

Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates

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SUMMARY

1. We conducted survey and transplant studies to determine whether colonization and residency on soft sediments by introduced, fouling mussels (*Dreissena polymorpha* and *D. bugensis*) were affected by physical disturbance, and whether *Dreissena* presence in turn influenced the diversity and population densities of other benthic invertebrates. Surveys revealed that colony density was typically higher at moderate depths than at shallower and greater ones. However, the largest, midsummer colonies and greatest coverage of sediments by mussels occurred at deeper sites.
2. Disturbance of transplanted colonies varied by depth and colony size, with deeper and larger colonies experiencing the lowest destruction rates. Colony destruction rate was positively correlated with current velocity adjacent to the lakebed.
3. Absence of mussel colonies at shallow sites was not determined by recruitment or substrate limitation, as recruit density was higher and sediment characteristics more suitable for postveliger settlement at shallow than at deeper sites. Rather, seasonal storms have much stronger effects in shallow than in deep water.
4. Mussel residency on soft sediment has profound effects on invertebrate biodiversity. Invertebrate species (taxon) richness and total abundance were positively correlated with mussel colony area. Mussel-sediment habitat supported between 462 and 703% more taxa, and between 202 and 335% more individuals (exclusive of *Dreissena*) than adjacent soft-sediment lacking mussels.
5. Results from this study illustrate that physical disturbance directly limits the distribution of mussels on soft sediments, and the diversity and abundance of other benthic invertebrates in consequence.

Keywords: mussel beds, *Dreissena*, biodiversity, Great Lakes, disturbance ecology

Introduction

Species introductions are a leading conservation problem, though they provide ecologists with unique insights into dynamics of community assembly and species interactions (e.g. Flecker & Townsend, 1994; Moyle & Light, 1996; Yan & Pawson, 1997; Ketelaars *et al.*, 1999). Two of the most important species introduced to the Great Lakes are the zebra mussel *Dreissena polymorpha* (Pallas) and the quagga mussel

Dreissena bugensis Andrusov. *Dreissena* spp. are 'ecological engineers' (Jones, Lawton & Shachak, 1997) in Lake Erie owing to their dramatic effects on seston availability and on the physical complexity of benthic substrates (e.g. Dahl *et al.*, 1995; Botts, Patterson & Schloesser, 1996; MacIsaac, 1996a; Klerks, Fraleigh & Lawniczak, 1996; Berkman *et al.*, 1998; Stewart, Miner & Lowe, 1998; MacIsaac *et al.*, 1999). The mussels have had far-reaching physical, chemical and biological impacts, including virtual extirpation of native bivalves. *Dreissena* forms very dense populations on most hard substrates in the western basin of the lake (MacIsaac *et al.*, 1992; Griffiths, 1993), though it occurs at much lower densities in the central and eastern

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basins (Dahl *et al.*, 1995). Quagga mussel distribution in Lake Erie is nearly a mirror image of that of the zebra mussel. It forms dense colonies on soft sediments (e.g. sand, mud) in the deeper eastern and central basins of the lake, but occurs at low density in the western basin (Dahl *et al.*, 1995; Dermott & Kerec, 1997).

Mortality in the *Dreissena* life cycle may exceed 99% during the transition from planktonic veliger to settled plantigrade mussel stages (Stańczykowska, 1977). Most young mussels die if they fail to locate suitable substrate upon which to settle and secure byssal threads (Stańczykowska, 1977). Lewandowski (1982) reported that macrophytes, mussel colonies and pebbles were more suitable settling substrates than gravel, sand and mud. Determinants of distribution and abundance of adult dreissenid mussels are less clear. Predation by ducks, crayfish and fish may reduce mussel abundance, though the effects may be ephemeral (Stańczykowska, 1977; Hamilton, Ankney & Bailey, 1994). Physical disturbance associated with waves determines distribution and abundance of *D. polymorpha* in nearshore, rocky habitat in western Lake Erie (MacIsaac, 1996b). Mellina & Rasmussen (1994) reported that substrate size explained between 38 and 91% of variability in *D. polymorpha* population density, with highest density occurring on boulders and lowest densities occurring on sand and mud. Likewise, Berkman *et al.* (1998) observed that *Dreissena* presence on soft sediments in western Lake Erie was positively related to particle size. Firm substrates including gravel, bedrock and clay constitute only 13% of benthic substrates in western Lake Erie, the remainder consisting of sand and mud (Hartman, 1973). The relative paucity of firm substrates could be an important determinant of mussel distribution in the basin because effects of wave disturbance should be greatest in shallow water bodies that lack holdfasts for attachment of mussel byssal threads.

Marine studies have demonstrated that physical destruction or translocation of mussel colonies may have adverse consequences on invertebrate communities owing to the complex habitat structure and food resources imparted by the colonies (Suchanek, 1981; Tsuchiya & Nishihira, 1985, 1986; Seed, 1996). In the Great Lakes, synoptic surveys have established that *Dreissena* benefits many species of benthic invertebrates in both shallow and deep, soft-bottom habitats (Stewart & Haynes, 1994; Botts *et al.*, 1996; Dermott &

Kerec, 1997). In addition, experimental studies have identified the mechanisms by which *Dreissena* presence benefits invertebrates in Lake Erie (Botts *et al.*, 1996; Stewart, Miner & Lowe, 1998). However, the direct effects of physical disturbance on the colonization ecology of *Dreissena*, and its indirect impact on biodiversity of other invertebrates, have not been explored in shallow, soft-bottom habitats. In this study we test the hypothesis that physical disturbance affects the spatial distribution of *Dreissena* colonies in western Lake Erie. We also test the hypothesis that mussel colonies enhance biodiversity of benthic invertebrates on soft sediments in relatively shallow water, and that physical destruction of mussel colonies indirectly impacts benthic communities.

Methods

Study Site

The study was conducted in the western basin of Lake Erie off the south-east shore of North Bass Island, Ohio. North Bass Island is a relatively large (2.4 km²) island located 13 km from the Ohio mainland. The lakebed at the study site consists of sand and sand-clay matrix from the surface to maximum depth (9.1 m). The site is protected from westerly winds but is fully exposed to easterly storms. During autumn 1995, waves generated by a hurricane-associated storm ranged from 2 to 5 m. Mussel beds that were virtually continuous at 9.1 m during August 1995 had been obliterated prior to June 1996 (A. Bially & H. MacIsaac, personal observ.), at which time we commenced our study of colony recovery.

Spatial Distribution of *Dreissena*

To assess the spatial distribution of *Dreissena* colonies (i.e. 'islands') in relation to depth, three transects were established on June 1, 4 and 12 1996, along a soft-sediment depth gradient (i.e. perpendicular to shore), off the south-east corner of the island. Terminal positions along transect lines were determined using a Geographical Positioning System (Garmin GPS 45). A 9-m² quadrat was deployed at every 1-m depth along the transect from 1.5 to 8.5 m depth. Locations of sampling quadrats were determined by driving a boat along the transect line and, using a depth finder (Hummingbird Wide 100 Portable) to establish sam-

pling stations, placing a weighted buoy in the water at appropriate depths. Quadrats were placed on the lakebed by anchoring the boat downwind of the buoys and, using SCUBA, lowering the quadrats off the north side of the boat adjacent to each buoy.

Dreissena colonies were videotaped by use of SCUBA and an underwater videocamera system. The system consisted of a high resolution black and white Sony camera (VCL-4800) and Sony 3.6-mm lens (VCL-SO3XM), housed in a waterproof case, and a Toshiba time-lapse S-VHS videorecorder (KV-6300A) operating at five frames per second. The videorecorder and camera were powered by a marine 12 V battery. A Sony Watchcam (EIA/CCIR) provided real-time observation on the boat. All video was recorded on S-VHS tape (ST-120; 3 M Corporation). The entire field sampling procedure was repeated on 12–19 August 1996, though only at two transect locations owing to time constraints. June and August samples were collected in the same vicinity, though exact transect positions varied slightly because our GPS unit was not equipped with differential capability.

Colonies were recorded during daylight hours by holding the camera 1-m off the lakebed. A numbered, white rectangular plate (90 cm²) was placed next to each colony for identification and to permit size calibration during subsequent image analysis. Video images were downloaded to a personal computer from the S-VCR using a Targa+ frame grabber. Colony images were then subjected to digital image analysis using Mocha 1.2 software (Jandel Scientific, San Raphael, CA). Three metrics were used to quantify mussel residency on soft sediments: the number of colonies m⁻² of lakebed, the surface area of individual colonies, and the proportion of lakebed covered by colonies in each quadrat. In determining the number of colonies per quadrat, we included all colonies that overlapped quadrat boundaries. In addition, if a colony overlapped quadrat boundaries, the entire colony was filmed and used to estimate the colony size–lake depth relationship. However, only portions of colonies within quadrat boundaries were included in assessments of total bottom coverage. Colony surface area appeared to be unrelated to colony volume because virtually all growth of colonies occurs in lateral directions (i.e. *x* and *y* planes).

Variation in colony density (colony number m⁻²), colony area and proportion coverage of lakebed by colonies, were separately analyzed using 3-way

ANOVA, with depth, transect number and study period (June, August) as categorical variables. Colony density and colony area were transformed as $\log(x + 1)$ prior to analysis to stabilize variance. Colony bottom coverage was transformed as arcsine squareroot proportion coverage prior to analysis. Because weather conditions varied between study periods, we also assessed whether an interaction existed between depth and study period for each of our colony metrics.

Species composition and size structure of mussel colonies were assessed by collecting three colonies from each of 5.5, 7.3 and 9.1 m depths. Differences among *D. polymorpha* and *D. bugensis* shell lengths in individual colonies were examined using paired *t*-tests, with Bonferroni-probability adjustments. Separate statistical comparisons were conducted for each depth.

Dreissena colony transplants

Two size classes of pizza pans (1257 cm² and 314 cm²) were used to collect eighteen large and eighteen small mussel 'colonies' at a deep site (9.1 m) adjacent to the transect sites where colonies were very large. After pans were placed under a large colony, colonies of the desired size were cut using a putty knife. Colonies and pans were stacked in water-filled 90-L PVC containers and brought to the surface. Six small and six large colonies were randomly selected and placed, without the pans, on soft sediment in a single line of uniform depth. Colonies were placed \approx 1.5 m apart, the order of which (large and small) was determined using a random number generator. This procedure was repeated at each of three depths (5.5, 7.3 and 9.1 m). Transplanted colonies were marked individually with rebars embedded vertically in sediment, 0.5 m on each side of each colony. Flagtape strips were added to rebar tips. Colony surface area and position relative to rebars were then recorded using the videocamera system. This procedure was carried out from July 10–22, 1996 and repeated August 6–19, 1996; inclement weather prevented SCUBA activities on August 18, thus duration of the transplant experiments differed by one day. Colonies were videotaped following 12 or 13 days' exposure to determine whether they were still in place, and whether their surface area had changed since deployment. Surface area was measured using image

analysis. We define colony destruction as removal of the entire colony from the filmed region. This definition seems suitable as colonies could rarely be located on sediment adjacent to the filmed zone. Moreover, it seems highly unlikely that voluntary movement by mussels could remove them from the filmed region because the mass burden imposed by colonial life exceeds the motility capability of individual mussels.

The proportion of large and small colonies destroyed during exposure was analyzed using ANOVA with colony size, transplant depth and date entered as categorical variables. The percentage colonies destroyed was standardized by dividing by the number of days of exposure (12 or 13). This value was then subjected to arcsine squareroot transformation prior to statistical analysis.

Current velocity was estimated 10 cm above the lakebed directly adjacent to the experimental transplant field. We attempted to measure velocity using dye flow fields, though these fields were too diffuse to allow accurate measurements. Thereafter we estimated velocity by displacement of near-neutrally buoyant fragments (≤ 0.10 g) of *Myriophyllum spicatum*. Velocity differences among depths were analyzed separately for each date using ANOVA and Bonferroni's multiple comparison tests. Measures of current velocity were made during relatively calm weather, though it is likely that velocity during storms is what potentially determines the fate of colonies on soft sediments.

Dreissena recruitment and sediment partitioning

We assessed the number of settling larvae and postmetamorphic *Dreissena* potentially available for recruitment because adult distributions of some invertebrates are affected by larval recruitment patterns (e.g. Gaines & Bertness, 1992). Potential recruitment was determined experimentally along the depth gradient by suspending white, nylon scouring pads (Halko Industries Ltd, North York, Ontario) 15-cm above the lakebed on 11 August, 1996. Two pads were suspended from each of four jumbo house bricks, and deployed at each of three depths (5.5, 7.3, and 9.1 m) adjacent to the experimental transplant field. Pads were 132 cm² in area and 0.7 cm thick, and were suspended in pairs above the bricks by small styrofoam floats with 9-kg monofilament line

(see MacIsaac, 1996b). Floats ensured that pads were exposed to water currents directly adjacent to the lakebed. Pads were retrieved following 7 days' exposure by use of SCUBA. To minimize loss of recruits on pads, sealable plastic bags were placed over individual pads and floats before monofilament lines from bricks were cut. Pads were floated into the inverted bags, which were then sealed and brought to the surface. Bag contents were preserved in 4% sugar-formalin solution. In the laboratory, mussel recruits were dislodged from pads by exposure to a strong current of tap water for 1 min per pad side (MacIsaac, 1996b). Dislodged recruits were retained on a 70- μ m sieve. Examination of rinsed pads under a dissecting microscope confirmed that all mussel recruits had been dislodged. Because large numbers of mussels settled on the pads, recruit number was estimated by three replicate subsamples, with replacement (MacIsaac, 1996b). Differences in recruitment across depths were analyzed using ANOVA and Bonferroni's multiple comparisons test. Recruitment (individuals cm⁻²) was log-transformed prior to analysis.

Mussel recruitment may be affected by substrate characteristics. We collected sediment from each sampling site by pushing a hand-coring device (98 cm²) 8–10 cm into the sediments at the locations where mussel colonies were transplanted. Sediment size composition was assessed in the laboratory using a series of sieves ranging between 4 mm and 90 μ m. This procedure involved mechanical agitation of 50 g of dried, animal-free sediment through stacked sieves for a 5 min period. Mass of sediment retained in each sieve was measured using a AND FX-200 digital electronic balance.

Invertebrate communities associated with Dreissena colonies

The relationship between mussel presence and invertebrate biodiversity was assessed by establishing a transect on July 31, 1996 along a soft sediment depth gradient off the south-east corner of North Bass Island. Invertebrate community diversity and abundance in *Dreissena* colonies with soft sediment were compared to values for soft sediment collected directly adjacent to the mussel colonies. Sampling was conducted at three depths (5.5, 7.3, 9.1 m) along the transect. Six colonies of various sizes were collected at each depth. In order to preclude con-

founding of colony area and distance from colonizing sources (MacArthur & Wilson, 1967), only those colonies that had approximately equal nearest-neighbour distances (30–50 cm) were collected; no isolated or highly clumped colonies were investigated. Thus, we have assumed biodiversity differences among colonies are related to depth or to colony area, and not to degree of colony isolation.

Prior to collection, mussel colonies were identified using numbered, white plates, and videotaped (as above). Whole *Dreissena* colonies were collected by positioning a large sealable freezer bag over the top of the colony. The identification plate, mussel colony, and 8 cm of sediment (collected by hand corer) from directly beneath the entire colony were placed in the bag. Bags containing colonies from each depth were then placed in a mesh bag and brought to the surface. At the surface, bags containing colonies were numbered, preserved in 4% sugar-formalin, and double bagged.

Colonies that were too large to fit into sealable bags were subsampled. Subsampling consisted of placing a subdivided 9-m² grid on top of the colony. Each segment of the grid was identified with a numbered plate and videotaped; area of each segment was subsequently determined using image analysis. Total colony area was established by summing values for each segment. Prior to collecting mussel colony subsamples, a random number generator was used to select nine points on the grid for subsample collections. Subsamples were collected by excising 98 cm² of colony and collecting 8 cm of sediment from below it with a hand corer. Species (taxon) richness and invertebrate abundances of each subsample were determined in the laboratory. Species (taxon) richness for whole colonies was determined by developing a saturation curve to describe the relationship between the number of non-redundant species (taxa) encountered in subsamples and the number of subsamples (ns) examined. Briefly, we used Bootstrap procedures to select subsamples for each of the one to nine subsample possibilities; the process was repeated ten times, with replacement. Results were subjected to non-linear regression analysis (species [taxon] richness = $22-5.243*ns^{-0.778}$; $r^2 = 0.80$) using Systat 7.0. We sampled large colonies using six subsamples; at this level of resolution, we expected to find 94% of the taxa in the colony. Colony diversity was therefore estimated as 106% of the value obtained from subsamples.

Invertebrates associated with mussel colonies were separated using a series of stacked sieves of mesh sizes 4 mm, 1 mm, 500 μ m, 250 μ m and 125 μ m. Contents retained on each sieve were further separated into dense and buoyant (i.e. animal and detritus) matter using the 'gold-panning' technique (Ciborowski, 1991), and placed into Petri plates. Invertebrates were sorted, identified and counted at 120 \times magnification using a dissecting microscope. No other clearing or preserving techniques was conducted on the invertebrate samples. Invertebrate classification was subject to the lowest possible taxonomic resolution for invertebrates preserved in 4% sugar-formalin. Invertebrates were identified using Merritt & Cummins (1995), Clifford (1991), Thorp & Covich (1991), Pennak (1989) and Witt, Hebert & Morton (1997). Hereafter all references to species or higher taxonomic levels are referred to as species (taxon) richness.

In addition to the six *Dreissena* colonies and associated sediments, we collected three sediment samples at each depth. All sediment samples were located adjacent to (< 1 m), but were free of mussel epi-bionts. Samples were collected with a hand-corer (98 cm²) to 8 cm depth. Taxa encountered in *Dreissena* colonies and in sediments are detailed in Appendix 1.

The relationship between species (taxon) richness and *Dreissena* colony area at different depths (5.5, 7.3, 9.1 m) was analyzed using ANCOVA, with colony area entered as a covariate. Both species (taxon) richness and colony area were log-transformed prior to analysis. The importance of mussel colony area and lake depth on total invertebrate abundance (excluding *Dreissena*) also was assessed using ANCOVA.

The importance of mussel colonies to benthic invertebrate communities at different depths was assessed by comparing species (taxon) richness on soft sediments with that on sediments and associated mussel colonies using 2-way ANOVA; substrate type (mussels vs. sediment) and depth were considered categorical variables. Richness values were divided by colony or sediment sample area prior to analysis. Likewise, total invertebrate abundance in soft sediment was compared to that in sediment and mussel colonies, at different depths, using 2-way ANOVA. *Dreissena* abundance and diversity (2 species) were excluded from consideration in both analyses. Invertebrate richness and total abundance were log-transformed prior to analysis to stabilize variance.

Results

Mussel distributions, vulnerability to disturbance, and recruitment

Dreissena distribution on soft sediments varied spatially, and, to a lesser extent, temporally (Fig. 1). Mussel colonies were never found on soft sediments in very shallow (< 3.5 m) water. Colony number was lowest at the shallowest (3.5, 4.5 m) and deepest (7.5, 8.5 m) sites, and greatest at mid-depths (5.5, 6.5 m). Mean colony area at different depths ranged from 7 to 1713 cm² in June, and 14–2150 cm² in August. The number of mussel colonies m⁻² differed among depths ($F = 4.85$, d.f. = 5,16, $P = 0.007$; Fig. 1a), but was independent of study period, transect surveyed and a depth by study period interaction ($P \geq 0.32$). Likewise, mean colony size (Fig. 1b) and proportion of bottom substrate inhabited by *Dreissena* colonies (Fig. 1c) were influenced only by depth ($P = 0.02$ and $P = 0.001$, respectively). Colony area tended to be highest at 6.5 and 8.5 m, though variation was very high even at these depths. Colonies at 7.5 m were very small during both surveys, indicating substantial 'local' effects. The effect of depth varied slightly

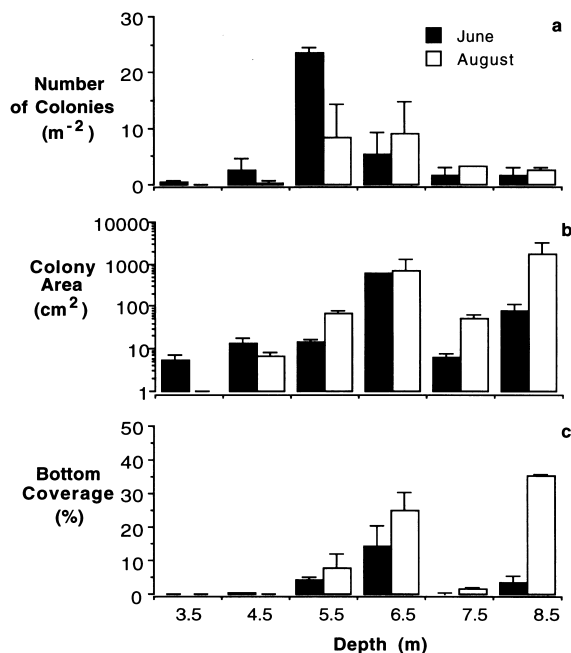


Fig. 1 Mean (+ SE) number of *Dreissena* spp. colonies m⁻² (a), area of individual colonies (b) and percentage bottom coverage (c) as a function of depth, for June and August 1996 surveys.

across time periods, though these interactions were not significant with respect to influence on mean colony size or percentage of sediment covered by mussel colonies ($0.064 < P < 0.072$). However, colonies tended to be larger and occupy a greater percentage of soft sediment in August than in June.

Mussel colonies were dominated (88%) numerically by *D. polymorpha* at all depths (Table 1). However, *D. bugensis* was significantly larger than *D. polymorpha* at each of the depths examined (paired *t*-tests, $P \geq 0.009$; Table 1). Consequently, the biomass contribution of *D. bugensis* would be much greater than its numerical contribution to mussel colonies.

Destruction of transplanted *Dreissena* colonies was related to depth and mussel colony size. The percentage of colonies destroyed per day was significantly lower at 9.1 m than at either of the shallower depths ($P = 0.003$; Fig. 2). Larger colonies were also less vulnerable to destruction than smaller ones ($P = 0.017$). Only 17 of 36 colonies that were deployed during July were recovered. Of those that were recovered, area declined across all depths, with losses ranging from 16% to 96%. Colony destruction rate was slightly but insignificantly lower during the transplant experiment conducted in August ($P = 0.159$), when 23 of 36 colonies survived transplant. Mean area of colonies that survived transplant at 5.5 and 9.1 m increased between 15 and 49%, while area of large and small colonies deployed at 7.3 m declined 79 and 86%, respectively. Patterns of colony destruction and changes in colony area during the two experimental periods correspond with milder weather during August than during July (Fig. 3).

Current velocity differed significantly between depths for both August periods (ANOVA, $P < 0.001$; Table 1). Current velocity was always highest at 7.3 m and lower at both 5.5 and 9.1 m sites (Bonferroni comparisons, $P = 0.01$).

Dreissena recruited rapidly on scouring pads deployed off the shore of North Bass Island during August, though differences among depths were evident. In contrast to mussel colony distributions, recruitment was higher at 5.5 m than at 7.3 and 9.1 m (Bonferroni test; $P = 0.01$; Table 1).

Recruitment patterns are consistent with assessments of sediment suitability for settlement. Sediment particle size typically decreased with increasing depth (Fig. 4). Shallow sites tended to have more coarse and less fine (< 125 μ m) sediment than deeper sites,

Table 1 *Dreissena* colony attributes and physical characteristics of study sites in Lake Erie. Area-adjusted species (taxon) richness and total density of invertebrates living in soft sediments or in association with mussel colonies and soft sediments. All values are mean (SE)

		Depth (m)		
		5.5	7.3	9.1
Species Composition	<i>D. polymorpha</i>	95 (1.3)	94 (3.0)	88 (3.5)
	<i>D. bugensis</i>	5 (1.3)	6 (3.0)	12 (3.5)
Mussel Size (mm)	<i>D. polymorpha</i>	12.5 (0.6)	12.7 (0.6)	11.2 (0.3)
	<i>D. bugensis</i>	24.2 (1.7)	20.8 (1.0)	19.8 (1.1)
Recruits (Indiv. cm ⁻²)	<i>Dreissena</i> spp.	5.9 (0.7)	3.9 (0.3)	1.7 (0.4)
Species (taxon) Richness (cm ⁻²)	Sediment	0.07 (0.00)	0.06 (0.00)	0.06 (0.01)
	Sediment + <i>Dreissena</i>	0.44 (0.09)	0.43 (0.18)	0.28 (0.10)
Invertebrate Density (Indiv. cm ⁻²)	Sediment	3.5 (1.2)	3.1 (0.7)	2.0 (0.4)
	Sediment + <i>Dreissena</i>	8.3 (2.8)	6.3 (1.2)	6.8 (1.5)
Current Velocity (cm s ⁻¹)	August 1	4.5 (0.4)	8.2 (0.4)	1.6 (0.4)
	August 12	1.4 (0.2)	4.4 (0.3)	3.2 (0.1)

particularly at the deepest site (8.5 m), and should have been more suitable for mussel settlement.

Invertebrate communities associated with *Dreissena*

Invertebrate species (taxon) richness in *Dreissena* colonies was related to colony area ($F = 13.05$, d.f. = 1,14, $P = 0.003$; Fig. 5) but not to lake depth ($F = 1.37$, d.f. = 2,14, $P = 0.873$). The highest richness

(22 taxa) was observed in the largest *Dreissena* colony surveyed (62 257 cm²), while the lowest richness (8 taxa) was observed in the smallest colony (8 cm²). The species (taxon) richness – colony area relationship revealed that even the smallest islands were expected to contain invertebrates in addition to *Dreissena* (Fig. 5a).

Total invertebrate abundance, excluding *Dreissena*, was also related to *Dreissena* colony area ($F = 180$, d.f. = 1,14, $P < 0.001$; Fig. 5b) but not to lake depth ($F = 0.05$, d.f. = 2,14, $P = 0.951$). Patterns of inverte-

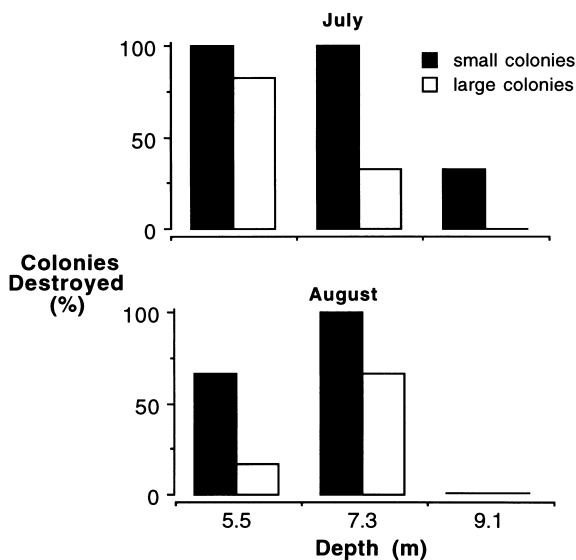


Fig. 2 Destruction of small and large *Dreissena* colonies transplanted during July and August 1996 in relation to depth. Colonies were deployed for 12 and 13 days, respectively.

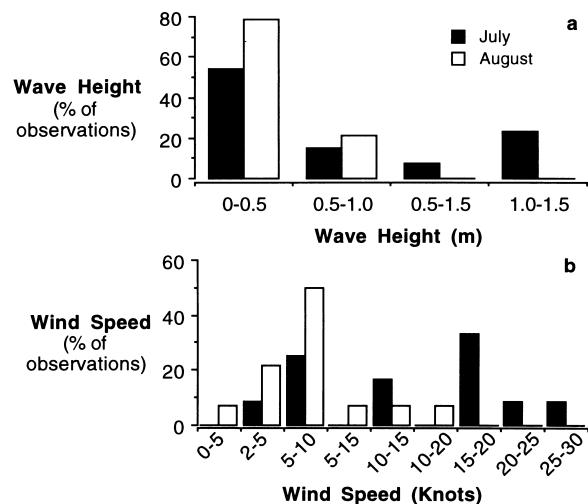


Fig. 3 Wave height (a) and wind speed (b) distributions at the study site during July and August periods that transplanted colonies were exposed.

brate abundance parallel those in *Dreissena* colony size. Mussel colonies at 5.5, 7.3 and 9.1 m averaged 51 (SE = 19), 8819 (8761) and 10437 (10363) cm², respectively; mean invertebrate abundances in *Dreissena* colonies and sediment at these sites were 365 (SE = 121), 41225 (40879) and 25547 (25118) individuals per colony. Variation in both colony size and invertebrate abundance at 7.3 and 9.1 m sites resulted from inclusion of one large colony at each depth. A recurrent group of invertebrates dominated samples collected at each depth. This group included the amphipods *Gammarus fasciatus* Say and *Echinogammarus ischnus* Stebbing, cyclopoid copepods, ostracods, oligochaetes, chironomids, the hydrozoan *Hydra*, and the planarian flatworm *Dugesia*. Densities of *Hydra* and *Dugesia* tended to be higher at greater depths and in larger *Dreissena* colonies. Abundances of *G. fasciatus*, oligochaetes and ostracods increased in relation to *Dreissena* colony area. All three groups were more abundant in large *Dreissena* colonies than in smaller ones. *E. ischnus* and cyclopoid copepod densities varied by neither depth nor mussel colony area.

Presence of *Dreissena* colonies had a marked effect on species (taxon) richness and abundance of benthic invertebrates (Table 1). For example, species (taxon) richness was influenced by the presence of mussels ($F = 10.9$, d.f. = 1, 23, $P = 0.003$), but not by lake depth ($F = 0.5$, d.f. = 2, 23, $P = 0.610$). Species richness values were 616, 703 and 462% higher in mixed

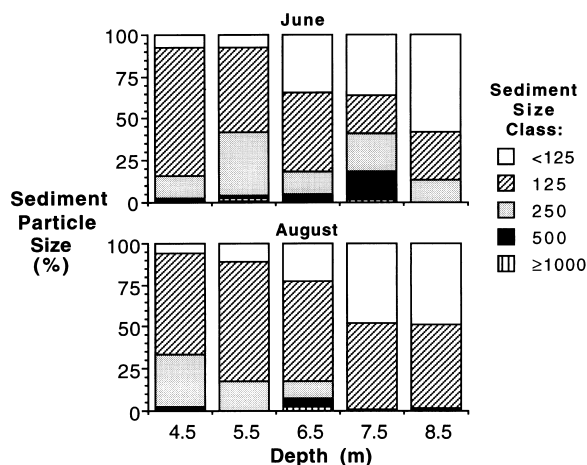


Fig. 4 Sediment particle size composition during June and August, in relation to depth. Samples were collected adjacent to the site where survey and experimental transplants were conducted.

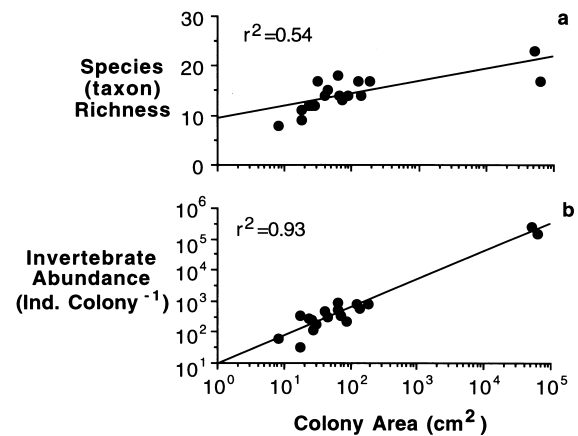


Fig. 5 Invertebrate species (taxon) richness (a) and total invertebrate abundance (b) (Individuals colony⁻¹) in relation to *Dreissena* colony area.

Dreissena colony – soft sediment habitat than in sediment alone at 5.5, 7.3 and 9.1 m, respectively (Table 1). Taxa found in *Dreissena* colonies but not in sediment included *Gammarus* and *Echinogammarus*, *Hydra*, *Dugesia*, Hirudinea (leeches), Zaitzevia (beetles), Hydropsychidae (caddis flies), Asselidae (isopods), and gastropods. As with species (taxon) richness, area-adjusted total invertebrate density, excluding *Dreissena*, was also related to the presence of *Dreissena* ($F = 10.2$, d.f. = 1, 23, $P = 0.004$) but not to collection depth ($F = 0.2$, d.f. = 2, 23, $P = 0.814$). Mean invertebrate density (individuals cm⁻²) was 239, 202 and 335% higher in *Dreissena* colony – soft sediment habitat than in soft sediment at 5.5, 7.3 and 9.1 m, respectively (Table 1). Taxa that exhibited the largest increases to the presence of *Dreissena* included *Gammarus*, oligochaetes and ostracods. Effects of mussel colonies were depth-dependent for some species. For example, increases in density of *Hydra* and *Dugesia* were limited to mussel colonies in deeper water. Interactions between mussel colony presence and depth may relate to changes in sediment characteristics. For example, the percentage of fine sediment (< 125 mm) was much lower (9.8%) at 5.5 m than at either 7.3 (27.5%) or 9.1 m (53.4%) depth.

Discussion

Physical disturbance has strong influences on species composition and community structure in many ecosystems. Physical disturbance associated with waves strongly affects invertebrate community com-

position in coastal zones of the Laurentian Great Lakes. Barton & Hynes (1978a,b) determined that fauna in wave-swept littoral regions of these lakes were characteristic of rivers, while taxa at less exposed sites were more representative of lake fauna. Studies of physical disturbance effects on benthic communities have been conducted primarily on marine ecosystems (Suchanek, 1981; Denny, 1995). Nehls & Thiel (1993) reported that severe storms destroyed 45 of 94 *Mytilus edulis* L. populations in the Wadden Sea, and that surviving colonies were found mainly in protected areas. Results from this study illustrate that *Dreissena* forms mixed-species colonies on soft sediment in Lake Erie even in relatively shallow (> 3.5 m) water. The distribution, size and aerial coverage of these colonies are, however, strongly related to lake depth and to the disturbance regimes that vary by depth. Examination of mussel colonies revealed that many lacked stones or pebbles that could serve as 'condensation nuclei' for growing mussel colonies. Rather it appears that shells of initial settlers may serve this function.

Earlier work established that distribution and abundance of *D. polymorpha* at shallow (0.8–2.8 m), rocky habitat in Lake Erie were also influenced by wave disturbance (MacIsaac, 1996b). Thus, wave disturbance affects distribution of *Dreissena* on both hard and soft substrates. However, because holdfasts for byssus attachment are scarce or absent on soft sediment, mussels can be dislodged more readily and are less likely to be found in wave-swept environments dominated by soft than by hard substrates. As evidence, we found an average of 70–482 mussels on individual rocks collected in nearshore, rocky habitat between 1.5 and 2.8 m depth (MacIsaac, 1996b), but never observed mussels on soft substrate in water less than 3.5 m depth in this study. Mussel colonies were first observed at \approx 3.5 m depth. These colonies were very small and typically occurred in small bowls or depressions in the sediment, apparently as a result of rolling on the bottom (Botts *et al.*, 1996).

Destruction of transplanted colonies was not a simple function of site depth. Although destruction rate was always lowest at the deepest site, the 7.3 m site had the highest values during August. Measurements of current velocity directly adjacent to the lakebed were also highest at this depth. All metrics of colony size in the population survey were also low or lowest at 7.5 m. Thus colonies at intermediate depth

appeared most vulnerable to disturbance associated with storms. We were unable to measure current velocity during the most ecologically meaningful time (i.e. during storms), though the depth contour in the channel between North Bass and Middle Bass Islands suggests that shear forces on the lake bed may be greatest at mid-depth. Reusch & Chapman (1997) also reported that patch area of *Mytilus* colonies on soft sediments in the western Baltic Sea was related to depth and presence of predators. While we cannot eliminate the possibility that predators (e.g. crayfish, fish, ducks) influenced mussel populations in this study, the close proximity of the sites at different depths suggests that predators should have had equal access to colonies throughout the study zone. It is unclear what happened to mussel colonies that were removed from sites of transplantation. Reusch & Chapman (1997) speculated that drift of dislodged colonies represented a primary mode of patch dispersal to new soft sediment habitats.

Facilitation of benthic invertebrates by mussels

Simberloff & Wilson (1969) regarded islands as patches of good habitat isolated by relatively inhospitable terrain. Mussel colonies may be considered biological 'islands' that provide refuge and or food resources for benthic invertebrates. Botts *et al.* (1996) demonstrated experimentally that *Dreissena* benefit amphipods, turbellarians, hydrozoans and oligochaetes by enhancing habitat structure, while chironomids apparently benefit from increased food supply. Likewise, Stewart *et al.* (1998) illustrated that amphipods, turbellarians and hydrozoans responded mainly to habitat structure, while *Microtendipes* chironomids and *Physella* gastropods responded to both food supply and habitat. Variability within treatments tended to be high in the latter study, potentially obscuring the role of food in facilitating invertebrates beyond the effect caused by increased habitat availability or complexity. For example, oligochaetes appeared to benefit from enhanced habitat and food supply, though responses were nonsignificant (Stewart *et al.*, 1998). González & Downing (1999) also determined that amphipods responded primarily to enhanced habitat structure associated with *Dreissena* colonies. Considering that amphipods (*Gammarus*, *Echinogammarus*), hydrozoans (*Hydra*), turbellarians (*Dugesia*) and oligochaetes

benefited most in this study, natural responses by Lake Erie taxa to invasion of soft sediment by *Dreissena* appear to be related principally to enhanced habitat structure.

Benthic invertebrates have also benefited from *Dreissena* invasion in eastern Lake Erie, Lake St. Clair and Lake Ontario (Dermott *et al.*, 1993; Griffiths, 1993; Stewart & Haynes, 1994). Dreissenid mussels account for more than 90% of biomass and production of benthic invertebrate communities in eastern Lake Erie, though total abundance of other invertebrates has also increased dramatically since mussels invaded the lake (Dahl *et al.*, 1995). However, Griffiths (1993) cautioned that some changes in invertebrate densities in Lake St. Clair may have resulted from long-term variation in water quality rather than invasion by *Dreissena*. Nevertheless, patterns established from numerous lakes invaded by *Dreissena* indicate a general, positive response by benthic invertebrates.

Marine studies provide complementary examples of facilitation of benthic invertebrates by mussel beds (Gunther, 1995; Seed, 1996; Svane & Setyobudiandi, 1996). For example, *Semimytilus* and *Perumytilus* mussels provide coarse-grained habitats and support high abundances of polychaetes in intertidal habitats in Peru (Tokeshi, 1995).

Benefits of mussels to invertebrates may depend on the size of mussel beds. Tsuchiya (1980) demonstrated that larger *M. edulis* colonies provided more microhabitats for invertebrates than smaller mussel beds. Likewise, macroinvertebrate diversity was positively associated with the size of bivalve (*Brachidontes*) colonies (Peake & Quinn, 1993). In this study, ostracods, oligochaetes and amphipods had higher densities in large mussel colonies than in smaller ones. Larger, more stable colonies may provide more complex structures, sediment or other debris that could be exploited by invertebrates (Seed, 1976, 1996; Tsuchiya, 1980). Alternatively, higher invertebrate diversity and population abundances in larger colonies may relate to colony age or to the duration it has been resident at a site. For example, older *Mytilus* colonies support higher levels of invertebrate species diversity than do younger colonies (Suchanek, 1978, 1985; Tsuchiya & Nishihira, 1985, 1986; Gunther, 1995). However, we found no evidence that smaller colonies were comprised of smaller and, presumably, younger mussels. Because smaller mussel colonies are more vulnerable to displacement than larger ones,

they may have been resident at a site for a shorter period.

Disturbance limits mussel facilitation

By limiting the distribution of *Dreissena* colonies, disturbance appears to indirectly affect the diversity of benthic communities and abundances of individual species (Fig. 2; Table 1). Turner *et al.* (1995) observed that benthic invertebrates were adversely affected when unstable *Mytilus* colonies were displaced by wave-associated disturbance. Gunther (1995) reported that diversity and abundances of invertebrates declined after storms dislodged *M. edulis* colonies on an intertidal sandflat.

The fate of displaced *Dreissena* colonies is not clear, though they may have been buried by settling inorganic sediments, transported to adjacent areas, or physically destroyed. Burial of mussels on soft sediments has been reported in marine systems (e.g. Reusch & Chapman, 1997). Renaud *et al.* (1997) observed that *M. edulis* occupying an artificial substrate below its natural distribution limit was buried by organic and inorganic sediment. Western Lake Erie is a relatively shallow basin with a mean depth of 7.3 m. Intense storms resuspend large quantities of sediment that could bury mussel colonies. However, the rapid recovery of mussel colonies during summer 1996 following an intense storm during autumn 1995, indicates that mussels likely repopulated the area by immigration of adult individuals or colonies rather than by larval settlement or postlarval drift (Gunther, 1995; Reusch & Chapman, 1997). Recolonization by adults is also suggested by size distributions of mussels recovered during 1996. Many *D. polymorpha* and *D. bugensis* individuals surveyed in colonies during summer 1996 were 10 mm or larger, indicating that they probably were not young-of-year mussels.

In contrast to the relatively persistent *Dreissena* colonies that occur on rocky substrates in Lake Erie, density and size of colonies on soft sediments exhibited substantial temporal variability. Because invertebrate diversity and total abundance were higher in the presence of mussels than in adjacent soft sediments, seasonal variation in mussel residency on soft sediments may influence local invertebrate diversity and abundance. Peake & Quinn (1993) also observed strong seasonal shifts in species diversity within mussel colonies. It remains unclear whether

the presence of *Dreissena* in basins with soft sediments results in an overall increase in invertebrate abundance, or simply results in seasonal 'focusing' of invertebrates to mussel colonies.

In summary, *Dreissena* may colonize soft sediments in relatively shallow water, though wave-associated disturbance affects the spatial distribution and size of colonies. Pronounced differences exist with respect to the density, size and spatial coverage of mussel colonies on soft sediments. Because mussel beds are strong facilitators of other benthic invertebrates, storms that destroy mussel beds also impact the diversity and abundance of benthic communities on soft sediments.

Acknowledgments

We thank R. Coulas, S. Roe, B. Ray, T. Mabee and K. Uriarte for SCUBA and field assistance. Logistical support was provided by staff of the Theodore Stone Laboratory, western Lake Erie. We are grateful to Dr Keith Bedford, Ohio State University, for permission to use archived weather data (<http://superior.eng.ohio-state.edu>). Thoughtful comments by two reviewers and C. Townsend improved the manuscript. This study was supported by research and equipment grants from NSERC, and by Environmental Youth Corps grants from the Ontario Ministries of Natural Resources and Environment, to HJM.

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(Manuscript accepted 20 July 1999)

Appendix 1 Lists of invertebrate taxa encountered amongst *Dreissena* colonies and in soft sediments. Species abundance codes, based on abundance in samples: * = absent, 1 = rare (< 5%), 2 = common (5–10%), 3 = dominant (> 10%)

Species (taxon)	Abundance in <i>Dreissena</i> colonies	Abundance in soft sediments
<i>Gammarus fasciatus</i>	3	*
<i>Echinogammarus ischnus</i>	1	*
<i>Hydra</i> sp.	1	*
Oligochaeta	3	2
Nematoda	1	3
<i>Dugesia</i> sp.	1	*
Hirudinea	1	*
Chironomidae	1	1
Cyclopoida	2	3
Calanoida	2	2
Harpacticoida	1	2
Ostracoda	2	3
Hydrobiidae	1	*
<i>Physa</i> sp.	1	*
Valvata	1	*
Ferrissa	1	*
Zaitzevia	1	*
<i>Hexagenia limbata</i> Serville	1	*
Hydropsycidae	1	*
<i>Oecitis</i> sp.	1	