quagga mussel
Zebra mussel
Nearshore phosphorus shunt
Mid-depth phosphorus sink

ABSTRACT

We determined the clearance rates of the profunda morph of the quagga mussel (*Dreissena bugensis*) using seston and *Cryptomonas ozolini*, a high-quality algal food, for the temperature range 1–7 °C, which is the full temperature range this morph is likely to experience during isothermal conditions or in the hypolimnion of deep lakes. Experiments at 3 °C with the shallow-water morph of the quagga and the zebra mussel provided very similar results. The clearance rates were combined with dreissenid abundance in 0–30 m, 30–50 m, 50–90 m, and >90 m depth zones of the southern basin of Lake Michigan to calculate a maximum (using *Cryptomonas*) and minimum (using seston) fraction of the water column cleared (FC) per day in the different depth zones at 3 °C to determine dreissenid impact on the spring phytoplankton bloom from 1994 to 2008. Starting in 2003 or 2004 with the replacement of zebra mussels by quagga mussels in shallow water and expansion of quagga mussel biomass in deep water, FC began to exceed likely phytoplankton growth in the 30–50 m zone. In 2007–2008, FC greatly exceeded likely phytoplankton growth by a factor of about 5 in the 30- to 50-m depth zone, where dreissenids were extremely abundant. Low FC in the offshore region led to the hypothesis of a mid-depth carbon (C) and phosphorous (P) sink caused by mussel uptake of seston-associated C and P that affected not only the mid-depth region, but also the offshore region "downstream" of the mid-depth zone.

Published by Elsevier B.V.

Introduction

Profound water-quality impacts of zebra and quagga mussels (collectively dreissenids) have long been recognized in shallow, nearshore areas, where they have been typically found in high abundance (e.g., Vanderploeg et al., 2002; Hecky et al., 2004). For example, dreissenid mussel filtering activities in bays and shallow areas have led to decreased chlorophyll *a* concentrations and increased water clarity (physical ecosystem engineering) in spring, and the promotion of harmful algal blooms (HABs) in summer consisting primarily of the toxic colonial cyanobacterium *Microcystis* through selective rejection of the large toxic colonies of this species (Vanderploeg et al., 2001, 2002, 2009). In addition to these filtering and physical engineering impacts, dreissenids have played a fundamental role in the re-engineering of nutrient cycling. Because of homeostatic nutrient excretion, in phosphorus-rich systems, dreissenids would tend to increase P availability as soluble P (and decrease N:P ratios); however, in P-poor systems, dreissenids excrete little P, so as to maintain constant concentrations in their tissues (Vanderploeg et al., 2002). Thus, depending on nutrient loading and mussel density, the dreissenid effects on nutrient cycling will vary across systems. Nutrient availability in turn can affect algal community composition, growth rate, and production (e.g. Vanderploeg et al., 2002).

Observed shifts in nutrients and production in the nearshore region can also affect offshore regions. Hecky et al. (2004) hypothesized that the collective impact of nearshore engineering of dreissenids has led to a "nearshore phosphorus shunt" retaining P (and C) at the expense of offshore areas. According to a series of hypotheses, P (both soluble and particulate) that would have moved from tributaries through the nearshore and then offshore is captured and held by the nearshore assemblage of dreissenids and their associated benthic community .

As a result of mussel feeding, excretion (soluble and particulate nutrients), and physical engineering (Vanderploeg et al., 2002) activities, both pelagic and benthic lower food web components (microzooplankton, mesozooplankton, and benthic invertebrates) have been appreciably affected (Fahnenstiel et al., 1995; MacIsaac, 1996; Lavrentyev et al., 1995; Vanderploeg et al., 2002). As a consequence, fish that depend on these energy pathways have also been negatively impacted (Strayer et al., 2004). During the proliferation of zebra mussels, food web impacts were mainly confined to bays or nearshore areas, with offshore impacts, other than the loss of *Diporeia*, being mostly equivocal (e.g., Vanderploeg et al., 2002).

Recently, however, extreme declines in chlorophyll *a* and increases in water clarity are apparent in deeper waters of the Great Lakes (e.g., Fahnenstiel et al., 2010; Kerfoot et al., 2010). In Lake Michigan, Fahnenstiel et al. (2010) document a major decrease in chlorophyll that occurred during the winter–spring transition with loss of the spring

* Corresponding author.
E-mail addresses: henry.vanderploeg@noaa.gov (H.A. Vanderploeg), jim.liebig@noaa.gov (J.R. Liebig), tom.nalepa@noaa.gov (T.F. Nalepa), gary.fahnenstiel@noaa.gov (G.L. Fahnenstiel), steve.pothoven@noaa.gov (S.A. Pothoven).

0380-1330/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.jglr.2010.04.005

phytoplankton bloom. In addition, there was a shift in phytoplankton composition with loss of large diatoms and an increase in colonial cyanobacteria (Fahnenstiel et al., 2010). It appeared that many of these offshore ecosystem changes occurred subsequent to the recent explosion and expansion of the quagga mussel "profunda" morph (deep-water phenotype) into deep waters.

The winter–spring transition is an important time for phytoplankton production and phytoplankton-mussel interactions in Lake Michigan, and dynamics during this period affect production throughout the year. Vanderploeg et al. (2002) argued that mussel filtering during the winter–spring transition (isothermal period) would be the most important time for impacting phytoplankton in deepwater systems like Lake Michigan, because the dreissenids would have access to the full water column during this well-mixed period, whereas during the stratified period, reduced vertical mixing would limit access to phytoplankton in the water column. Strong support for a well-mixed water column is given by a number of recent studies, particularly those associated with the Episodic Events Great Lakes Experiment (EEGLE), that clearly demonstrated that properties like chlorophyll concentrations are constant from top to bottom and that currents have the same direction and speed from top to bottom, thus implying a mixed condition (e.g. Fahnenstiel et al., 2000; Beletsky et al., 2003; Rao et al., 2004; Vanderploeg et al., 2007; Kerfoot et al., 2008, 2010).

After autumn turnover–typically occurring at 5 °C in December–isothermal conditions begin to prevail (e.g., Brooks and Torke, 1977). The intense winds at this time tend to promote complete mixing even before the water cools to the temperature of maximum density, 4 °C. Both water temperature and light decrease together until the winter solstice (e.g., Brooks and Torke, 1977; Scavia and Fahnenstiel, 1987; Vanderploeg et al., 2007). After the winter solstice, water temperature continues to decrease slowly until April reaching a typical minimum of 2 °C in offshore waters (e.g., Brooks and Torke, 1977; Vanderploeg et al., 2007), but solar radiation and photoperiod slowly increase. Until recently, depth-integrated chlorophyll concentration increased steadily with increasing light availability throughout the winter–spring transition, reaching maximum yearly concentration in late spring before stratification or about the same time (Brooks and Torke, 1977; Scavia and Fahnenstiel, 1987; Fahnenstiel et al., 2010). Much of the time during the isothermal period, lake temperature hovers near 3–4 °C. In summer, dreissenids in the hypolimnion would typically be exposed to temperatures around 4–5 °C.

There are four hypotheses for the recent offshore decrease in the spring phytoplankton concentration: (1) the direct impact of mussel filtering as they move into deeper water, (2) sequestering of nutrients by the nearshore shunt, (3) a decrease in P loading over time, and (4) sequestering P by the mussels or community associated with them in deep water. Of particular concern here is the first hypothesis, since mussel filtering has an immediate direct impact on phytoplankton mortality. Two major necessities for evaluating the role of mussel filtering on phytoplankton concentration are: (1) specifying mussel clearance rates at low temperatures during the winter–spring transition and in the hypolimnion during summer, and (2) specifying some appropriate measure of population abundance from which to project the impact of clearance rates. Complicating the first necessity is the very important effect of food quality, which can be more important than temperature (Vanderploeg et al., 2009).

Unfortunately, there is almost no information on dreissenid feeding at low temperatures, that is, temperatures below 8 °C (Reeders and Bij DeVaate, 1990; Vanderploeg et al., 2009). Also, many investigators report mussel abundance only as numerical density, which is problematic in that mussel clearance varies with mussel size (e.g., Kryger and Riisgard, 1988). To help gain insight into these hypotheses, particularly the first, we determined the clearance rates of dreissenid mussels at low temperatures (1–7 °C). To deal with the problem of food quality we examined the feeding rate response of mussels on natural seston as well as on an ideal food that was representative of the assemblage before expansion of the mussels into deep water. This information was combined with recently determined depth distribution of mussel densities, lengths, and weights in the southern basin of Lake Michigan (Nalepa et al., 2010) to project a filtering impact to different depth regions in 1994–2008.

Methods

The study site, collection methods, and handling

Mussels and water were collected in Lake Michigan at M45 (43 11.29°N, 86 25.92°W) a site on the 45-m deep depth contour approximately 4 nautical miles west of Muskegon, MI, on four dates during April to September 2008 (Fig. 1). This site was chosen because it has been a part of both pelagic and benthic monitoring programs (Vanderploeg et al., 2007; Nalepa et al., 2006) and displayed increased mussel densities (Nalepa et al., 2006) and decreased chlorophyll *a* (Chl), likely associated with the increase in mussels. All mussels at this site, as well as other sites in Lake Michigan, were the profunda morph of the quagga mussel (*D. bugensis*) characterized by a long incurrent siphon and a modoliform shell (Nalepa et al., 2010).

Water and mussels were collected in the morning and transported to NOAA's Great Lakes Environmental Research Laboratory (GLERL) in Ann Arbor, MI, where they arrived by late afternoon for re-acclimation in preparation for the seston feeding experiments using methods similar to those of Vanderploeg et al. (2001, 2009). Mussels were collected by benthic sled, and immediately upon collection, were wrapped in moist paper towels and placed in a cooler. Ice or cold gel packs were placed above the mussels for transport to keep them near ambient, cool temperatures. Water was collected in a 30-L Niskin bottle, transferred into 25-L carboys, and placed in coolers to maintain ambient temperature. During isothermal conditions, water was collected from the middle of the water column. During times the water column exhibited stratification, water was collected from the middle of the hypolimnion.

Feeding experiment overview

Two kinds of feeding experiments were conducted. The first used natural seston, that is, the water collected at M45 from April to November 2008 (Table 1). The second used cultured *Cryptomonas ozolini*, a highly desirable food (Vanderploeg et al., 2001, 2009) suspended in filtered (0.2 μm) lake water. *Cryptomonas* and other cryptophytes are a common part of the phytoplankton assemblage during the winter spring transition (Bundy et al., 2005). *Cryptomonas* was presented at a chlorophyll concentration between 0.8 and 3.0 μg L^{-1} (Table 2), values that bracket those found during the winter–spring transition (Vanderploeg et al., 2007) before the massive expansion of dreissenids, and are below values that saturate feeding (Vanderploeg et al., 2001, 2009).

The usual premise of exploring the effect of temperature on clearance rate is that clearance rate is a function of filter area and of ciliary beat rate, which is a function of temperature (e.g., Kryger and Riisgard, 1988; Jones et al., 1992; Lei et al., 1996). It has been argued from extensive data on the marine mussel *Mytilus edulis* that mussel filter area approximates the "square law", which means that filter area is proportional to L^2, where L is mussel length (e.g., Jones et al., 1992). Some results for dreissenid mussels appear to be consistent with this observation. Lei et al. (1996) observed that filter area in zebra mussels was proportional to $L^{1.90}$. Mussel clearance has also been expressed on a per weight (W) basis, which would be consistent with biomass varying with the cube of length. Jones et al. (1992) observed that clearance rate in the marine mussel *Mytilus edulis* was proportional to $W^{0.67}$ therefore, weight-specific rates, i.e., normalizing clearance rates to weight would imply that clearance rate per unit biomass would vary with $W^{-0.33}$. Likewise, Baldwin et al. (2002) reported that for the