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Negative effect of zebra mussels on foraging and habitat use by lake sturgeon (Acipenser fulvescens)

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ABSTRACT

1. Lake sturgeon (*Acipenser fulvescens*) are threatened or endangered throughout much of their range. Juvenile sturgeon utilize sandy and silty habitats extensively during their growth. Invasive zebra mussels change the nature of sandy and silty habitats because they settle on and coat the habitat with the shells of living and dead individuals. The potential impacts of this increased habitat complexity on lake sturgeon is unknown.

2. Juvenile lake sturgeon habitat choice was assessed in laboratory experiments, and zebra mussel impact on the foraging success of juvenile lake sturgeon on three different prey species was measured.

3. Sturgeon foraging on chironomids was virtually eliminated by 95% zebra mussel cover of the sand floor of the foraging arena, and 50% cover reduced foraging significantly. Foraging on more mobile prey items (amphipods and isopods) was essentially eliminated by either 95% or 50% zebra mussel cover of the arena floor. In habitat choice experiments, sturgeon avoided the zebra-mussel-covered habitat more than 90% of the time.

4. This combination of zebra mussel avoidance and reduced foraging in the presence of zebra mussels may be detrimental to sturgeon restocking programmes utilizing smaller sturgeon in zebra-mussel-infested waterways.

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KEY WORDS: invasive species; endangered species; lake sturgeon; foraging; predator-prey; habitat structure; zebra mussel; soft sediment

INTRODUCTION

The impacts of zebra mussels on North American aquatic food webs, hard-substrate habitat complexity, and human use of aquatic habitats and water has, for some time, received considerable attention in the scientific literature and in the popular press. More recently, the scientific community has turned its

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attention to the effects of zebra mussels on soft-sediment communities (Dermott and Munawar, 1993; Dermott and Kerec, 1997; Bially and MacIsaac, 2000; Beekey *et al.*, 2004a). Zebra mussels spread across soft sediments from isolated colonies, forming thick, dense layers that effectively carpet the benthos and convert the habitat to a more complex form. The effects of this conversion from soft, simple habitat to a complex, consolidated habitat has increased benthic macroinvertebrate density and diversity (Bially and MacIsaac, 2000; Beekey *et al.*, 2004a). Whether this increased macroinvertebrate density translates into a net benefit for benthic fish will probably depend on the feeding habits and habitat use of the species in question (Beekey *et al.*, 2004b).

Among benthic-feeding fish, lake sturgeon (*Acipenser fulvescens*) are of particular concern. Lake sturgeon are native to lakes and large rivers in the Atlantic watershed of North America including the Hudson Bay, Laurentian, and Gulf of Mexico catchments (Lee *et al.*, 1980). Through much of this range, lake sturgeon populations have been reduced from viable populations to threatened or endangered status owing to over-fishing and habitat destruction (Auer, 1999). Zebra mussels now co-occur with lake sturgeon over much of their range, including the Laurentian Great Lakes and portions of the Mississippi and Hudson Bay catchments, and may represent a novel threat to lake sturgeon. Whereas zebra mussels co-occur with lake sturgeon in all of the major Atlantic coast catchments, many areas of lake sturgeon habitat or potential habitat remain zebra-mussel-free within these major catchments.

Juvenile sturgeon use protrusible mouth parts to forage for macroinvertebrates in sand and silt. Burrowing mayflies (Ephemeroptera: *Hexagenia*) are common in sand and silt and were found in the guts of the majority of juvenile sturgeon sampled by Beamish *et al.* (1998). Jackson *et al.* (2002) found that most smaller (<600 mm TL) sturgeon consumed amphipods and that larger sturgeon (>600 ml TL) also included large numbers of zebra mussels in their diets. Zebra mussels have the potential to affect sturgeon reintroduction programmes by impeding the foraging success of stocked juvenile sturgeon. Zebra mussel colonies on soft sediments may impede foraging success by blocking access to infaunal invertebrates and preventing juveniles from successfully capturing epifaunal invertebrates within zebra mussel colonies. Furthermore, juvenile sturgeon may not even recognize zebra mussel colonies as potential foraging grounds.

To assess the potential impact of zebra mussels on juvenile sturgeon, laboratory foraging trials and habitat choice experiments were conducted. Foraging trials were run on sand with high, low, or zero density of zebra mussels. Three different macroinvertebrate prey species were used, each with a different mode of habitat use. In separate experiments, sturgeon were placed in tanks with a choice of sand, gravel, and zebra mussel habitats and their position was recorded at regular intervals.

METHODS

Organisms

Sturgeon used in the experiments were young-of-the-year (TL \bar{x} = 167 mm; range 136–186 mm) obtained from the Pittsford National Fish Hatchery in Vermont. The sturgeon were handled at all times in accordance with guidelines for animal care established by the University of Vermont's Institutional Animal Care and Use Committee. They were held in continually aerated, dechlorinated tap water and fed on commercial trout food and frozen bloodworms. Macroinvertebrate prey items were from the following sources: chironomids (*Chironomus* sp.; length range 4–8 mm) were raised in bulk cultures in the laboratory; isopods were purchased (*Asellus communis*; length range 4–11 mm) from Connecticut Valley Biological Supply Company; amphipods (*Gammarus minus*; length range 4–8 mm) were collected from springs in Pennsylvania. Zebra mussels were collected from areas of soft sediment in Lake Champlain using scuba and rinsed free of macroinvertebrates and fine sediments using dechlorinated water prior to use. Mussels

damaged or killed during the collection process were discarded to preserve water quality in the experimental tanks.

Prey species were selected on the basis of differences in their modes of habitat use, which may influence how zebra mussels affect sturgeon foraging success. Larval chironomids burrow in soft sediments and are relatively immobile. Isopods are typically found crawling on and under hard benthic substrates and are not usually found under soft sediments. Amphipods are the most mobile of the selected invertebrates. Amphipods are active swimmers and crawlers and make short excursions from the benthos into the water column.

Foraging experiments

All foraging trials were run in continuously aerated dechlorinated water in 8-L circular plastic microcosms (27 cm diameter; 14 cm depth) with approximately 2.5 cm depth of washed sand on the floor. The factors in this experiment were zebra mussel density (absent, 50% zebra mussel cover, and 95% zebra mussel cover; percentage cover estimated by inspection), and predator presence or absence. Control microcosms lacking the predator are essential for evaluation of macroinvertebrate recovery and have been also been advocated for other reasons (Roa, 1992). The full factorial design yields a total of six treatments and six replicates were run for each prey species.

For each prey species, three replicates were run on each of two days with the treatments randomly arrayed on a bench top. The prey species were of different sizes, may or may not vary in palatability to sturgeon, and were not always simultaneously available. For these reasons and because only 18 sturgeon were available, the experiments were not designed to compare statistically the effects of prey species on sturgeon foraging. To eliminate potential impacts of differential foraging success in one experiment on sturgeon appetites in the next, sturgeon were returned to a common holding tank and fed frozen bloodworms six times daily for 2 to 4 days between experiments. The sturgeon were then held without food for at least 12 hours prior to the foraging trials. They were then randomly assigned to treatments in such a way that any potential appetite differences would not bias any particular treatment.

Separate Kruskal–Wallis tests were used to determine the impacts of predator presence and zebra mussel treatment on the density of each of the three prey species after sturgeon foraging. For each prey species, all predator treatments were first pooled and compared with all prey treatments using the Kruskal–Wallis test. To measure the effects of zebra mussel treatment on foraging, the three zebra mussel treatments with foragers present were compared using a Kruskal–Wallis test.

Prior to the experiments, brief, unreplicated trials were used to determine appropriate prey densities and foraging trial durations that would leave some prey remaining in all treatments at the end of each experiment. Based on these pilot data, 70 chironomid larvae were added per microcosm (effective density 1223 individuals per square metre) 24 hours before the experiment to allow for burrowing time. Because amphipods and isopods are larger than chironomids and fewer tend to be consumed by sturgeon, 30 individuals were added to each microcosm (effective density 524 individuals per square metre) at least 2 hours before the predator was introduced. Trials with chironomid prey were run for 8 hours and those with amphipods and isopods were run for 6 hours.

A single sturgeon was added to each predator microcosm at the beginning of the foraging trial. Each forager was used once only for a given prey species. After the foraging period, the sturgeon were removed, weighed (wet weight to nearest 0.1 g), measured (standard length to nearest 0.1 mm), and returned to a holding tank. The remaining prey items were recovered and counted by sieving the contents of each microcosm.

Habitat choice

Habitat choice experiments were run in six 43.2-L circular tubs (61 cm diameter). Sand, zebra mussels, and gravel were placed in three segments of equal area on the bottom of each tub. The gravel selected was black

shale from Lake Champlain in the same size range as zebra mussels. These choices were offered to separate differences in preference for habitat structure from preference for, or avoidance of, zebra mussels. Unlike the foraging experiments, the zebra mussels and gravel in the habitat choice experiments were placed directly on the tub floor without an underlay of sand.

A single sturgeon was placed in each tub and allowed to acclimatize for 4–6 hours before observations were recorded. The position of each sturgeon relative to the three habitats offered was recorded every 30 minutes for 24 hours. In cases where the sturgeon lay across two habitat types, the habitat upon which the fish's head rested was considered to be the habitat of choice. Unlike observations from previous experiments on other species (Beekey *et al.*, 2004b) the sturgeons spent a large portion of their time up in the water column, adding a fourth category to the data set.

The null hypothesis in this experiment was that the sturgeon would spend equal time in each of the habitats. The number of observations of fish in each habitat was compared with that predicted by the null hypothesis using *G* tests. Unlike chi-square values, individual *G* statistics and their associated degrees of freedom are additive and they can be summed to yield a meaningful aggregate statistic with increased statistical power (Sokal and Rohlf, 1995). The *G* statistics from each fish were summed to test for homogeneity among habitat choices to determine if fish spent different numbers of observations in each of the three habitats. A replicated goodness-of-fit test was used to test whether there were differences among fish in their habitat use. Having no basis for predicting the frequency of observations of fish in the water column, pelagic observations were excluded from the data set for both of the analyses.

RESULTS

Foraging experiments

Sturgeon reduced the density of all three prey items (Kruskal–Wallis tests, $p < 0.001$ in all cases; Table 1(A); Figure 1). For all three prey species, there were significant differences in the numbers of prey individuals remaining among the three zebra mussel treatments (Kruskal–Wallis, $p < 0.003$; Table 1(B)) with fewer prey remaining in the bare sand treatments (Figure 1). There were few differences in the numbers of amphipods

Table 1. (A) Results of Kruskal–Wallis test for the effects of sturgeon foraging on density of remaining prey after 24-hour foraging bout. A statistically significant result indicates a difference between treatments with and without sturgeon, confirming predation. (B) Results of Kruskal–Wallis test for the effects of zebra mussels on prey remaining in sturgeon treatments after foraging. A statistically significant result indicates that there were differences in foraging success among the three densities of zebra mussels

(A)			
	Amphipods	Isopods	Chironomids
<i>H</i>	25	15.7	16
d.f.	1	1	1
<i>p</i> value	<0.001	<0.001	<0.001
(B)			
	Amphipods	Isopods	Chironomids
<i>H</i>	11.7	13.7	13.6
d.f.	2	2	2
<i>p</i> value	<0.003	<0.002	<0.002

EFFECT OF ZEBRA MUSSELS ON LAKE STURGEON

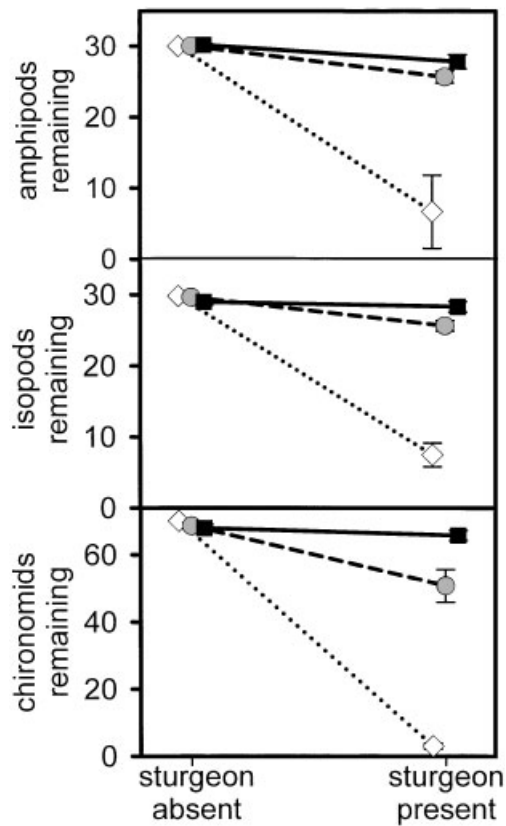


Figure 1. Numbers of prey items remaining after 8 hours (in amphipod and isopod trials) or 6 hours (in chironomid trials) of sturgeon foraging. Black represents 95% zebra mussel cover treatment, grey represents 50% mussel cover, and white represents bare sand. The left sides of the graphs represent procedural controls designed to measure investigator success at recovering prey from the experimental tanks. Treatments with foraging sturgeon present are represented on the right-hand side of the figure. Differences between the slopes of the lines in the figure indicate differential foraging success among treatments.

and isopods remaining between high- and low-density zebra mussels. More chironomids were consumed in low-density zebra mussels than in the high-density zebra mussel treatment (Figure 1).

Habitat choice

The number of observations of fish in each of the three benthic habitats was significantly different from a null model of equal time spent in each habitat ($p < 0.001$, $G = 291.6$, $df = 24$). Of the benthic observations of fish, 65.7% were in sand, 25.8% were in gravel, with the remaining 8.5% in zebra mussels (Figure 2). The number of observations of fish up in the water column had a diurnal pattern, with most sturgeon being benthic between 8:00 and 19:00, becoming more pelagic in the evening and through the night and early morning (Figure 2).

DISCUSSION

The presence of zebra mussels reduced foraging success of juvenile sturgeon; this result is similar to observations on other predator species tested thus far: (yellow perch *Perca flavescens* (Mayer *et al.*, 2001;

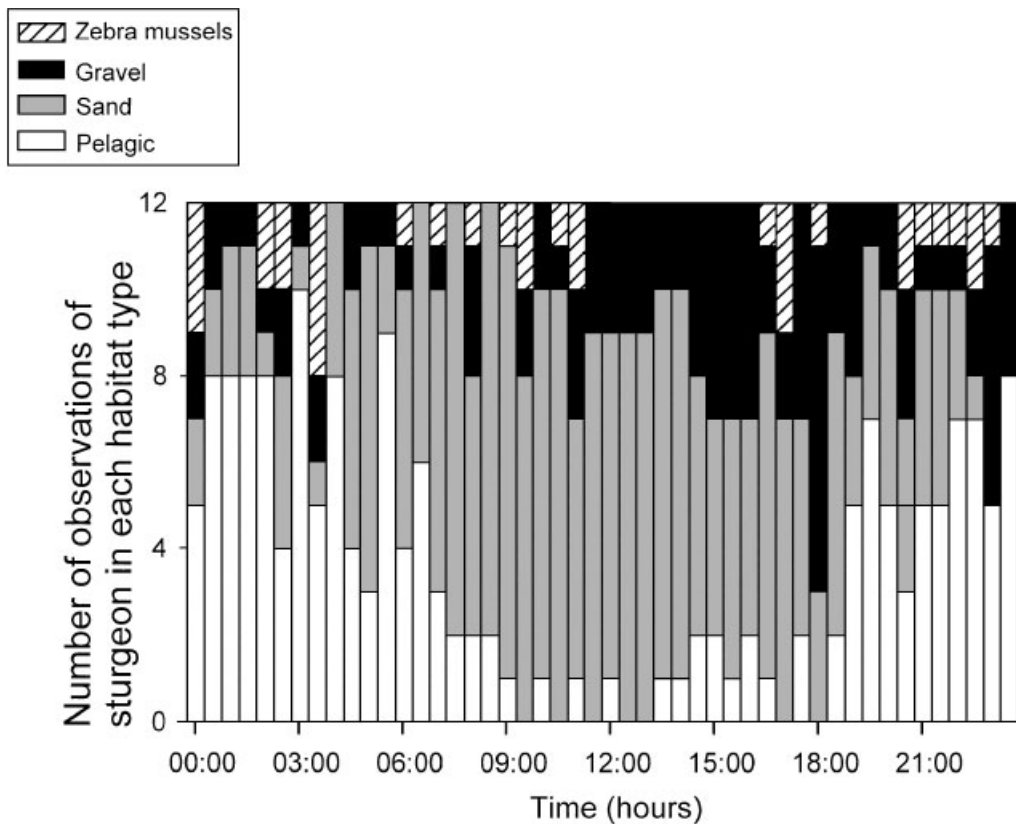


Figure 2. Number of observations of sturgeon in each of four possible habitats in circular arenas. There were a total of 12 fish observed in separate arenas. Fish positions were observed every 30 minutes. Hatched bars represent number of fish observed on zebra mussels, black represents fish on gravel, grey represents fish on sand, and white represents pelagic fish.

Cobb and Watzin, 2002); bluegill *Lepomis macrochirus* (González and Downing, 1999); sculpin *Cottus cognatus*, logperch *Percina caprodes*, bullhead *Ameiurus nebulosus*, and crayfish *Orconectes* sp. (Beekey *et al.*, 2004b)). In contrast to other predator species, however, reduced foraging success in sturgeon was most pronounced with amphipod and isopod prey. Sturgeon foraging on these species was dramatically reduced by the presence of even 50% zebra mussel cover. In previous work, sculpin, logperch, and bullhead foraging on amphipods was reduced by between 30% and 85% (Beekey *et al.*, 2004b), whereas sturgeon foraging on the same prey was reduced by more than 90% in the current study. This difference may be attributed in part to a strong tendency for the predator species used in the former study to spend time on zebra mussel colonies, in contrast to the avoidance of zebra mussels by sturgeon (see below).

When foraging on chironomids, sturgeon had slightly higher success in tanks with 50% zebra mussel cover than with 100% cover. Higher success with patchy zebra mussel cover may in part be explained because chironomids burrow into the sand, become essentially sessile, and are not particularly attracted to the zebra mussel patches. Bare sand patches among the zebra mussel habitat would thus present access to food resources for sturgeon. Unlike chironomids, amphipods are attracted to zebra mussels (Cobb and Watzin, 2002, Van Overdijk *et al.*, 2003) and may use the nooks and crannies as cover from predation. The same may well be true of isopods given their mobility, but data to test attraction of isopods to zebra mussels were not collected during this study. Increased sturgeon foraging success on chironomids with reduced zebra mussel coverage is consistent with results from the three fish species examined by Beekey *et al.* (2004b).

In sharp contrast to the results of previous studies of habitat choice in fish (Cobb and Watzin, 2002; Beekey *et al.*, 2004b) and crayfish (Beekey *et al.*, 2004b), juvenile sturgeon in the current study avoided zebra mussels in favour of the other available habitats. All of the other species, when offered choices between zebra mussels and other substrates, showed a marked preference for zebra mussel habitat. Fish may be attracted to mussels because of increased macroinvertebrate abundance, because mussels are a potential food source, or because increased habitat structure provides cover. Young-of-the-year sturgeon of the size used in this study are too small to consume zebra mussels (Jackson *et al.*, 2002, unpublished observations), and the stimulus to seek infaunal food may be a higher priority than the need to avoid predators in complex habitats. Peake (1999) convincingly demonstrated a strong preference of sturgeon for sand over plastic, rock, or gravel. These results confirm a preference for sand and furthermore suggest that zebra mussels may render sandy habitats unappealing to young-of-the-year sturgeon.

This combination of zebra mussel avoidance and reduced foraging success has the potential to exert a negative impact on sturgeon. While distributions of sturgeon are not well understood, and may vary by location, they appear to concentrate in depositional areas that are suitable for foraging (e.g. Thomas and Haas, 2002). Larval and juvenile sturgeon tend to move steadily downstream after hatching, so that young-of-the-year reside near river mouths; for example, sturgeon 20–76 cm long in Lake Nipigon were generally found on shoals near river mouths (Scott and Crossman, 1973; Auer and Baker, 2002). Becker (1983) noted that juvenile sturgeon age 1+ are found in lentic habitat with adults. Zebra mussels and quagga mussels (*Dreissena bugensis*) are found on soft sediments as shallow as 3 m (below the wave disturbance zone), and as deep as 90 m (Dermott and Munawar, 1993; Coakley *et al.*, 1997; Dermott and Kerec, 1997), so their range of potential impact overlaps the distribution of juvenile sturgeon except in rivers and on the shallower portions of river deltas. Restoration of sturgeon populations in the Great Lakes basin and Finger Lakes of New York generally involves stocking of age-0 sturgeon in rivers to reduce hatchery effects on behaviour (e.g. Carlson, 2000); once these stocked individuals migrate into lakes, their ability to find foraging areas and food may be compromised by zebra mussels and consequently their growth rates and survival may be reduced. Because zebra mussels supplement the benthic food web at the expense of the pelagic web (Lowe and Pillsbury, 1995) there may be a net gain for sturgeon populations, but this depends either on successful growth of juveniles to a size category that can utilize zebra mussels, or on behavioural shifts to utilize the macroinvertebrates inhabiting zebra mussel beds.

There is no known management solution to reduce densities of zebra mussels in the wild, therefore restoration plans for sturgeon that involve stocking could be modified to focus stocking on larger individuals (i.e. age 1+). This strategy has the added advantage that sturgeon larger than 600 ml TL can utilize zebra mussels for food (Jackson *et al.*, 2002). Therefore, even if the effects observed on age-0 sturgeon are also found in larger sturgeon, the loss of access to infaunal prey may be offset by their access to abundant zebra mussels. Impacts of zebra mussels on naturally spawned sturgeon cannot be so readily circumvented, and may reduce juvenile survivorship. Field observations of juvenile sturgeon foraging behaviour, growth, and survival in areas where they co-occur with zebra mussels are needed to determine whether there are impacts on wild populations from mussel-modification of the benthos. However, such observations would, in most areas, be complicated by the rarity of lake sturgeon.

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