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Eradication of colonizing populations of zebra mussels (Dreissena polymorpha) by early detection and SCUBA removal: Lake George, NY

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ABSTRACT

1. Since their introduction to North America, zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) have rapidly colonized North American fresh waters. Strategies for limiting the economic and ecological impacts of zebra mussels exist, but there are few examples where once zebra mussels have invaded a natural body of water they have been removed or managed without the use of ecologically destructive methods. The first successful attempt to eradicate a colonizing population of zebra mussels using SCUBA is reported here. Studies were conducted in Lake George, NY.
2. Since zebra mussel larvae had been detected prior to the discovery of adults in Lake George, a comprehensive management programme for zebra mussels was in place when mussels were found in 1999, at a single location in the southern part of the Lake (Lake George Village site). Efforts were quickly launched to remove as many mussels as possible by SCUBA with the intent of minimizing the risk of the population reproducing and establishing a permanent presence in the Lake.
3. Population size at the discovery site was initially estimated at fewer than 30 000 animals. Between 1999 and 2007 more than 21 000 animals were removed from the site, over 90% of them shortly after the colony was discovered. Continued monitoring of the site for larvae, recruitment, and growth suggests that the animals have not successfully reproduced since the project began. Since detection at the Lake George Village site, six separate colonizing populations at other locations in the lake were found and similar removal efforts appear to be having comparable success.
4. This study demonstrates that the combination of early detection, suboptimal habitat, proactive establishment of a rapid response and management plan, and cooperation of a comprehensive network of stakeholders can prevent a successful zebra mussel invasion.

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INTRODUCTION

Native to the drainage basins of the Black, Caspian and Aral Seas, zebra mussels (*Dreissena polymorpha* Pallas, 1771) were introduced to much of Europe by the mid-1800s (Ludyanskiy *et al.*, 1993), and to North America by 1986 (Hebert *et al.*, 1989) or earlier (Carlton, 2008). Since their introduction, zebra mussels have rapidly colonized many of the fresh waters of the eastern USA and south-eastern Canada. As expected, dreissenids are expanding their range westward (Bossenbroek *et al.*, 2007). A thousand miles further west than previously reported, the closely related quagga mussel was found in Lake

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Mead in January 2007 (Stokstad, 2007) and has been spreading since then. A year later, zebra mussels were reported in central California (Benson, 2009).

Water bodies can support zebra mussels when calcium concentrations are greater than $12\,\mathrm{mg\,L^{-1}}$, pH is greater than 7.4, salinity is less than 3 ppt, annual water temperatures do not exceed 30°C, nutrients are sufficient to support significant photosynthetic biomass, and hard substrates with extensive littoral zones are available (Morton, 1971; Ten Winkel and Davids, 1982; Sprung and Rose, 1988; Kovalak, 1989; Smirnova and Vinogradov, 1990; O'Neill and MacNeill, 1991; Sprung, 1993). The importance of these parameters has been confirmed and further refined by statistical analyses of the observed occurrence of zebra mussel populations in Europe (Ramcharan *et al.*, 1992a, b), North America (Hincks and Mackie, 1997), and using bioassays (Frischer *et al.*, 2005). With regards to Lake George, the Ramcharan *et al.* model indicates a low risk of zebra mussel establishment and predicts moderate population densities in the event of an invasion (Frischer *et al.*, 2005).

The success of zebra and quagga mussels is due in large part to their high reproductive capacity achieved through broadcast spawning that facilitates wide dispersal of planktonic larvae and the ability of juveniles and adults to attach to overland vectors. Because zebra mussels have encountered very little competition with native species or mortality from predators or parasites in North America, they have been extremely successful as an invasive species (Casagrandi *et al.*, 2007). Restrictions to the expansion of their North American range have been due to the limits of their own biology.

Several control strategies for zebra mussel have been developed (see discussions in Nalepa and Schloesser, 1993; Claudi and Mackie, 1994; D'Itri, 1997) owing to the large economic impact of mussel fouling in industrial facilities that depend on water intake (Connelly *et al.*, 2007). However, for open water bodies these approaches are generally not suitable as they can be ecologically damaging, expensive, and ineffective. The only accepted practical approach for preventing and managing dreissenid invasions in open waters is thought to be by prevention-oriented management including public outreach and education (Frischer *et al.*, 2005). The increasing use of public signage and wash stations at potential introduction points (e.g. boat launches) are examples of this strategy. However, these efforts only limit the introduction and spread of invasive species, so control approaches are also needed to prevent, manage, and eradicate dreissenids in open water systems.

A growing number of success stories regarding the eradication of invasive species, particularly on islands (Veitch and Clout, 2002), generate optimism that action taken against invasives may be rewarded. In addition to results on islands, successes have been achieved in mainland lakes and rivers (Britton *et al.*, 2008), in marine environments (Culver and Kuris, 2000; Wotton *et al.*, 2004), on land (Simberloff, 1997), in wetlands (Gosling and Baker, 1989), and with plants (Simberloff, 2003). Despite evidence that eradication of biological invasions is possible under certain circumstances (Myers *et al.*, 2000; Simberloff, 2002), eradication is often not considered because the conventional wisdom is that once established invasive species cannot be eliminated. However, because the ongoing cost of managing invasives can be substantial (Pimentel *et al.*, 2005), total eradication may be the most economically prudent way to manage invasive populations. One essential criterion for successful eradication is the early detection of invasive introductions allowing action to be taken while the problem is relatively small (Dewey and Andersen, 2004; Roche *et al.*, 2009). In part, early detection is dependent on an effective monitoring and education programme. Once invasives are found, rapid response is necessary in order to deal with the invasion before it becomes unmanageable (Westbrooks, 2004; Anderson, 2005). Most successful eradication strategies involve aggressive action focused on vulnerable life stages with the goal of limiting reproduction and population expansion (Shea, 2004; Pardini *et al.*, 2008). Such strategies require a thorough knowledge of the biology and ecology of the invasive species to maximize the efficiency of the response while minimizing unwanted secondary impacts (Zavaleta *et al.*, 2001; Sebert-Cuvillier *et al.*, 2007; Gray *et al.*, 2008).

In this study physical removal of mussels using SCUBA was explored to eliminate zebra mussels from Lake George, NY, USA. Lake George is a 51 km long oligo- to mesotrophic glacial lake located in the south-eastern corner of the Adirondack Park in northern New York State, between latitude 43° 25–49′ N and longitude 73° 26–42′ W. The lake is a tourist destination, providing recreational venues including boating, camping, fishing, hiking and diving. Proximity to several zebra mussel colonized water bodies (<40 km: Lake Champlain, Hudson River, Glen Lake, Saratoga Lake) increases the risk of zebra mussel introduction. While establishment of zebra mussels in Lake George may be limited by the prevailing water chemistry, specifically low calcium concentration (Frischer *et al.*, 2005), micro-habitats including areas where calcium enriched ground and stormwater enter the lake may be conducive to *Dreissena* establishment.

The detection of zebra mussel larvae (veligers) in Lake George has been reported previously (Frischer *et al.*, 2002), indicating that zebra mussels are being transported into the lake. Additional studies suggested that humans are the primary introduction pathway of zebra mussels since most observations of veligers occurred near marinas and areas of heavy boat use (Frischer *et al.*, 2005). In response to the detection of zebra mussel veligers in Lake George, and because it is close to waters that are heavily infested with zebra mussels, beginning in 1995 a network of researchers, managers, and citizen stakeholders was established to help protect the lake from a zebra mussel invasion. Management efforts included regular monitoring as well as public education and outreach, with the goal of prevention and/or early detection of any zebra mussel introductions (Frischer *et al.*, 2005). In 1999 adult zebra mussels were found. This discovery resulted in immediate public concern, support for action, and the initiation of a mitigation response.

Although it is commonly assumed that elimination of established zebra mussel populations is not possible, in this study the conventional wisdom is challenged. Here the hypothesis is tested that early detection and then the removal of a large fraction of a colonizing invasion of zebra mussels is a viable tool for eradicating a founding zebra mussel population and is a possible management strategy for prevention of successful establishment of mussels in freshwater bodies.

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MATERIALS AND METHODS

SCUBA survey and removal

Adult zebra mussels were first found on 18 December 1999 at a private marina in the Village of Lake George at the south end of the Lake (43° 25′N; 73° 42′W). The serendipitous discovery was made by SCUBA divers from a local not-for-profit underwater archaeological organization (Bateaux Below, Inc.) conducting a benthic clean-up. Shortly after discovery, preliminary SCUBA surveys defined an affected area of *ca* 3900 m^2. In order to conduct a systematic survey and guide removal efforts, after initially surveying the area the site was divided into nine sections which were delineated with rebar and nylon line (Figure 1). SCUBA divers worked within these sections to locate and remove as many mussels as possible. In late 1999, and until June 2000, divers focused on areas of high *Dreissena* concentrations, but surveys of the entire site were also completed. During this period, an area of approximately 140 m^2, straddling Sections 4 and 5, was identified as having the highest density of mussels. This area was called the 'hotspot' and, while divers examined the whole site thoroughly, removal efforts during the first year concentrated on this region. In subsequent years, divers

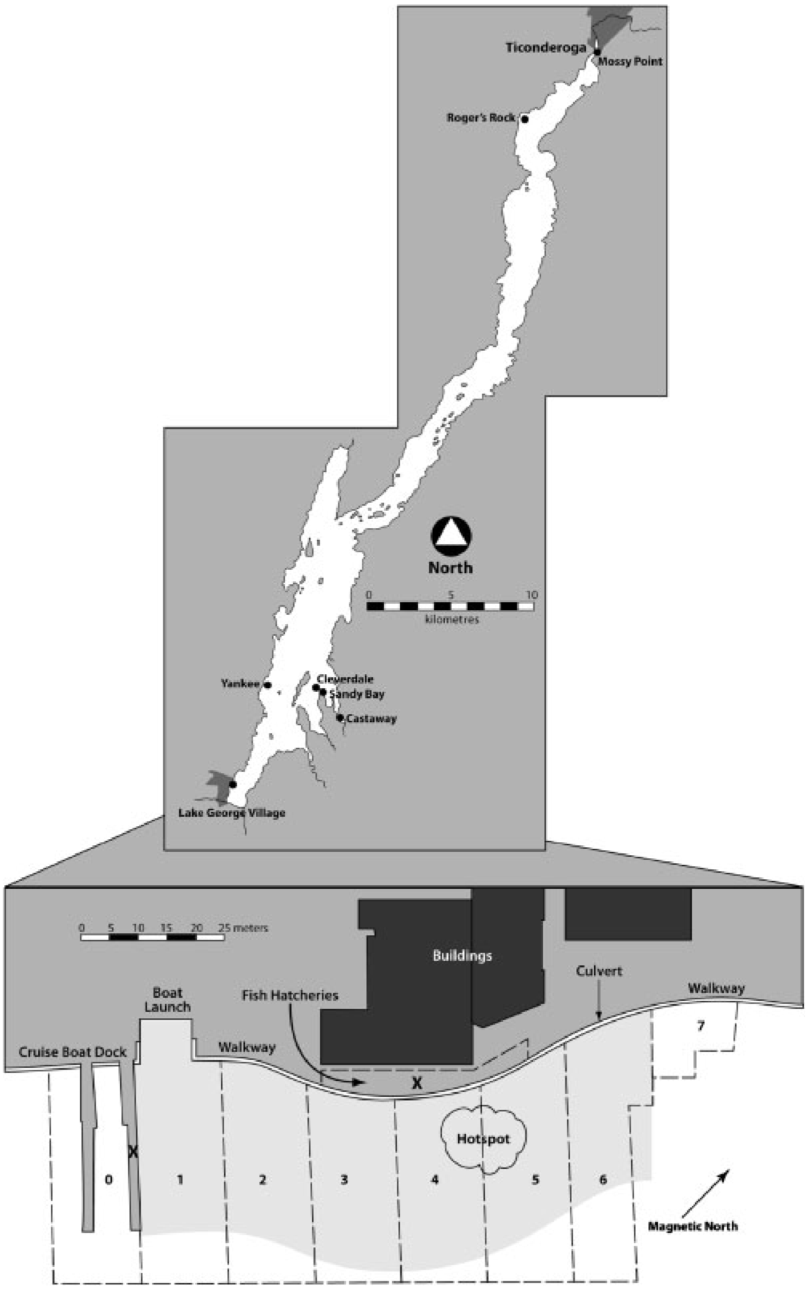

Figure 1. Schematic of Lake George Village site located in the south-western portion of Lake George, NY. Lake George is bounded by small population centres on the north at the Village of Ticonderoga and on the south at the Village of Lake George. Site survey sections are shown as well as the location of shoreline features including the boat launch, cruise boat dock, concrete walkway, fish hatcheries, and the location of the spat traps (X) and culvert. The lighter shaded area delineates the extent of the sample matrix for calcium concentration. The location of the Lake George Village site is shown with respect to Lake George. The location of other sites where zebra mussels have been found in Lake George are also indicated (●).

systematically and repeatedly searched and removed mussels from the total area. Sections searched and dive times were recorded, with a large fraction of the dives undertaken by scientific divers volunteering their effort. At six other sites where zebra mussels were later found in Lake George (Figure 1), a similar protocol was employed with regularly repeated dives at each site. Before the removal of zebra mussels from Lake George, a permit was obtained as required by the New York State Department of Environmental Conservation.

Population structure and growth

In addition to recording the number of mussels removed and the site section from which they were taken, shell lengths were determined to estimate population structure and growth. During the first collection season approximately 16% (3051 of 19 176) of the mussels removed were randomly selected and measured. After the first year, with a diminishing number of mussels recovered, all were measured. Annual growth rates were estimated each spring, as the difference in median size between years. Mussel lengths were determined using a dial caliper (Mitutoyo Corporation, Kanagawa, Japan).

Water chemistry

Because low calcium concentration is a primary factor limiting recruitment of zebra mussels in Lake George (Frischer *et al.*, 2005), during the initial three years of the study, calcium concentrations at the Lake George Village site were measured to determine whether conditions there might have resulted in elevated levels that could support zebra mussel colonization. A 0.3 m steel culvert drains surface water and groundwater to the lake at this location. Water samples (140) were collected in 50 mL sterile polycarbonate tubes from the culvert and from an evenly distributed spatial matrix along the shoreline and out to 30 m offshore (Figure 1). Samples were collected in December 1999, August 2000, and August 2001 and were acidified with nitric acid to a final concentration of 0.1%. Calcium concentrations were determined using a Perkin-Elmer Atomic Absorption Spectrophotometer (Model 5100 PC, Perkin-Elmer, Norwalk, CT) following the US EPA method 215.1 (1983). Analyses were carried out in the Keck Water Quality Laboratory at Rensselaer Polytechnic Institute.

Veliger and recruitment monitoring

When water temperatures were above the spawning threshold of 12°C (Jantz and Neumann, 1998; Wacker and von Elert, 2003) at the Lake George Village site, the occurrence of zebra mussel veligers was monitored by examining plankton samples using cross-polarized light microscopy. Samples were collected from 1 m below the surface directly over the hotspot, where the water was 2 m deep. From May 15th to August 25th 2000, samples were collected almost every day, with a total of 87 samples examined during this period. During the summer months of 2001 to 2007, samples were collected bi-weekly. All plankton samples were collected as previously described (Frischer *et al.*, 2002) by filtering 200 L of water through a 44 μm mesh size plankton net (Wildco, Madison, WI) and concentrated to 50 mL. Unpreserved samples were examined for veligers within 24 h, also as previously described (Frischer *et al.*, 2002).

Settlement and recruitment of juvenile zebra mussels were monitored using custom designed collectors (24.9 × 11.1 × 13.5 cm) that contained eight removable stainless steel plates (7.7 × 12.7 cm) as previously described (Frischer *et al.*, 2005). Two collectors were placed at the Lake George Village site and settlement plates from each collector were exchanged and examined each spring and autumn. One collector was positioned 1 m above the lake bed adjacent to the boat slip under the cruise boat dock, and a second collector was suspended in the fish hatcheries underneath the walkway, 8 m from the hotspot (Figure 1). The presence/absence of zebra mussel recruits was determined by microscopic examination of each plate.

Statistical analyses

The relationship between mussel removal rates and effort was estimated by fitting a single parameter exponential ($y = ae^{-bx}$) function to removal and mussel recovery data, where y = the number of mussels, x is a time parameter, and a and b are solved regression coefficients. Best fit parameters were identified by maximizing regression correlation coefficients using the non-linear regression procedures available in the software package SigmaStat V.3.00 (SPSS, Inc., Chicago, IL). Estimation of population structure was determined based on the lengths of animals collected during the first project year (winter 1999 and spring 2000) prior to any biases being introduced by mussel removal. Whether there were multiple size cohorts present was assessed by examining the normality, modality, and skew of size frequency histograms. Analyses were facilitated using the normality assessment procedures in SigmaStat. Comparisons of size of animals collected at different locations within the study site and over the study period were carried out using analysis of variance (ANOVA) and t-tests as appropriate, also using the SigmaStat software.

RESULTS

Distribution and removal

Shortly after the discovery of zebra mussels at the Lake George Village site, a survey of the area indicated that mussels were confined to a relatively small geographic area and that their distribution was patchy. Based on this information, it was concluded that the best eradication potential was for SCUBA divers to remove the mussels prior to the spring when spawning was expected. These efforts (until June 2000) resulted in the elimination of approximately 90% (19 176) of mussels found at the site during the entire study period. Two hundred and seventy six hours spent by divers underwater (dive hours) were expended during this period. The largest number of mussels was located in the hotspot within Sections 4 and 5 (Figure 1). Over the full study period, 77.3% (16,432) of the mussels were extracted from these sections (Figure 2), most of which were taken from the hotspot. Following initial removal efforts, monitoring and extraction continued in the spring and autumn (when the lake was ice free but recreational activities were minimal). From October 2000 to September

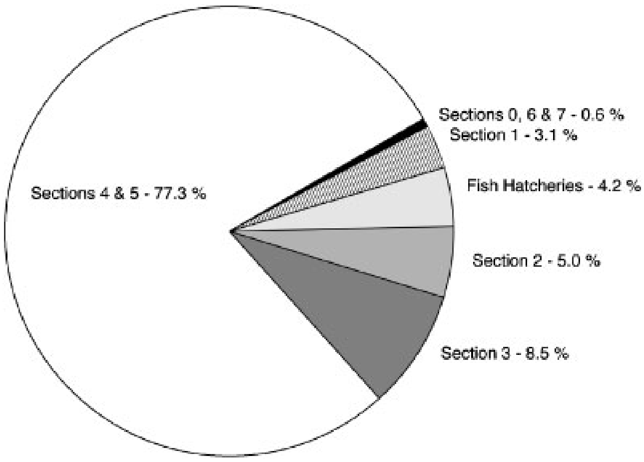

Figure 2. Percentage removal of zebra mussels from each survey section at the Lake George Village site. Prior to the establishment of the survey and removal sections in April 2000, 269 mussels (1.3% of the total) were removed from the site and are not indicated here.

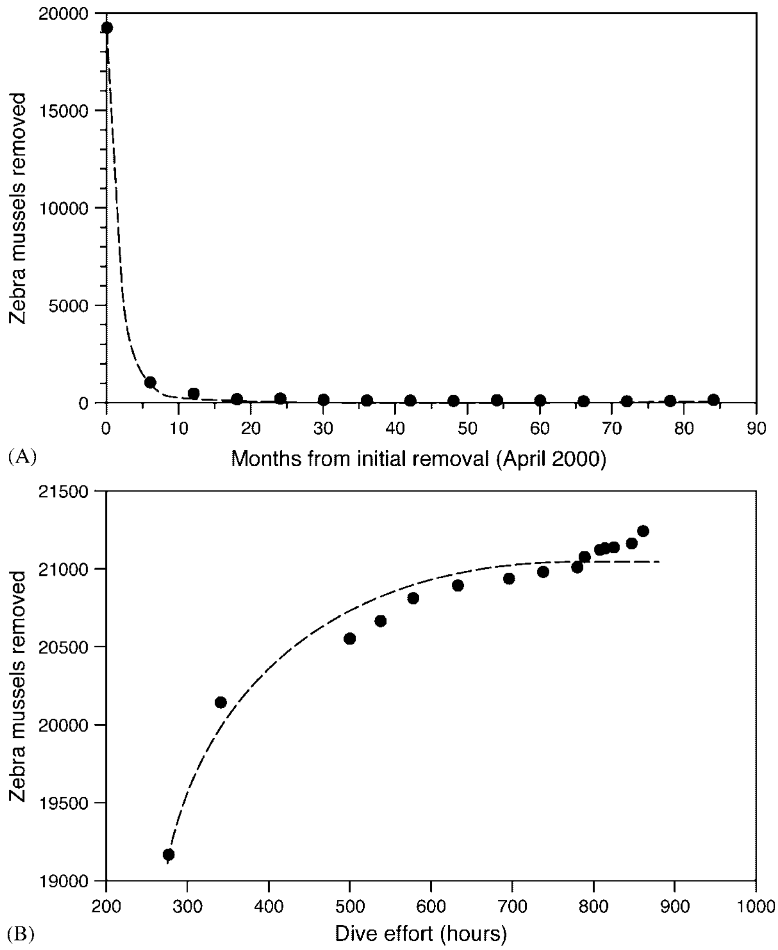

Figure 3. Zebra mussel removal from the Lake George Village site as a function of time from the initiation of the removal effort in early Spring 2000 (A). The removal rate was defined by a single parameter exponential decay function [mussels removed = $19176^{e\text{-}0.49}$] ($r^2 = 0.999$). Zebra mussels removed from the Lake George Village site as a function of dive effort (B). The removal rate was defined by a single parameter exponential growth function [mussels removed = $2.1 \times 10^4 * (1^{-e-8.65 \times 10-3} *$ dive hours)] ($r^2 = 0.942$).

2007, an additional 584 dive hours were expended and an additional 2076 mussels were eliminated (Figure 3). A total of 21 252 mussels were removed in 860 dive hours.

Removal over time followed an exponential decay function (Figure 3A, $r^2 = 0.999$) with an estimated half of the population removed in less than 2 months (1.38 months)

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from the start of the project. Mussel removal was also exponentially related to removal effort, with removal rates approaching asymptotic levels after 500 hours (Figure 3B, $r^2 = 0.942$).

Introduction, growth, and reproduction

In order to estimate the time of introduction and to determine whether or not multiple age cohorts were present, assessments were made of the size distribution of the zebra mussels that were removed during the first season. The shell lengths of approximately 16% of the mussels collected from April to June 2000 were measured. The median size of these mussels was 12.7 mm with a mean of 13.0 ± 2.7 mm. The population exhibited a unimodal normal distribution indicative of a single age class (Figure 4). Although removal efforts after the first year probably biases the interpretation of later size structure data, unimodal size distribution continued in all subsequent years suggesting that successful spawning and/or recruitment had not occurred. The median size of zebra mussels subsequently removed continued to increase, and by the spring of 2006 was 29.0 mm (Figure 5). Based on these measurements, *in situ* growth rates were estimated to be 2.8 mm year^{-1} in the first year of the project, decreasing by an order of magnitude to 0.17 mm year^{-1} in the final study year.

With the exception of a single veliger detected in a plankton sample in August 2004, there was no evidence of veligers or settlement at the Lake George Village site. Occasional inspections down-current to the south and at the margins of the site revealed no evidence of recruitment. Thus, it appears

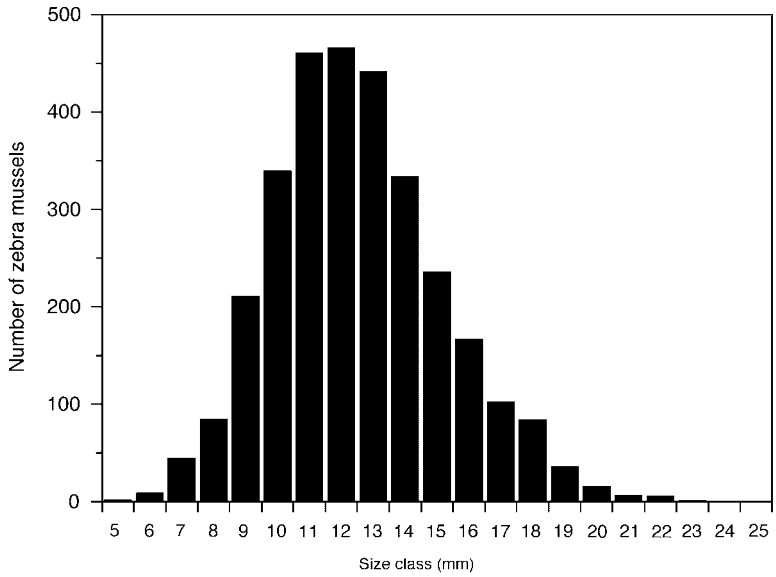

Figure 4. Size distribution of zebra mussels removed during the spring of 2000 from the Lake George Village site.

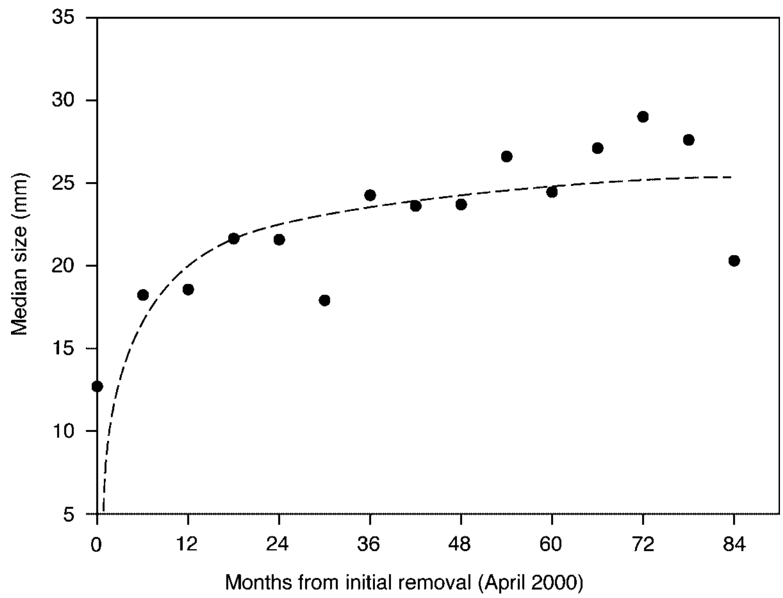

Figure 5. Growth of zebra mussels estimated from shell length of zebra mussels removed from the Lake George Village site from April 2000 to September 2007. Growth was predicted by a single parameter hyperbola function [shell length = 26.15*months/3.67+months].

that further reproduction and recruitment have not been successful since eradication efforts began.

Given the importance of low calcium concentrations as a limiting factor for zebra mussel growth, calcium concentrations at the Lake George Village site were measured during the first three years of the study, to determine whether they were elevated where zebra mussels were found. Calcium concentrations of water flowing from the culvert at this site were typically higher than the average concentration in the lake. Culvert calcium concentrations in December 1999, August 2000, and August 2001, for example, ranged from 13 to 35 mg L^{-1} higher than those measured along the shoreline (Table 1). Furthermore, in two out of three years (1999 and 2001) calcium concentrations measured at the shoreline were significantly higher compared with offshore (8–30 m) concentrations ($P<0.001$) (Table 1) and were significantly above the mid-lake average of 10.7 mg L^{-1} (Momen *et al*., 1996). These differences cannot necessarily be attributed to seasonal variation or groundwater input rates, since in 1999 samples were collected during December whereas in 2000 and 2001 samples were collected in August. Although it is not possible to ascertain water conditions when zebra mussels were introduced, the results indicate that groundwater and runoff contributions of calcium fluctuate considerably and may have elevated shoreline concentrations sufficiently to support zebra mussel recruitment at the Lake George Village site.

Additional invasions in Lake George

Since the identification of the Lake George Village site infestation, six additional zebra mussel colonies have been discovered in Lake George (Figure 1, Table 2). Five of these locations have boat launch facilities (Castaway, Mossy Point, Roger's Rock, Sandy Bay and Yankee) and one is at a privately owned boat house (Cleverdale). Each colony appears to have small populations (<2000 animals) and at these sites as many mussels as possible were immediately removed (Table 2). As is the case at the Lake George Village site, there has been no evidence of successful recruitment, however a small number of animals most likely remain at each site. Removal of any additional zebra mussels at these sites will be continued in an effort to prevent permanent colonization and spread.

Table 1. Calcium concentrations at Lake George Village site (1999–2001)

27/12/99	n	[Ca]+/−SD (mg L^{-1})	Min [Ca] (mg L^{-1})	Max [Ca] (mg L^{-1})
Date and location				
Culvert	1	47.01	na	na
Shoreline	14	11.89 (0.72)	9.98	12.51
Offshore	27	11.14 (0.32)	10.08	12.01
31/8/00				
Culvert	1	25.08	na	na
Shoreline	12	11.63 (0.64)	11.14	13.51
Offshore	34	11.37 (0.53)	10.77	14.02
9/8/01				
Culvert	1	48.35	na	na
Shoreline	13	13.10 (0.35)	12.25	13.66
Offshore	37	12.67 (0.23)	12.24	13.11

n: number of samples. na: not applicable. numbers in parentheses are standard deviation of the mean. Culvert: Groundwater and runoff outflow drain located at shoreline of Lake George Village site.

DISCUSSION

This study was conducted to test the hypothesis that early detection and then rapid removal of a significant fraction of a population of zebra mussels is a feasible management approach for the prevention of new zebra mussel infestations and a viable strategy for eradicating a founding zebra mussel population.

Rationale for an eradication attempt

Conventional wisdom holds that once populations of zebra mussels are established in natural water bodies they are impossible to control. However, based on three observations, we believed it might be possible to remove enough mussels to reduce the population density to the point where successful reproduction and sustained recruitment would be impeded in Lake George. First, in general Lake George provides less than ideal conditions for the spread of zebra mussels. Bioassays have shown that adults can grow and survive in Lake George water, but veligers do not recruit well because of the low calcium concentrations (Frischer *et al*., 2005). Therefore, it seemed likely that mussels might not have spread beyond the immediate area, making SCUBA removal practicable. Second, since 1995 the monitoring programme in Lake George revealed very few veligers (Frischer *et al*., 2005), and no adult zebra mussels have been observed in an ongoing large-scale benthic survey of Lake George (*unpublished data*). In this study 346 survey transects (50 m each) distributed throughout the lake have been examined by SCUBA divers. Therefore, it seemed conceivable that this was the first significant introduction to the lake. Third, surveys conducted when zebra mussels were discovered in Lake George suggested that colonization was limited to a relatively small area. Although theoretically one male and one female mussel could produce a large number of new animals, it is more likely that for fertilization to occur a large, tightly grouped population of mussels is required. However, critical densities for successful *Dreissena* reproduction are poorly understood.

Introduction into Lake George

Based on initial surveys of the Lake George Village site and an accounting of the mussels removed during the study period, the total population size at the time of discovery was estimated to be in the order of 20 000 to 30 000 animals. At the time of discovery the size distribution of the population was unimodal, lacking both tail and skew, and it seemed unlikely that >20 000 animals were introduced simultaneously. Thus, based on their

Table 2. Zebra mussel occurrence in Lake George

Location	Latitude °N	Longitude °W	Date mussels discovered	Mussels removed (as of Sept 2007)
Lake George Village	43° 25′	73° 43′	19/12/99	21252
Cleverdale	43° 29′	73° 39′	20/07/04	1364
Mossy Point	43° 49′	73° 26′	10/11/04	1503
Sandy Bay	43° 28′	73° 38′	01/05/06	377
Roger's Rock	43° 48′	73° 29′	15/06/07	12
Yankee	43° 30′	73° 41′	23/09/07	7
Castaway	43° 28′	73° 38′	25/09/07	17

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size and average growth rates it was speculated that the population discovered in 1999 was the result of an introduction in 1997 or 1998 followed by one successful recruitment season. The colonies that were found later were also at high risk locations (mostly marinas or boat launches). Due to the considerable distance between each location, it seems likely that these colonies resulted from independent introductions.

Was water chemistry conducive for zebra mussel establishment?

Because the calcium concentration of Lake George is below the level thought to be supportive of zebra mussel populations, it was somewhat surprising to discover a population that apparently resulted from at least one significant recruitment event. However, calcium concentrations in the lake vary considerably due to the underlying lake geology and to tributaries that can drain calcium-enriched groundwater into the lake. Elevated calcium concentrations in groundwater are common in Lake George and the Adirondack region (Fuhs, 1972; Sutherland *et al.*, 2001). Thus, at sites near lake tributary outlets, especially in locations where marinas and boat ramp facilities are nearby, the risk of zebra mussel introduction is highest. Therefore, continuing surveillance efforts in Lake George concentrate on these locations.

Analysis of water calcium concentrations at the Lake George Village site during this study suggested that nearshore concentrations of dissolved calcium may have been elevated when zebra mussels were introduced. Furthermore, a substantial inter-annual variation in shoreline calcium concentration was observed over the three-year period from 1999–2001, with shoreline concentrations in August 2001 above the theoretical zebra mussel limiting concentration of $12\,mg\,L^{-1}$ ($13.1\,mg\,L^{-1}$, Table 1). Thus, it seems likely that micro-environments in Lake George, where calcium concentrations might have been sufficiently elevated, can support zebra mussel populations and, once established, zebra mussels can survive, grow, and perhaps even successfully reproduce. If this was the case at the Lake George Village site, it does not rule out a scenario whereby, after initial high levels during invasion, calcium concentrations may have dropped in succeeding years, eliminating the chance for further successful recruitment and thereby ensuring the eventual collapse of the population, even if the mussels had not been removed.

Removal from Lake George

Removing zebra mussels by SCUBA was an extremely labour intensive process. In this study 860 dive hours were logged, surveying and removing mussels from the Lake George Village site. However, the amount of effort needed to prevent the mussels from successfully reproducing may be significantly less than this (Figure 3A). For example, more than 90% of the recovered population was removed during the 276 dive hours before the Spring 2000 spawning season. Since then, only 2076 more animals were removed and no other high density patches were found. However, present knowledge must be balanced with a lack of knowledge after the first removal season of how many mussels had been missed. Given the zebra mussel's highly fecund nature and with the danger of this population 'bouncing back' from a radically diminished one to an exploding one, it was necessary to be vigilant. To date, these efforts appear to have been sufficient to prevent reproduction.

In confined, industrial facilities, methods such as heat treatment, chemical disinfection, acoustics, and biocides have been effectively used to control and manage zebra mussel populations (see discussions in Nalepa and Schloesser, 1993; Claudi and Mackie, 1994; D'Itri, 1997). Nevertheless, these methods are likely to be less practical for use in large, open systems because of their expense and potential for negative ecological impacts. Therefore, it is critical to continue development of methods for control and management of zebra mussels in open water systems.

There have been only two substantiated reports of mussel eradication in open water bodies, and both used chemical treatments. In Australia, colonization by a close relative of the zebra mussel, *Mytilopsis* sp. (black striped mussel), was eradicated by treatment with $CuSO_4$ in 1999 (Bax, 1999; Bax *et al.*, 2002). In 2005, zebra mussels were reported to have been eradicated from a Virginia quarry by elevating potassium concentrations (Virginia Department of Game and Inland Fisheries, 2009). In the present study, the first report is provided of a non-chemical and environmentally non-destructive strategy that has proved successful in preventing a new colonization of zebra mussels in an open natural system. Additional strategies have been explored, such as the use of benthic barrier mats (thick plastic sheets placed on the lake bed to smother living organisms underneath) to kill zebra mussels in pilot studies in Saratoga Lake, NY (Braithwaite, 2003). These approaches have not yet been applied on a large scale.

Cost considerations

Removal effort costs included diving, shore support, data logging, water sample collection and analyses, and reporting. For the Lake George Village site the total number of dive hours was 860. An additional 99 dive hours were logged in association with the other six sites. Shore support included diver logistic assistance, equipment and sample handling, outreach to and education of interested observers. Diver support and diver out-of-water time was estimated to be 400% of underwater time. Sample analyses and record keeping was estimated to be 200% of underwater time. Overall, the largest cost associated with this eradication approach was labour. If funding had been required to cover all labour expenses, the total would have been prohibitive. However, the strategy to involve the community and the ability to mobilize qualified volunteers made the project possible. Actual labour costs included one full-time scientist and a small amount of support for several other professionals. The importance cannot be overemphasized of good public relations, proactive planning, cultivation of a local sense of ownership, and optimism that the problem is manageable (Simberloff, 2009).

Is eradication possible? Mission accomplished in Lake George?

It is commonly understood that humans are the primary vector promoting the introduction of zebra mussels to non-colonized water bodies (Carlton and Geller, 1993; Johnson and Carlton, 1996; Johnson and Padilla, 1996; Johnson *et al.*, 2006). More specifically, in Lake George the highest risk of zebra mussel introduction occurs at marinas and locations where boats are

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introduced to the lake (Frischer *et al*., 2005). Consistent with this, the Lake George Village site is located in the busiest and most densely populated part of the basin at an active marina and boat launch facility.

The critical factors for success in eradicating a new zebra mussel colony are early detection, fast action, and application of a management strategy that prevents successful reproduction and recruitment. In the case of Lake George, because a broad-based surveillance programme and contingency response plan were in place when zebra mussels were discovered, it was possible to mount a SCUBA-based removal programme while the population was still relatively small. A critical component to this project's successful eradication probably stems from the sub-optimal conditions that exist in Lake George. However, it was not possible to determine whether veligers were produced at the Lake George Village site but failed to survive and settle, or if they did not form at all owing to insufficient density of eggs and sperm in the water column. Likewise, because the spat traps were located so close to the colony, it is difficult to conclude definitely that the Lake George Village animals did not reproduce or contribute to other populations in the lake, although this is unlikely based on downstream surveys for additional mussel colonies. Nevertheless, to date, all evidence suggests that the colony of mussels at the Lake George Village site is no longer viable and therefore, although a small number of animals probably remain at this site, the population is likely to attenuate as the animals age and die.

There is great variation in the literature for reported growth rates and longevity of zebra mussels (Karatayev *et al*., 2006). In oligo-mesotrophic lakes, growth rates of young animals range from 7 to 20 mm per year (Mackie, 1991; Dorgelo, 1993). Longevity of zebra mussels has been reported to range from 1 to 19 years with an average of 7.4 years (Mackie *et al*., 1989; Karatayev *et al*., 2006). It is recognized that both growth and longevity depend greatly on environmental conditions and that growth rates are relatively slow when water temperatures and nutrient concentrations are low (Karatayev *et al*., 2006), such as are found in Lake George (Momen *et al*., 1996; Eichler, 2009). Based on this information we have postulated that mussels were introduced to the Lake George Village site in 1997 or 1998, and that if further introductions are prevented, the eradication of zebra mussels at the Lake George Village site appears to be plausible.

Although the zebra mussels at the Lake George Village site are being successfully eliminated, six additional small colonies have been identified at other lake locations during the last eight years. Therefore, it may be that zebra mussels within Lake George function as a metapopulation (Hanski, 1999). However, since there has been no evidence of zebra mussels at 346 other sites distributed throughout the lake that have been carefully surveyed, it is reasonable to consider the seven locations as independent populations. Nevertheless, because of the possibility that a metapopulation may exist and the probability of independent introductions, the Lake George zebra mussel management programme involves the continued search for and removal of other zebra mussel colonies. As occurred at the Lake George Village site, each of these other colonies appears to be small and limited in area. Removal of animals by SCUBA seems to have been successful in preventing the permanent establishment of zebra mussels in Lake George. However, these experiences also suggest that even with education, outreach, and preventative measures, the threat of re-introduction remains. Perhaps 'Mission Accomplished' can never be claimed, but the prevention of colonization may well be possible with a long-term commitment to monitoring and rapid remedial action.

Practical applicability

In light of the continuing western US expansion of zebra and quagga mussels beyond the 100th meridian (Stokstad, 2007) and the large number of currently uninfested (but at risk) water bodies in North America, the need for effective aquatic invasive species prevention and eradication approaches is acute. In this study, it was demonstrated that, if detected early and removed before extensive reproduction, it is possible to prevent a successful invasion of zebra mussels. The applicability of this approach to individual ponds, lakes and reservoirs must be evaluated case by case, but the success of this strategy challenges the conventional wisdom that permanent zebra mussel colonization at a site, once introduced, is inevitable. This knowledge should empower future researchers, managers, and stakeholders to consider eradication programmes and the development of new approaches to facilitate these goals.

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