Effects of predation by fish and wintering ducks on dreissenid mussels at Nanticoke, Lake Erie[1]

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Abstract: Dreissenid mussels in the Laurentian Great Lakes are preyed on by fish and diving ducks, but predators' roles in structuring Great Lakes' mussel populations are unclear. In Europe, predation impacts on zebra mussels are most pronounced on lakes where waterfowl winter. Using cages which excluded either fish and diving ducks or only diving ducks, we examined effects of these predators on both zebra mussels and quagga mussels (*Dreissena polymorpha*, *D. bugensis*) at Nanticoke, Lake Erie, where ducks both stage and winter. We arrayed cages at two sites, one within, and one adjacent to, a winter ice-free hole created by a generating station's coolant water discharge. At the ice-free site, predation by diving ducks reduced numbers of both mussel species substantially, and especially numbers of larger mussels. At the ice-covered site, residual effects of predation by ducks the preceding fall depended on rock size: numbers of large mussels declined on large rocks. Predation by fish reduced quagga but not zebra mussel abundance at the ice-covered site. Effects appeared to be most pronounced on the smallest mussel length class, but characterizing length-class preferences was difficult because effects on large mussels were sensitive to rock size: large mussels were removed from small rocks. At both sites, prior correlations between the number of quagga mussels on a rock and the size of that rock weakened or broke down completely following predation. Our results extend previous work on zebra mussels to include the quagga mussel, and show experimentally the potential of both predator groups, but especially wintering diving ducks, to affect local density, demography, and substrate-specific occupancy of dreissenid mussels.
Keywords: Dreissena polymorpha, Dreissena bugensis, Aythya spp., Aplodinotus grunniens, predation.

Résumé : Dans les Grands Lacs, bien que les moules de la famille des Dreissenidae subissent la prédation par les poissons et les canards plongeurs, le rôle précis des prédateurs dans l'établissement de la structure de population des moules demeure nébuleux. En Europe, les impacts de la prédation sur les moules zébrées sont plus prononcés dans les lacs où la sauvagine hiverne. L'effet des prédateurs sur les moules zébrées et les quagga (*Dreissena polymorpha, D. bugensis*) a été examiné à Nanticoke, au lac Érié, où les canards hivernent. Pour ce faire, des cages ont été utilisées, excluant les poissons et les canards plongeurs ou les canards plongeurs uniquement. Des cages ont été disposées à deux sites, un vis-à-vis et l'autre adjacent à une zone d'eau libre de glace créée par la décharge des eaux de réfrigération d'un générateur. La prédation par les canards plongeurs a significativement réduit les effectifs des deux espèces de moules dans le site sans glace, en particulier les individus de forte taille. Chez le site couvert de glace, les effets résiduels de la prédation par les canards l'automne précédent dépendaient de la taille des rochers sur lesquels les moules étaient accrochées : les effectifs des moules de grande taille ont décliné davantage sur les gros rochers. La prédation par les poissons a réduit l'abondance des quagga, mais pas des moules zébrées dans le site couvert de glace. Les effets semblaient plus prononcés chez les plus petites classes de taille. Cependant, l'existence de prédation différentielle selon la classe de taille était difficile à établir puisque la prédation sur les moules de grande taille dépendait de la taille des rochers : les grandes moules étaient retirées des petits rochers. Des corrélations entre le nombre de quagga sur un rocher et la taille du rocher établies avant la prédation perdaient leur signification après la prédation et ce, aux deux sites étudiés. Nos résultats étendent la portée d'études précédemment réalisées sur les moules zébrées, tout en incluant les quagga. Ainsi, le potentiel de deux groupes de prédateurs, mais surtout celui des canards plongeurs en hivernation, d'affecter la densité locale, la démographie, ainsi que le patron d'occupation de substrats spécifiques des moules de la famille des Dreissenidae a été démontré expérimentalement.
Mots-clés : Dreissena polymorpha, Dreissena bugensis, Aythya spp., Aplodinotus grunniens, prédation.

Introduction

The appearance of zebra mussels (*Dreissena polymorpha*) and congeneric quagga mussels (*D. bugensis*) in the Laurentian Great Lakes has been among the most widely reported of recent species introductions to North America. Zebra mussels were introduced in 1985 or 1986 (Hebert,

Muncaster & Mackie, 1989) and have since spread rapidly through the lower Great Lakes and several adjacent watersheds, colonizing primarily shallow, near-shore areas. They may eventually colonize most lakes and slow-flowing rivers of temperate North America (Strayer, 1991). Quagga mussels were first found in 1991 (May & Marsden, 1992), and now occur from Quebec City, on the St. Lawrence River, to western lake Erie (Mills *et al.*, 1993). Quagga mussels dominate deeper, offshore waters of lakes Erie and Ontario, but also co-occur with zebra mussels near-shore. Because they arrived first and have spread further, most research has focused on zebra mussels.

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Many indigenous predators, but particularly molluscivorous waterfowl and fish, now include dreissenid mussels in their diets, some to the near-exclusion of alternate, traditional prey. Migratory diving ducks, among them greater and lesser scaup (*Aythya marila, A. affinis*), common goldeneye (*Bucephala clangula*), bufflehead (*B. albeola*), oldsquaw (*Clangula hymenalis*), and white-winged scoter (*Melanitta deglandi*), prey on zebra mussels during fall staging periods (Wormington & Leach, 1992, Mitchell & Carlson, 1993; Hamilton & Ankney, 1994; Hamilton, Ankney & Bailey, 1994; Knapton, 1994; Shular, 1994; Custer & Custer, 1996). Of Great Lakes fish, freshwater drum (*Aplodinotus grunniens*), yellow perch (*Perca flavens*), common carp (*Cyrinus carpio*), and pumpkinseed (*Lepomis gibbosus*) prey on dreissenid mussels in the field (Spataru, 1967; French, 1993; French & Bur, 1993; Tucker, Cronin & Soergel, 1996; Boles & Lipcius, 1997; Morrison, Lynch & Dabrowski, 1997). Both waterfowl and fish are size-selective predators of zebra mussels. To date, predation on quagga mussels has not been considered. Predation by fish and by diving ducks may play an important role in determining local outcomes of dreissenid mussel introduction. However, the nature and magnitude of predation effects on mussel equilibrium size distributions, densities, and relative abundances remain unclear.

Studies on zebra mussel populations in European lakes provide a broad range of estimates of predation impact. The mussels have spread through Europe over the past 200 years; there, as in North America, both fish and diving waterfowl forage extensively and size-selectively on zebra mussels (reviewed in Pliszka, 1953; Geroudet, 1966; Jacoby & Leuzinger, 1972; Stanczykowska, 1977; Geroudet, 1978; Mackie *et al.*, 1989; Mitchell, 1995; and bibliography in Limanova, 1968). Fish predators may limit mussel densities in some areas, although published results are equivocal (Florescu, 1970; Draulans and Wouters, 1988; Bij de Vaate, Greijdanus-Klass & Smit, 1992; Karnaukhov & Karnaukhov, 1993; Smit *et al.*, 1993). Impact estimates for waterfowl predators range from negligible to reductions in excess of 90%, with the greatest percent declines occurring in lakes where waterfowl winter (Pedroli, 1981; Suter, 1982a-c; Piesik, 1983; Zuur, Suter & Kramer, 1983; Bij de Vaate, 1991; Cleven and Frenzel, 1993; and reviews in Stempniewicz, 1974; Stanczykowska, 1977; Mackie *et al.*, 1989; Stanczykowska *et al.*, 1990; Mitchell, 1995). In some cases, the entire mussel population disappears from near-shore areas where waterfowl forage (Jacoby & Leuzinger, 1972; Burla & Lubini-Ferlin, 1976) and, during particularly harsh winters, waterfowl may then starve (Suter & Van Eerden, 1992). These results suggest that seasonal variation in the intensity of predation may be important. However, predation studies in European lakes have been observational. Either waterfowl have been observed foraging in an area and concurrent declines in mussel abundance have then been attributed to predation, or predation's impact has been estimated from the number of predators present and their presumed daily intake.

Only one study has experimentally measured waterfowl predation's impact on dreissenid mussels: Hamilton, Ankney & Bailey (1994) used exclosure cages to restrict foraging activity by diving ducks during a fall staging period

at Point Pelee, Lake Erie. By that season's end, mussel biomass was 53% lower beside cages than beneath cages, with a disproportionate reduction in the biomass of mid-sized, 10-15 mm, zebra mussels. After a winter during which the field site was ice-covered and therefore free of duck predation, this difference had disappeared. Thus, predation by diving ducks had a substantial, but temporary, effect on the mussel population. Using a similar experimental design through the summer, Hamilton (1992) found no indication of fish predation effects. In contrast, Boles & Lipcius (1997), again using cage exclosures but in the Hudson River Estuary, estimated that fish predation reduced zebra mussel abundance by 14% over a two-week period.

The goal of this study, suggested by the observational work in European lakes, was to examine the role of overwinter predation on dreissenid mussels in North America. To that end, we applied Hamilton, Ankney & Bailey's (1994) experimental approach at a site where diving ducks not only stage, but also winter. Wintering of waterfowl on the Laurentian Great Lakes has been reviewed by Prince, Padding & Knapton (1992). As long as the lakes remain ice-free, birds can move freely along the shoreline. When the near-shore area is ice covered, though, they are restricted to ice-free holes created by turbulence or by warm water discharges from industrial plants and generating stations (Reed, 1971; Freedman & McKay, 1977; Goodwin, Freedman & McKay, 1977; McCullough, 1984; Gebauer, Dobos & Weseloh, 1992; Custer *et al.*, 1996). Access to an abundant prey resource, like dreissenid mussels, may be particularly important to wintering diving ducks as their metabolic requirements are higher in cold weather (Nilsson, 1970; Smith & Prince, 1973; Suter & Van Eerden, 1992). Based on observations in European lakes, these are the circumstances under which local regulation of dreissenid mussels by waterfowl predators may be most likely.

Material and methods

STUDY SITE AND EXPERIMENTAL DESIGN

Our field site, Nanticoke, is on the northeast shoreline of Lake Erie at the northeastern end of Long Point's outer bay, where a coal-powered generating station releases heated water from its condensor cooling system into the lake (Figure 1). Prevailing winds and currents push the plume of warmer water eastward into Outfall Bay or, less frequently, southward (offshore) (Burchat, 1984). In years when ice cover is extensive, this plume forms an ice-free hole to which wintering greater and lesser scaup and bufflehead, species known to prey on zebra mussels elsewhere on the Great Lakes, are restricted (McCullough, 1984). These ducks also use Nanticoke during a three-month fall staging period, peaking in late October or early November, and for a brief spring migration in April (McCullough, 1981; Prince, Padding & Knapton, 1992). Table I summarizes reports of diving ducks observed at Nanticoke over the course of this study. (Because scaup forage nocturnally through the winter [Nilsson, 1970; McNeil, Drapeau & Goss-Custard 1992], we did not attempt to quantify predation pressure through observations of foraging birds. Table I is intended to give a qualitative sense of the site's use by
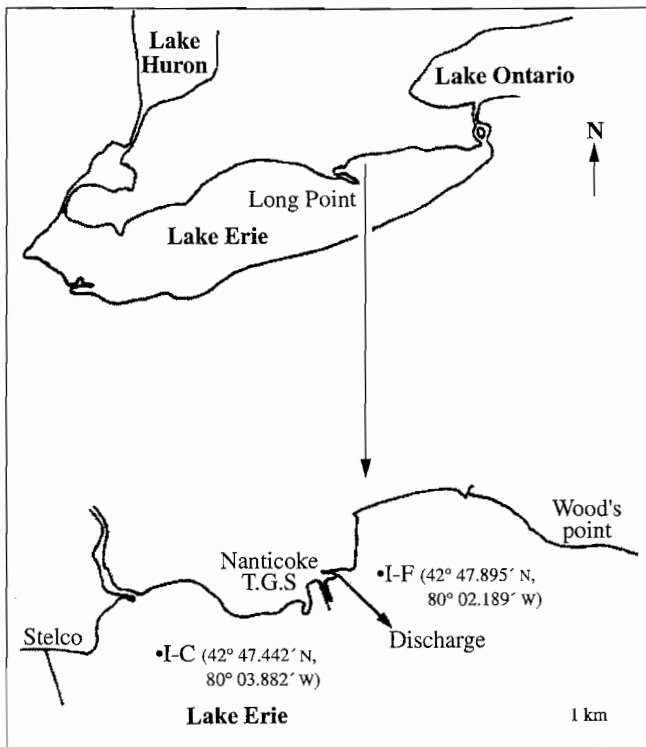
FIGURE 1. Location of the study site, Nanticoke, on the north shore of Lake Erie, and of the two sites near the Nanticoke Thermal Generating Station where waterfowl and fish exclosure cages were placed. Near the mouth of the discharge canal, Site Ice-Free ('I-F' on the figure) remained open and accessible to waterfowl year-round, whereas Site Ice-Covered, ('I-C'), west of the generating station, was ice-covered through the winter.

TABLE I. Reported counts of scaup, common goldeneye, and bufflehead at Nanticoke (the 10 km stretch of shoreline between Stelco Pier, west of the generating station, and Peacock Point, east of the station) during the course of this study. The source of the estimate is given as: DD: D. Dennis (unpubl. data); JSM: J.S. Mitchell (pers. observ.); MS: M. Street (pers. comm.).

Date	Scaup spp.	Common goldeneye	Bufflehead	Source
27 Oct 93	0	40	65	DD
10 Nov 93	130	21	0	JSM
16 Nov 93	150	50	190	DD
23 Dec 93	2550	38	174	DD
12 Jan 94	2000	0	0	JSM
24 Jan 94	124	64	129	JSM
21 Feb 94	2500-3500	0	0	MS
24 Feb 94	250-350	0	0	MS
17 Mar 94	40	493	50	DD
30 Mar 94	10	327	326	DD
15 Apr 94	0	417	350	DD

waterfowl). Freshwater drum, one of the main fish predators on zebra mussels in the Great Lakes, are also present at Nanticoke (Mitchell, 1995). Zebra mussels first appeared at Nanticoke in 1989 (Griffiths *et al.,* 1991) and quagga mussels, in 1992 (Mills *et al.,* 1993; but see Domm *et al.,* 1993). Quagga mussels are now the more abundant of the two dreissenids (Mitchell, Knapton & Bailey, 1996).

To estimate the impact of predation on zebra and quagga mussels at Nanticoke, we deployed exclosure cages similar to those used by Hamilton, Ankney & Bailey (1994). Half

the cages were designed to exclude both diving ducks and fish, and half, ducks only. Our goal was to estimate the impacts of duck and fish predation at Nanticoke through the fall and winter. This study provided the first opportunity to examine predation impacts on quagga mussels, all previous research having looked exclusively at zebra mussels. It also revealed unexpected interactions between the extent to which mussels were grazed from a rock and the size of that rock.

CAGE DESIGN

Exclosure cages used in these experiments were modified from those used in Hamilton, Ankney and Bailey's (1994) study of duck predation on zebra mussels at Point Pelee. Hamilton (1992) determined that confounding effects (*i.e.,* effects not due to predation) were slight using these cages and tended to mask, rather than augment, effects attributed to predators. The cages are square, angle iron frames (1.5 m × 1.5 m) on 30 cm legs. Construction netting (4 cm mesh) fastened over the top of each frame prevents diving ducks from foraging beneath cages. On cages intended to exclude fish as well as diving ducks, we extended the netting down all sides of the frame, such that the netting was flush with the substrate. French & Bur (1993) found that freshwater drum, which we expected to be the most important fish predator of dreissenid mussels at Nanticoke, began consuming zebra mussels once 25 cm long. Drum this large could not swim through the 4 cm construction netting mesh. Small pumpkinseed and perch might have been able to pass through the netting, but their contribution to the overall effect of fish predation should not have been appreciable; while sampling, we saw no pumpkinseed and few perch.) The sides of cages intended to exclude only ducks were left open. We secured cages to the lake bottom by hammering metal poles into the substrate at the corners of the cage (Site Ice-Free) or using guy lines run from diagonally opposite corners of the cages to cinder blocks 3 m away (Site Ice-Covered). We refer to cages intended to exclude duck but permit fish access as top-only exclosures, and to cages intended to exclude both ducks and fish as full exclosures.

In October 1993, we arranged six top-only and six full exclosures at each of two sites (24 cages total). The first site was southeast of the warm water discharge canal's mouth, and was therefore expected to remain ice-free through the winter (Site Ice-Free). The second site was west of the generating station and unaffected by the warm water discharge, so that ice cover was expected (Site Ice-Covered) (Figure 1). Both sites were in 7 m of water and both consisted of loose cobble overlying a silt/clay substrate. We placed cages such that sufficient cobble was present beneath each cage to allow for sampling. At Ice-Free, we could locate only one 'patch' with a sufficient cobble density. The area of this patch required placement of cages approximately 3 m apart. Cobble cover was not a concern at Ice-Covered, but we elected to use a similar cage distribution. Based on Ontario Hydro's investigations of the warm water plume at Nanticoke, temperatures at Ice-Free might occasionally have been raised by up to 4°C above those at Ice-Covered (Burchat, 1984). We recorded bottom temperature on several occasions while collecting samples but never observed temperature differences greater than 1°C between sites. Mussel density is not affected by warm water discharges, although growth rates can be (Kornobis, 1977; Draulans &

Wouters, 1988; Stanczykowska, Lewandowski & Ejsmont-Karabin, 1988). Because our approach used mussel number, rather than biomass (see below), temperature differences between the sites are unlikely to have seriously affected our results, although differences in mussel growth rates could conceivably have affected length class-specific impact estimates.

SAMPLING PROCEDURE

SCUBA divers collected rocks and placed each in a separate plastic bag while underwater, being careful not to displace the attached mussels. The sampling unit was therefore all the mussels on an individual rock. Rocks collected beneath a cage were selected by placing a 1 m² quadrat, subdivided into a 1 dm × 1 dm grid, over the centre of that cage and taking rocks closest to predetermined, random grid coordinates. To avoid any possible edge effects, no rocks were collected from beneath the outer 25 cm of the caged area. For samples collected adjacent to cages, the same procedure was used, but with the quadrat placed 1 m from the cage in a predetermined, random direction. At the surface, water was drained from the bags and replaced with sufficient 70% ethanol to immerse the rock and its attached mussels. We collected one sample at each cage location in mid-October, 1993, and two beneath and one adjacent to each cage in late May, 1994. Subsequent handling errors left us with 11 October samples from Site Ice-Free and 11 from beneath top-only exclosures at Site Ice-Covered, but with 12 in all other groups (94 samples in total).

Mussels were scraped from each rock and separated by species (quagga mussel or zebra mussel) using differences in shell morphology (May & Marsden, 1992; Domm *et al.,* 1993; Pathy & Mackie, 1993). Each mussel was measured under low power (6.4×) of a dissecting microscope using a *camera lucida* and Digitize software (Version 1.3,® Hopcroft, Zoology, University of Guelph). The surface area of each scraped rock was estimated by wrapping the rock in foil and then comparing the weight of the foil to that of a known foil area (Reice, 1980).

STATISTICAL ANALYSES

Analyses were performed using SYSTAT (Wilkinson, 1989). From each sample and for each mussel species, we counted the number of mussels in each of five length classes: 2-6 mm, 6-10 mm, 10-14 mm, 14-18 mm, and > 18 mm. Mussels less than 2 mm long were ignored because we wanted to ensure that all mussels counted were settled, rather than post-veligers, and because of difficulties distinguishing the two species when < 2 mm. Caloric value increases exponentially with shell length (Draulans & Wouters, 1988), so mussels less than 2 mm long are unlikely to be of importance for waterfowl or fish (Prejs, Lewandowski & Stanczykowska-Piotrowska, 1990).

To determine whether excluding predators affected mussel abundance, we ran Model I Multivariate Analyses of Covariance (MANCOVAs) separately on log-transformed counts of quagga mussels and of zebra mussels from the May samples. To test for an effect of duck predation, we compared samples collected beneath top-only exclosures with samples collected adjacent to cages. We then compared samples collected beneath top-only exclosures with those collected beneath full exclosures to test for an incremental effect of fish predation. Predictors used in the models were site (Ice-Free and Ice-Covered), cage treatment, and log-transformed rock surface area. Site was considered to be a fixed factor and rock surface area, a covariate. All interactions between factors were initially included in the models. Non-significant interactions were then sequentially removed (highest order first) and the revised model was re-run. We found significant interactions between cage treatment effects and effects of the covariate, rock size (see Results), and used univariate regressions of log-transformed mussel abundance on log-transformed rock surface area as an aid to understanding those interactions.

Two elements of this approach warrant further mention. First, we collected samples in October (immediately prior to cage deployment) so that we could quantify total percent declines. We did not use the October data in statistical analyses. Initially, we had hoped to collect a late December sample as well, and were concerned that removing additional rocks from beneath cages in October might leave too few rocks remaining for subsequent samples. Our approach assumes that, prior to caging, there were no systematic differences between caged and uncaged rocks. An alternative approach, where samples from both dates are included and a predation effect appears as an interaction between date and treatment, reduces overall power because of the additional interaction terms. Second, by not including cage as a factor, we have ignored potential variation among cages within a site. Given the distribution of cages necessitated by substrate availability at Ice-Free, rocks collected adjacent to one cage might be as close to its neighbour, making it inappropriate to pair samples collected adjacent to cages with those collected beneath a specific cage.

Results

The 1993-1994 winter was harsh and ice-cover was extensive nearshore. Wintering diving ducks were restricted to ice-free holes, including that created by warm water discharged from the generating station at Nanticoke. Rafts of diving ducks were often seen at the Nanticoke ice-free hole (Table I). Site Ice-Covered was inaccessible to ducks from early January until mid-March. In contrast, Site Ice-Free was rarely, if ever, ice-covered.

In late February, 18 scaup and 1 bufflehead were found dead in the discharge canal at Nanticoke. At least some of these birds had apparently died of starvation (D. Campbell, pers. comm.). The birds, and others collected earlier, contained large numbers of dreissenid mussel shell fragments (Mitchell, Bailey & Knapton, 1999). Mitchell (1995) also found dreissenid mussels in freshwater drum collected at Nanticoke the preceding fall.

Quagga mussels were more abundant at Site Ice-Free than at Ice-Covered, and at both sites were more abundant than zebra mussels (Figure 2). Zebra mussels were much more abundant at Ice-Covered than Ice-Free. We collected few large mussels of either species. The largest quagga mussel found was 24 mm long, the largest zebra mussel, 22 mm.
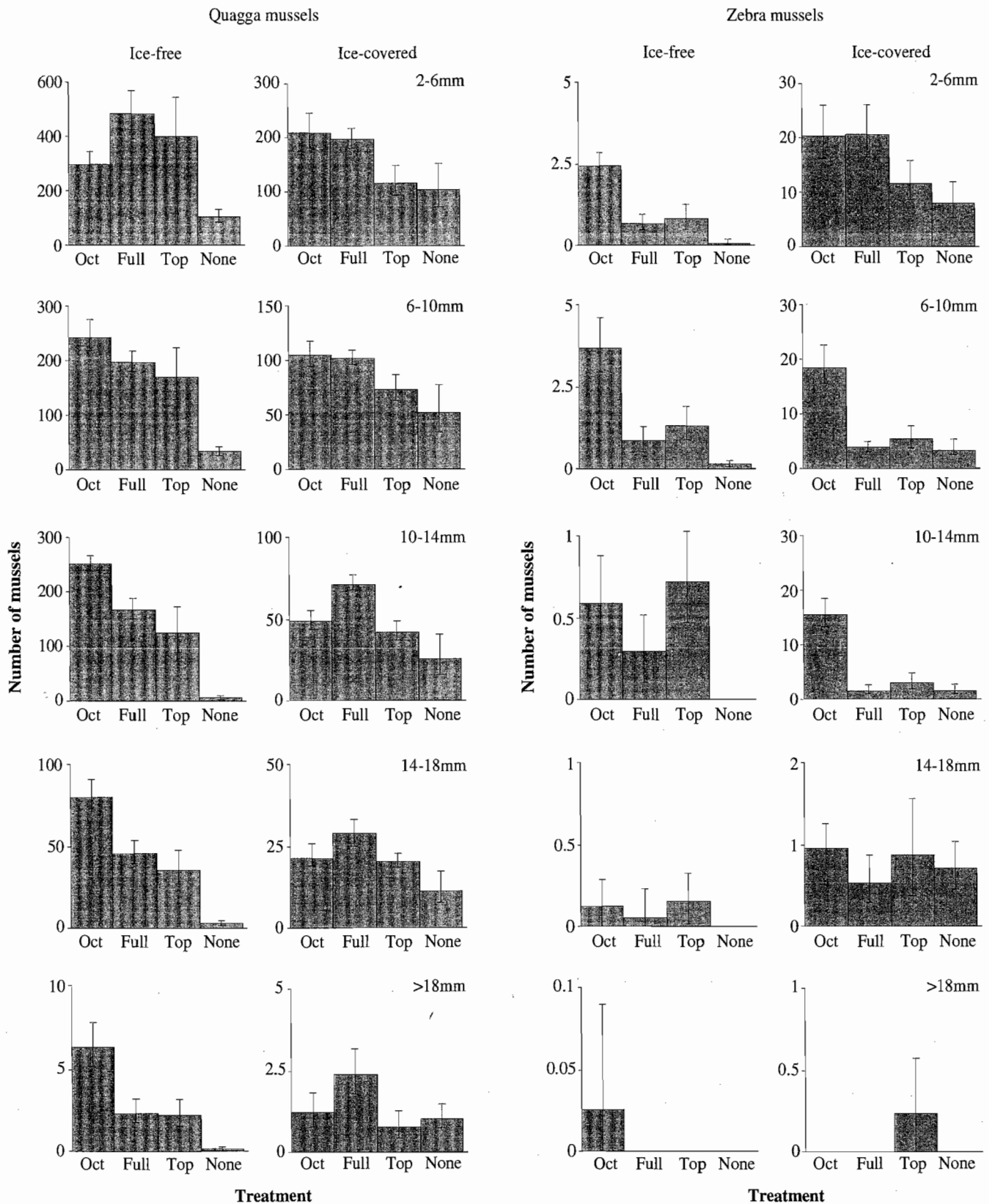
FIGURE 2. Adjusted mean number of quagga mussels and zebra mussels found on rocks in October, prior to cage placement (Oct), and, the following spring, beneath fish exclosures (Full), beneath waterfowl exclosures (Top), and adjacent to exclosures (None). Site Ice-Free was accessible to waterfowl predators through the winter; Site Ice-Covered was not. Plotted are the mean number of mussels and the standard error of that mean. Since rock surface area varies, the numbers of mussels have been standardized to that for the mean rock surface area (279 cm^2). Error bars are not symmetric about the mean because the analysis used log-transformed data. Eleven rocks were collected for the October estimate at Ice-Free and for the May waterfowl exclosure estimate at Ice-Covered. All other samples used 12 rocks. Note that the y-axis scale varies among mussel size classes.

EFFECT OF ROCK SIZE

Interactions with rock surface area (Table II) complicated the interpretation of exclosure cage effects. Correlations between mussel abundance and rock size varied with season, site, mussel species, and mussel size (Figure 3). In October, quagga mussel abundance was correlated with rock size at both sites. Beneath full exclosures, and with the exception of 2-6 mm quagga mussels at Site Ice-Free, abundance and rock size were still correlated in May. Beneath top-only cages, though, and particularly outside cages, that correlation broke down. In spring samples collected outside cages, rock size did not explain more than 5% of any length class's abundance at either site.

In both October and May samples, correlations between zebra mussel abundance and rock size were generally much weaker than for quagga mussels. The only exception was the 2-6 mm length class in October at Site Ice-Free. Like quagga mussels', zebra mussel abundance was consistently uncorrelated with rock size in May samples. For zebra mussels, though, October correlations were also weak.

EFFECT OF PREDATOR EXCLOSURES

To estimate the impact of predation, we standardized observations to the overall sample mean rock surface area (mean: 279 cm^2, range: 58 - 696 cm^2). (Rocks collected did not differ significantly in surface area among treatment groups [ANOVA; F = 1.7, df = 4,66; p = 0.15]). Note that, because predation affected prior relationships between rock size and mussel abundance, the expected effect on a given rock depends on that rock's size.

QUAGGA MUSSELS

An interaction with site was significant or suggestive both for the comparison between top-only and no cage treatments (waterfowl excluded) (p = 0.05) and that between full and top-only cages (both waterfowl and fish excluded) (p = 0.1) (Table II).

Duck predation: At Site Ice-Free, quagga mussels were significantly more abundant on rocks collected beneath top-only cages than on rocks collected outside those cages (Table II, Figure 2). This result was independent of rock size. All length classes were affected (univariate F-tests, p < 0.001). Effect magnitude varied: relative to beneath top-only exclosures, numbers of 2-6 mm quagga mussels on uncaged rocks declined by 74% (of the upper value). Six-10, 10-14, 14-18, and > 18 mm quagga mussels declined by 78, 92, 90, and 93% respectively.

At Site Ice-Covered, interpretation of diving duck predation effects was complicated by a significant interaction with rock surface area (Table II). The interaction was significant for > 18 mm quagga mussels (univariate F-test, p = 0.01) and suggestive for 14-18 mm mussels (p = 0.14). The interaction between cage treatment and rock size was not significant for smaller quagga mussels, nor was the direct effect of cage treatment when the interaction term was removed and the model re-run with the two largest length classes excluded (Table II, Figure 2).

Fish predation: When numbers of quagga mussels beneath full cages were compared with those beneath top-only cages to test for an incremental effect of fish predation, the site-specific results were reversed. At Site Ice-Free,

TABLE II. Results of MANCOVAs testing for abundance differences between cage treatment groups at the Ice-Free and Ice-Covered sites. Samples collected beneath top-only cages were compared with samples collected outside cages to assess effects of predation by ducks. Samples collected beneath full cages were compared with samples collected beneath top-only cages to assess fish predation's effects. Where an interaction with the covariate was not significant, the model was re-run without that interaction to evaluate the direct effect of cage treatment. Where the interaction was significant (for quagga mussels at Ice-Covered), results of univariate F-tests indicated that this interaction was limited to larger mussel length classes. MANCOVAs were then re-run using only smaller mussels. The *a priori* prediction is of full > top-only > no cage abundance, so p-values for cage treatment's effect are one-tailed. The exception is fish predation's effect on zebra mussels at site Ice-Covered, where the two-tailed value has been used because the direction of the observed effect was not consistent across length classes (Figure 2). Given the *a priori* prediction, this p-value should be treated as neither significant nor suggestive. lrsa: log-transformed rock surface area.

|		SITE ICE-FREE			SITE ICE-COVERED		
	Λ	df	p	Λ	df	p	
PREDATION BY DUCKS ON QUAGGA MUSSELS (site*treatment*lrsa: Λ = 0.74; df = 5,35; p = 0.05)							
lrsa*treatment	0.71	5,16	0.3	0.38	5,15	0.007	(all length classes)
				0.93	3,17	0.18	(2-14 mm)
treatment	0.28	5,17	< 0.001	0.89	3,18	0.24	(2-14 mm)
PREDATION BY FISH ON QUAGGA MUSSELS (site*treatment*lrsa: Λ = 0.78; df = 5,35; p = 0.1)							
lrsa*treatment	0.87	5,16	0.8	0.46	5,15	0.03	(all length classes)
				0.98	2,18	0.85	(2-10 mm)
treatment	0.88	5,17	0.4	0.78	2,19	0.04	(2-10 mm)
PREDATION BY DUCKS ON ZEBRA MUSSELS (site*treatment*lrsa: Λ = 0.85; df = 5,35; p = 0.3) (site*treatment: Λ = 0.9; df = 5,36; p = 0.54)							
lrsa*treatment	0.85	4,17	0.56	0.67	5,15	0.25	
treatment	0.56	4,18	0.02	0.92	5,16	0.46	
PREDATION BY FISH ON ZEBRA MUSSELS (site*treatment*lrsa: Λ = 0.85, df = 5,35, p = 0.37) (site*treatment: Λ = 0.86, df = 5,36, p = 0.34)							
lrsa*treatment	0.76	4,17	0.29	0.67	5,15	0.26	
treatment	0.96	4,18	0.97	0.61	5,16	0.12 (two-tailed)	
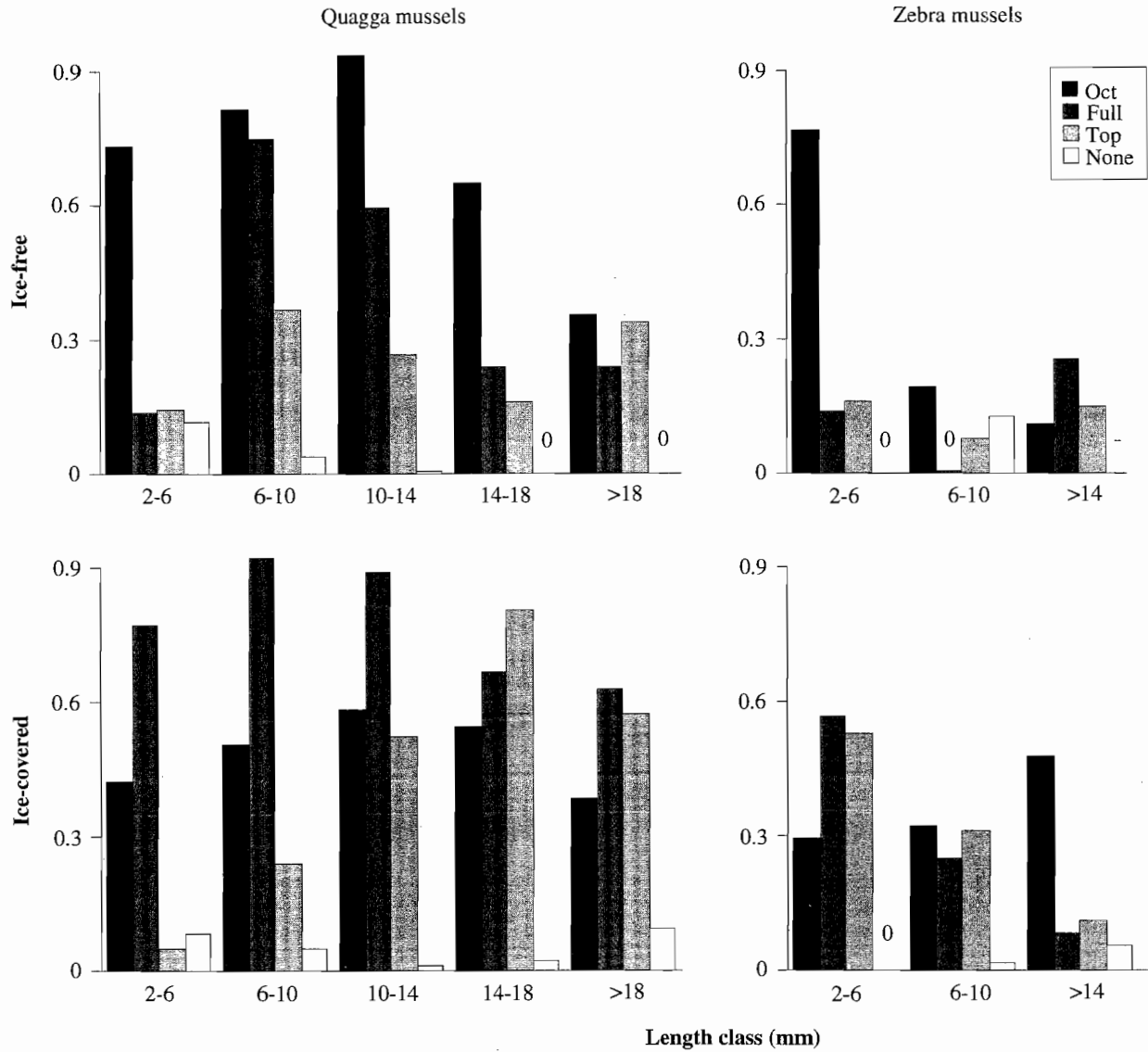
FIGURE 3. Adjusted r^2 values from regressions of each length class's abundance against rock surface area (both variables log-transformed). Because zebra mussels longer than 10 mm were rare, 10-14, 14-18, and > 18 mm length classes have been pooled. "0" indicates $r^2 = 0$. "-" indicates that no mussels of that length class were present in the sample. For adj. $r^2 < 0.16$, the relationship is non-significant.

although quagga mussels of all length classes were more abundant beneath full than top-only exclosures (17-25%), this trend did not approach statistical significance (Table II, Figure 2).

In contrast, the treatment by rock size interaction was significant at Site Ice-Covered (Table II). For fish, as for diving duck effects, this result was driven by numbers of larger mussels: the interaction term was significant for 14-18 mm quagga mussels and suggestive for > 18 mm mussels (univariate F-tests, $p = 0.03$, $p = 0.13$). The univariate statistic for 10-14 mm mussels was not statistically significant ($p = 0.23$) but its multivariate equivalent remained suggestive when this length class was included in the analysis ($p = 0.1$). For those three length classes, the regression slope of quagga mussel length class abundance *versus* rock size was steeper in the top-only cage treatment group than in the full cage treatment group, such that, on the smallest rocks

sampled, mussel abundance was greater beneath full than beneath top-only cages, while on the largest rocks sampled, abundances beneath the two cage types were similar (Table III). That is to say, on small rocks but not on large rocks, numbers of quagga mussels > 10 mm were reduced when subject to fish predation. Caging's effect was independent of rock surface area for 2-6 and 6-10 mm quagga mussels, which were significantly more abundant when both fish and ducks were excluded than when only ducks were excluded (2-6 mm: 41%, $p = 0.03$; 6-10 mm: 27%, $p = 0.05$) (Figure 2).

ZEBRA MUSSELS

For zebra mussels, interactions with site were not significant (Table II). Nor, when these terms were removed and the models re-run with sites pooled, were differences between treatment groups apparent. Despite this, we elected

TABLE III. Regression parameters for the three largest quagga mussel length classes at Site Ice-Covered. 'ln(number)' refers to log-transformed mussel abundance on a rock and 'lrsa' to log-transformed rock surface area. Quagga mussels > 14 mm were not included in the analysis of differences between top-only and uncaged treatments, and mussels > 10 mm were not included in the analysis of differences between full and top-only cages because, in both cases, interactions between the effect of cage treatment and that of rock size were attributed to these length classes.

| | 10-14 mm | | 14-18 mm | | > 18 mm | |
	ln(number)	r^2	ln(number)	r^2	ln(number)	r^2
Fall	-1.205 * lrsa + 0.911	0.54	-2.859 * lrsa + 1.062	0.50	-5.445 * lrsa + 1.111	0.32
Full	-1.205 * lrsa + 0.976	0.88	-2.030 * lrsa + 0.956	0.63	-6.298 * lrsa + 1.337	0.59
Top-only	-4.537 * lrsa + 1.476	0.47	-8.651 * lrsa + 2.082	0.78	-14.108* lrsa + 2.612	0.52
None	1.551 * lrsa + 0.309	< 0.01	0.567 * lrsa + 0.351	< 0.01	-1.356 * lrsa + 0.371	< 0.01

to split the data by site to facilitate comparisons with quagga mussel results. Because zebra mussels were rare, particularly larger length classes and particularly at Site Ice-Free, these results may be less reliable than those for quagga mussels.

Duck predation: At Site Ice-Free, zebra mussel results were qualitatively similar to those for quagga mussels: relative to their abundance beneath top-only exclosures, 2-6, 6-10, and 10-14 mm zebra mussels declined by 86, 86, and 100% respectively (univariate F-tests: $p < 0.05$) (Table II, Figure 2). Larger zebra mussels were too rare at Site Ice-Free for a test to be meaningful (three mussels > 14 mm collected beneath top-only cages *versus* none collected outside cages). At Site Ice-Covered, cage treatment effects were not detectable.

Fish predation: No incremental effect of excluding fish was detectable at either site (Table II, Figure 2). Although differences in zebra mussel abundance between full and top-only cages at Site Ice-Covered were pronounced, the direction of effect was not consistent across length classes.

Discussion

DUCK PREDATION

Differences in the effects of top-only exclosures between the two sites are consistent with predation by wintering diving ducks at Site Ice-Free, and an over-winter release from duck predation at Site Ice-Covered due to that ice. At Ice-Free, both quagga and zebra mussel numbers declined outside cages relative to their numbers beneath top-only exclosures, while at Ice-Covered, effects on quagga mussels were less pronounced and were restricted to mussels 14-18 mm long. Our estimates of duck predation's impact at Ice-Free (reductions of 74-93% for quagga mussels and 86-100% for zebra mussels, depending on mussel length class) are of similar magnitude to estimates from European lakes. We conclude that, when accessible stretches of shoreline are restricted, predation by wintering diving ducks can cause dramatic, localized declines in the abundance of both mussel species. Note, as caveat to this conclusion, that our assessment of ice cover's effect is based on a single contrast between paired sites. Differences other than ice cover may be responsible for the observed differences in caging's effect between the sites. While this limitation is unavoidable (we had only one ice-free hole with which to work), repetition of the study at other winter ice-free holes would be necessary to eliminate the alternative.

Our estimates of duck predation's impacts are particularly useful because they can be attributed directly to predation,

whereas estimates from European lakes are observational, being based on correlations of mussel population declines and the presence of waterfowl (Suter, 1982a,b; Bij de Vaate, 1991; Cleven & Frenzel, 1993) without accounting for other causes of mortality. For example, Suter (1982a,b) attributes to duck and coot predation a 97% over-winter decline in zebra mussel biomass in the River Rhine near Lake Constance. In contrast, Suter's (1982c) estimate of waterfowl consumption of mussels, based on waterfowl counts and estimated daily intakes, predicts a predation impact of less than 50%. Differences between mussel abundance in fall samples and that beneath full exclosures in spring samples make clear the risk of attributing all mortality to predation. At Site Ice-Free, we would have underestimated predation's impact on 2-6 mm quagga mussels, which were more abundant beneath full exclosures in spring than they had been the preceding fall, and overestimated predation's contribution to declines of larger mussel length classes, which decreased in abundance beneath full exclosures.

SPECIES-, PREY SIZE-, AND ROCK SIZE-SELECTIVE PREDATION BY DUCKS

At Site Ice-Free, percent declines of quagga and zebra mussels were similar, which suggests that ducks did not discriminate between the species. At Site Ice-Covered, effects were significant (but complicated by the effect of rock size) only for quagga mussels. However, all zebra mussel length classes at Site Ice-Covered were more abundant beneath than beside top-only exclosures. A preference for quagga mussels is possible as zebra mussels' flattened ventral surface allows them to 'hug' the substrate more firmly than can quagga mussels (Mills *et al.*, 1993). Draulans (1982), though, found that the time required for captive tufted ducks (*Aythya fuligula*) to disengage zebra mussels from a substrate was minimal, and did not affect prey profitability. Furthemore, Mitchell & Knapton (1993) concluded that weight:length relationships for quagga and zebra mussels at Nanticoke were similar, and that caloric values would likewise be similar. We conclude that waterfowl foraged without regard for mussel species.

Ducks did select among mussel length classes. At Site Ice-Free, declines attributed to duck predation were greatest for larger quagga and zebra mussels, exaggerating a demographic skew towards smaller mussels. Likewise, the only detectable effect of duck predation at Site Ice-Covered, an interaction between cage treatment and rock size, was restricted to quagga mussels > 14 mm long. This is the pattern expected if ducks selected large mussels and then, through the winter at Site Ice-Free, broadened their diets to include

smaller mussels as the density of larger prey declined. Preferred zebra mussel length classes vary among waterfowl species and among sites (reviewed in Mitchell, 1995) but, for scaup in the Great Lakes, 'medium'-sized mussels tend to be preferred (Custer & Custer, 1996: 8-12 mm; Hamilton & Ankney, 1994: 8-14 mm, depending on spp., site, and year; Hamilton, Ankney & Bailey, 1994: 11-13 mm). Draulans (1982, 1984; but see De Leeuw & Van Eerden, 1992) argued that tufted ducks selected smaller mussels to limit the risk of accidentally accepting mussels too large to handle efficiently. Large mussels are rare at Nanticoke; the largest we collected was 24 mm. Scaup may be able to forage profitably on larger mussels at Nanticoke than elsewhere because there is little risk of encountering mussels too large to handle. While we favour this explanation, the same pattern, of larger effects on larger mussels, could also come about under non-selective predation if larger mussels are less mobile than smaller mussels (see below).

Estimates of duck predation's impact were sensitive to rock surface area. Excluding Site Ice-Free's rare zebra mussels, mussel numbers in the fall samples were correlated with rock surface area for all length classes of both species, whereas samples taken outside cages the following spring were not (Figure 2). This result implies that the intensity of duck predation on large as compared to small rocks was not proportional to initial differences in mussel abundance on large and small rocks. At Site Ice-Free, the effect may be a consequence of predation's intensity: waterfowl consumed almost all available mussels at the site, and more mussels were available for consumption on larger rocks. The pattern held, though, at the ice-covered site, where the effect of duck predation was much less pronounced. Larger rocks may be more easily detected by diving ducks or ducks may actively avoid smaller rocks because, with fewer mussels attached to them, a preferred length class is less likely to be found. Regardless of the underlying reason for rock size effects, their consequence is that our methodology will tend to underestimate duck predation's impact, as there is an upper limit on the size of rocks which a diver can handle.

FISH PREDATION

At Site Ice-Covered, we attribute differences in quagga mussel abundance between full and top-only exclosures to predation by fish. Smaller quagga mussels were less abundant where fish could forage than where they could not (2-6 mm: 41%, 6-10 mm: 27%). For larger quagga mussels at Site Ice-Covered, effects depended on rock size. Zebra mussels at the ice-covered site were unaffected by fish predation. At Site Ice-Free, no incremental effect of excluding fish was detectable for either mussel species. Although the effect of fish predation at Site Ice-Covered was much less than that of diving ducks at Site Ice-Free, it was a source of substantial quagga mussel mortality. Moreover, predation by fish may be less localized than that by wintering ducks. The effect did not approach that reported by Boles & Lipcius (1997) who, also using exclosure cages, estimated that fish predators reduced mussel numbers in the Hudson River estuary by 14% in two weeks. Molluscivorous fish may be more abundant, or alternate prey less abundant, at Boles & Lipcius's study site than at Nanticoke. That study's methodology may also have facilitated fish predation: rocks

were collected, some of the attached mussels removed, and the rocks then returned to the field site. That approach may have weakened the remaining mussels' attachment to their substrate and/or created an 'edge' on the remaining mussel clump, such that the remaining mussels were more accessible to predators. Hamilton (1992) did not detect an effect of predation by fish through the summer on mussel densities at Point Pelee, when fish might be more active, but also when alternate prey might be more abundant. Based on our results, predation by fish through the fall and winter did effect quagga mussel abundance at Nanticoke, but not at the ice-free hole.

The absence of an effect of fish predation at Site Ice-Free was surprising. Drum and perch were encountered at both sites while sampling and, while these events were not recorded, no between-site differences stood out. Fish at Site Ice-Free would have had access to an alternate resource: along with coolant water, the generating station discharge canal expels dead fish which have passed through the station's pumps (Foster & Wheaton, 1981). McCullough (1984) discussed utilization of this resource by mergansers at Nanticoke; presumably, it would also be of value to (live) fish.

SPECIES-, PREY SIZE-, AND ROCK SIZE-SELECTIVE PREDATION BY FISH

Fish predation affected quagga but not zebra mussel abundance. Although ease of detaching mussels from the substrate may not be relevant to ducks, it may be to fish predators. French & Love (1995) and Prejs, Lewandowski & Stanczykowska-Piotrowska (1990) both argue that ease of detaching zebra mussels from their substrate helps to explain avoidance of large zebra mussels by fish predators. A similar explanation may apply to species-selective predation by fish at Nanticoke.

Preferred quagga mussel sizes were difficult to assess for fish because, for larger length classes, the magnitude of fish predation's impact depended on rock size (see below). Rock size was not relevant for the two smallest mussel length classes at Site Ice-Covered, and here, percent reductions of 2-6 mm quagga mussels were greater than of 6-10 mm mussels. Fish predation on these two length classes was sufficiently intense at the ice-covered site to weaken substantially or remove entirely a correlation between mussel abundance and rock size. French & Love (1995) did not find zebra mussels longer than 22 mm in Lake Erie freshwater drum, and argued that this reflected avoidance of the largest mussel length classes. Morrison, Lynch & Dabrowski (1997) concluded that smaller drum selected small (< 6 mm) zebra mussels, while larger individuals avoided mussels > 13 mm long but preyed on smaller mussels in proportion to their availability; the authors reported qualitatively similar results for perch. In Poland, Prejs, Lewandowski & Stanczykowska-Piotrowska (1990) found that mussel prey size preferences of roach varied with fish size, but that roach avoided small zebra mussels in favour of those 11-17 mm long. Even in the absence of confounding rock size effects, then, local effects of predation by fish will be sensitive to both the size and species composition of fish predators. At Nanticoke, those fish predation effects appear to be most intense on smaller quagga mussels.

Whereas ducks foraged more intensively on larger rocks, effects of fish predation were greatest on smaller

rocks. At Site Ice-Covered, this led to significant or sugges-tive interactions between rock size and cage treatment effects on quagga mussels > 10 mm long. We argued above that diving ducks might locate larger rocks at a dispropor-tionate frequency. While it's possible that fish predators actively seek out smaller rocks, where ducks have been less active, it's unlikely, particularly as ducks and fish appear to be concentrating on prey of different sizes. A more likely explanation is that fish encounter and forage from rocks at a rate independent of rock size. For larger, infrequently con-sumed prey, this would lead to greater percent declines on rocks initially occupied by fewer mussels, while for smaller, preferred length classes, predation's impact might break down relationships with rock size. Again, regardless of the reason for rock size effects, an upper limit on the size of rocks collected will lead us to, in the case of fish predation, overestimate effects.

MUSSEL POPULATION RECOVERY FROM PREDATION

We attribute the effect seen at Ice-Free to wintering birds, but might still have expected to see greater residual effects of predation by ducks staging at Ice-Covered the preceding fall. Hamilton, Ankney & Bailey (1994) also reported that, after a predation-free winter, zebra mussels at Point Pelee had by spring recovered completely from a substantial decline in mussel biomass caused by staging diving ducks predation in the fall. Why should a persistent predation impact require that predation continue through the winter? Hamilton, Ankney, & Bailey hypothesized that zebra mussels outside cages at Point Pelee realized faster spring growth rates because the local population density was lower than that beneath cages. We can rule out this interpretation because our analysis used mussel number, not biomass. A more likely explanation is that mussels move. Cleven & Frenzel (1993) and Suter (1982a) suggested that mussel population recoveries from intense over-winter waterfowl predation could be due to mass migrations of one-year-old mussels from outside their study sites. Similarly, Dermott *et al.* (1993) concluded that pre-settlement recovery of near-shore zebra mussel populations in Lake Erie from winter ice scour was due to smaller-scale move-ments of young individuals from beneath rubble and from within bedrock fissures. These authors attribute recovery to recolonization of exposed near-shore areas by mussels previously occupying either depth or microhabitat refugia. If spring recoveries from fall predation are due to recolo-nization, then lasting predation impacts hinge not only on the intensity of predation, but also on its duration: predation must continue for a long enough period to not only remove mussels from exposed areas, but also to deplete the stock of mussels recolonizing that area from refugia. Dramatic effects of winter predation on dreissenids are then observed because, over the course of the winter, the mussel supply in refugia becomes exhausted. Alternatively, if restocking from refugia is a slow process, predation over-winter may be too recent an event for restocking to have occurred. Cleven & Frenzel (1993), Suter (1982a), and Dermott *et al.* (1993) all note that smaller mussels are more mobile than older, larger individuals. If small mussels move, we may underestimate impacts of duck and fish predation on those length classes: ducks' apparent preference for larger mus-

sels may not be as pronounced as it appears from our data and fish predation may be even more skewed towards smaller quagga mussels.

Implications

Patterns of predation attributed to fish and diving ducks suggest the two predator groups' foraging niches overlap less than were both to forage non-selectively. Diving ducks select large mussels while fish either have no preference or prefer smaller mussels. Fish prey on zebra mussels while ducks show no preference. Diving ducks remove mussels from larger rocks, while fish may prefer to graze mussels from smaller rocks. Impacts of diving ducks are most pro-nounced at the ice-free site, while fish predation effects are most apparent at the ice-covered site. Complementary feeding habits may lead to greater impacts on mussel populations than might be the case if those habits were more similar.

We expect predation impacts, even those of wintering diving ducks, to be localized and of short duration. Effects will be localized because the ice-free holes are the excep-tion. Effects will be of short duration because, although diving ducks can remove virtually all large, reproductively mature mussels, the spatial scale involved is small relative to the mobility of larval mussels. Recruiting zebra mussels (and presumably quagga mussels) settle preferentially on substrates with an intermediate existing mussel density (Chase & Bailey, 1996). Thus, even in the absence of short-term recovery through migration of settled mussels from refugia, larval recruitment through the summer could com-pensate for localized losses to predators the previous fall and winter.

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