EXOTIC INTERACTIONS: ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) SURVIVAL, SETTLEMENT, AND GROWTH IN THE BEDS OF NONNATIVE WATER CHESTNUT (*TRAPA NATANS*) VERSUS NATIVE WATER CELERY (*VALLISNERIA AMERICANA*) IN THE HUDSON RIVER

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Abstract. Both the zebra mussel (*Dreissena polymorpha*) and water chestnut (*Trapa natans*) have had profound effects on the Hudson River since their invasions, and their influences on the indigenous system have been well documented. How they may relate to one another, however, is less known. This project sought to determine if growth, survival, and/or settlement of the zebra mussel are higher in *Trapa* stands than in beds of the native water celery (*Vallisneria americana*). Dissolved oxygen levels were significantly lower (6.5 ± SE vs. 8.1 ± SE) in *Trapa* than *Vallisneria*, but several measures of food availability did not differ between vegetation types. Mussels placed in four pairs of *Trapa* and *Vallisneria* sites showed lower survivorship in *Trapa*, and there was a trend towards greater settlement of new mussels in beds of *Vallisneria*. These results suggest a negative interaction between these two invasive species.

INTRODUCTION

In the freshwater tidal Hudson River, two nonnative species—the zebra mussel and Eurasian water chestnut—have profoundly changed ecosystem dynamics and become subjects of great scientific concern since their arrival and establishment in the 20th century (Strayer et al. 1999, Caraco et al. 2000, Strayer, Hattala, and Kahnle 2004). The two species exert remarkably similar effects on the Hudson, via different mechanisms, and have collectively cost industry and municipalities billions of dollars in removal costs nationwide. Yet, the connection between them has not been thoroughly explored. Invasion biology typically examines the effects of a nonnative on an indigenous system. Because ecological invasions are not isolated phenomena, to study concurrent exotics' influence on each other is also imperative.

The zebra mussel (*Dreissena polymorpha*), a colonial bivalve that creates dense aggregations on natural and manmade surfaces, arrived in North America from eastern Europe in the late 20th century in freight ballast water and subsequently has spread throughout the Great Lakes and major United States watersheds. The tidal Hudson River was invaded in May 1991, and since September 1992, the zebra mussel has become one of the most influential organisms in the Hudson, reaching average densities of 2000 individuals per square meter (Strayer 1999).

Purposefully introduced to New York State, the Eurasian water chestnut (*Trapa natans*, hereafter referred to as *Trapa*) entered the Hudson watershed in 1879 and spread into the river itself after the 1930s. The aquatic plant is distinguished by its sharp, four-pointed nuts and floating rosette leaves, which form a dense mat on the water's surface and consequently shade out native submerged aquatic vegetation (SAV). Nuts prove a hazard to swimmers and rosettes obstruct waterways; at one time, one of the major ingredients the infamous Agent Orange herbicide was employed to curb this plant's expansion (Hummel 2004).

At first, the impacts of *Trapa* may seem counterintuitive to the survival of the zebra mussel. Dense patches of the water chestnut's floating rosettes are capable of intercepting over 99% of incident sunlight (Caraco and Cole

2002). Thus, they may consequently displace other, submerged, macrophytes and phytoplankton (the zebra mussel's food source) by creating atypically dark conditions in the water column. Because *Trapa* leaves lie at the air-water interface, photosynthetic oxygen is vented to the atmosphere, and the oxygen used by underwater *Trapa* respiration is hence not replaced. Hypoxic or anoxic conditions that may be detrimental to sensitive fish or invertebrates may therefore result (Caraco and Cole 2002). Some patches of water chestnut in the Hudson continue to grow in area, replacing formerly dominant vegetation, primarily *Vallisneria* (Strayer et al. 2003, Nieder et al. 2004, Strayer, Hattala, and Kahnle 2004).

The zebra mussel, however, has exerted remarkabe effects on the Hudson River similar to those of *Trapa*. Phytoplankton and small zooplankton populations have fallen by 80-90% as a result of the mollusks' filter feeding (Strayer et al. 1999), and a decline in dissolved oxygen has been attributed to this organism because of its high respiratory demand (Caraco et al. 2000). Synergistic relationships between *Trapa* and *Dreissena* in terms of phytoplankton and oxygen depletion, however, have not been examined, although diminished impacts on phytoplankton and fish are seen southward of river kilometer 100, beyond the ranges of the greatest mussel and *Trapa* abundance (Walton 1996, Nieder et al. 2004).

That *Trapa* serves as zebra mussel habitat in the Hudson has been established. A survey by Strayer et al. (2003) compared the benthic and epiphytic invertebrate communities supported by *Vallisneria* and *Trapa* beds at Cruger Island and Esopus Meadows. The highest densities of zebra mussels were found to exist on the benthos of *Trapa* habitat, with *Trapa* supporting higher invertebrate density and comparable diversity to *Vallisneria* overall (although community structure was different).

The reason behind the trend in zebra mussel abundance documented by Strayer et al. is unknown, although the provision of higher standing substrate biomass could be an influential factor (Caraco and Cole 2002). One unverified explanation is that the mussels' preference for habitat is, at least to some degree, influenced by the availability of light. Several studies have demonstrated the zebra mussel to be strongly photophobic (Zhang, Stevens, and Wong 1998, Kobak 2001, Toomey, McCabe, and Marsden 2002). In laboratory experiments, zebra mussels exhibit strong negative phototaxis and grow faster in dim, sheltered conditions. Zhang, Stevens, and Wong (1998) even recommend that illumination be considered as a deterrent mechanism to zebra mussel settling.

The habitat characteristics created by *Trapa* have been shown to vary considerably from those provided by the dominant native form of submerged aquatic vegetation (SAV), water celery (*Vallisneria americana*). These characteristics may also strongly influence the habitat preference of zebra mussels. For this project, the impact of the differing plant beds on light availability, dissolved oxygen (DO), particulate matter, chlorophyll *a* concentrations, and zebra mussel survival, growth, and settlement were examined.

To test the influence of the two vegetation types on the zebra mussel, this project developed according to the following three hypotheses: (1) The growth, survival, and/or settlement rates of zebra mussels are higher in *Trapa* beds; (2) These rates are lower in *Trapa* beds; or (3) There is no difference between the two vegetation beds in terms of these rates, the null hypothesis.

Study Area

I used 1997 GIS data and 2002 aerial photos to select four pairs of nonnative *Trapa* and native *Vallisneria* beds in the Hudson: three pairs were small to medium-sized, but I also chose one large pair to serve as a case with extreme conditions (Table 1). Any characteristics typical of the vegetation type presumably would be magnified with the bed size. According to Hummel (2004), however, turbidity, dissolved organic carbon, nitrate, ammonium and phosphate are not significantly affected by *Trapa* bed size.

METHODS

Mussels were detached from rocks collected by a professional diver on 20 June from the Hudson at the following locations: Poughkeepsie, Port Ewen, Stuyvesant, Castleton, Stockport, Coxsackie, and Albany. They were refrigerated temporarily in damp paper towel and then transferred to tubs containing aerated water from the Hudson and Wappinger Creek. Between 65 and 100 mussels, measured to 0.1 mm with calipers, were placed in each of 8 plastic mesh bags containing a small chain of ~2.5 cm^2 plastic tiles. Mesh bags were closed with monofilament and deposited in each vegetation bed on 6 July 2005 to remain in the field for a duration of 27 days. Bags were suspended about a half-meter above the substrate from platforms (based on a model used by Findlay, Schoeberl, and Wagner [1989]) that were equipped with eight ceramic tiles also seeded with zebra mussels.

Dissolved oxygen readings were taken at the sites on approximately a weekly basis, along with water samples that I filtered back at the lab to measure chlorophyll *a*, suspended matter, and organic matter concentration. Light meters were left in the field for about one week to continuously record the light conditions.

Some platform tiles were collected from the field after a period of 13 days for visual examination. At the end of 27 days, the mussels contained in the mesh bags were brought back from the Hudson and remeasured. I also examined the bags themselves and all of the mussels within them (live or dead) for new settlers under the stereoscope. ANOVAs (Analyses of Variance) were performed using STATISTICA software.

RESULTS

Habitat Characteristics

As established by other researchers, dissolved oxygen concentrations were found to be significantly lower in the exotic *Trapa* beds compared to *Vallisneria*. The size of the bed seems to influence the relationship dramatically, for when Inbocht and Cheviot (the largest beds) are considered, the statistical significance of the difference between vegetation is greater: $p = 0.00593$, as compared to $p = 0.0139$ when they are removed from the analysis (Figure 1). Because DO measurements were always made at flood tide, mean concentrations are shown greater than 5 mg/L. They do not reflect, therefore, the extreme oxygen deprivation (and perhaps even anoxia) mussels actually experienced in the *Trapa* beds at low tide during the experiment (documented by Caraco and Cole 2002).

ANOVA revealed no significant relationship between vegetation type and either chlorophyll *a* concentration or total suspended matter concentration. Organic matter was found to be significantly higher in *Trapa* only when the largest beds were not considered: among the small beds, ANOVA shows the relationship between the concentration of organic matter and the vegetation type to be significant, with *Trapa* containing the greater density of organic matter ($p = 0.00583$). Yet, when the large beds are included in the analysis, the relationship becomes insignificant ($p = 0.91758$). The cause of this phenomenon is uncertain.

Suspended matter concentrations were found to not relate to vegetation type, whether or not the largest beds were included in the analysis (included, $p = 0.233$; excluded, $p = 0.115$). However, visual analysis of tiles brought back from the field on 19 July revealed that platforms in *Trapa* beds remained clear of sediment, while tiles in *Vallisneria* beds (especially those from Bridge and Cheviot sites) were heavily fouled with fine sediment, and consequently harbored populations of burrowing midge larvae.

Results from the measurement of light levels proved inconclusive. The total light detected by the light meters on three reference days was very similar among the vegetation types. Yet many factors (including weather and tide) may have affected these results in unforeseen ways, and therefore I do not believe that the data collected truly reflects the actual pattern of light penetration in *Trapa* and *Vallisneria*. It would seem, though, that light is not as major a player in the survival of the zebra mussel in the Hudson as I had previously supposed, since light readings for the native *Vallisneria* were lower than expected.

Survivorship

Mussel survivorship was calculated as the ratio of the number of living mussels recovered in mesh bags from experimental sites to the number of mussels initially placed in those bags. Survivorship ranged from 28.8% to 44.9% and was greatest overall in *Vallisneria* sites. With the large beds included in the analysis, the link between zebra mussel survivorship and vegetation type is statistically significant (ANOVA, $p = 0.0399$). The large beds seem to drive this relationship, for when they are removed from consideration, the relationship becomes statistically insignificant ($p = 0.192$). The largest *Trapa* bed and largest *Vallisneria* bed were at opposite ends of the data spectrum, with the largest nonnative bed, Inbocht, having the lowest survivorship (28.8%) and the largest native bed, Cheviot, having nearly the highest (43.0%) (Table 2, Figure 2).

Comparison of dissolved oxygen and mussel survivorship yields a pattern of overall higher survivorship occurring with higher levels of dissolved oxygen. The correlation between survivorship and DO (including the large beds in the analysis) tends toward significance ($p = 0.072$), although with more experimentation, I believe the connection here would only be strengthened. Since zebra mussels have been shown to have a high oxygen demand (Caraco et al. 2000), it seems logical that their survival in the two vegetation types could be oxygen-limited (Figure 3).

No significant correlations were found between survivorship and chlorophyll *a*, organic matter, or suspended matter levels ($p = 0.533$, $p = 0.771$, $p = 0.895$, respectively).

Settlement

I also found zebra mussel settlement to be related to vegetation type, with higher numbers of settlers found in the native *Vallisneria.* A Wilcoxon test gauging the link between settlement and vegetation type yielded a p value of 0.057, indicating that with further experimentation, a more statistically convincing relationship may be found between zebra mussel settlement and *Vallisneria*.

As also exhibited by survivorship data, the two largest vegetation sites are at the extreme ends of the spectrum, with zero settlers found in the mesh bag from the largest nonnative bed and the most settlers (37) found in the largest native bed (Table 3). Settlement was not statistically correlated with any habitat characteristics, although there was a weak association with DO ($p = 0.066$).

Growth

No significant relationship was found between the change in median shell length within mesh bags and the vegetation type in which the bags remained for 27 days. The size distribution of the mussels before they were deployed places most individuals in the 5-10 mm size class, with the median at about 13. At the end of the field trial, the size distribution of the mussels is nearly indistinguishable between vegetation types (Figure 4). In both the exotic and native beds, most mussels were in the 10-15 mm size and the overall median did not change, although histograms of post-deployment mussels better fit the expected normal curve. I cannot be certain of the causes of mortality (upon inspection during remeasurement, the smallest and largest individuals seemed to have experienced the most death), and so these data neither support nor contradict the hypothesis that mussel growth rates differ between the two main vegetation types. With a longer field duration and higher numbers of specimens, the results may be more convincing.

DISCUSSION

The findings of this study appear to support hypothesis 2. I found zebra mussel survivorship and settlement to actually be lower in beds of the exotic water chestnut. This trend seems to be associated with the availability of dissolved oxygen, but I cannot assume that the relationship is cause/effect. The native water celery (*Vallisneria*) tends to consistently have higher oxygen supplies, and the zebra mussel has been known to require a great deal for its metabolism (Caraco and Cole 2000, 2002). The high oxygen demand of the mussel would presumably make *Vallisneria* a preferred mussel habitat to *Trapa*.

Yet, this experiment does not recreate natural conditions since mussel specimens were not permitted to choose their habitat. It is possible that *Trapa* may still indeed be attractive habitat due to its provision of shadowed, abundant, and stable substrate. The needs for space, food, DO, and light may all interact to dictate the attractiveness of this vegetation.

Hypoxia in some *Trapa* beds (or at least their edges) may also be ameliorated by the influx of oxygen-rich waters from exterior *Vallisneria* beds during flood tide (S.E.G. Findlay, personal communication). This spatial arrangement of beds and resulting DO exchange could make *Trapa*, or at least those beds of a small or moderate size, a more attractive habitat to oxygen-sensitive organisms than supposed.

Because of the complexity of the Hudson's ecosystem dynamics, on both the large and small scale, comprehension of the interactions between concurrent exotics is imperative for truly understanding how invasions contribute to chemical and food web alterations. The conduction of surveys akin to that performed by Strayer et al. (2003) in more sites across a greater number of beds, and including DO assessment, would better gauge the actual numbers of mussels attached to *Trapa* or *Vallisneria* leaves across the freshwater tidal Hudson. Experiments that follow up those conducted by Kobak (2001) and Toomey, McCabe, and Marsden (2002) to determine the light tolerance threshold of the zebra mussel would also provide insight into the contribution of darkness to the habitat selections made by this species.

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APPENDIX

TABLE 1. Size, species, and location of experimental vegetation beds in the Hudson River

Assigned Bed Name	Vegetation Type	GPS coord. (UTM, NAD83)	Area (m^2)
Inbocht Bay	*Trapa natans*	591424, 4668574	2.1 million
Cheviot	*Vallisneria americana*	590790, 4665309	680 000
Esopus Creek Mouth "North"	*Trapa natans*	588304, 4657409	2002 data unavailable
Esopus Creek Mouth "South"	*Trapa natans*	588229, 4657281	4 308
Glasco	*Vallisneria americana*	587822, 4655048	96 393
Cruger Island VA	*Vallisneria americana*	588700, 4654249	18 703
Cruger Island TN	*Trapa natans*	588809, 4653344	17 015
Kingston-Rhinecliff Bridge	*Vallisneria americana*	588310, 4649143	23 375

Note: Size estimates based on 2002 GIS data.

TABLE 2. Zebra mussel survivorship and settlement in experimental beds

Vegetation Bed	Vegetation Type	Mussel Survivorship	Mussel Settlement
Inbocht Bay	*Trapa*	28.8%	0
Kingston-Rhinecliff Bridge	*Vallisneria*	30.0%	7
Esopus Creek Mouth "North"	*Trapa*	31.9%	5
Cruger Island TN	*Trapa*	32.3%	1
Esopus Creek Mouth "South"	*Trapa*	33.0%	6
Cruger Island VA	*Vallisneria*	39.7%	2
Cheviot	*Vallisneria*	43.0%	37
Glasco	*Vallisneria*	44.9%	32

Note: Beds are listed in ascending order of zebra mussel survivorship.

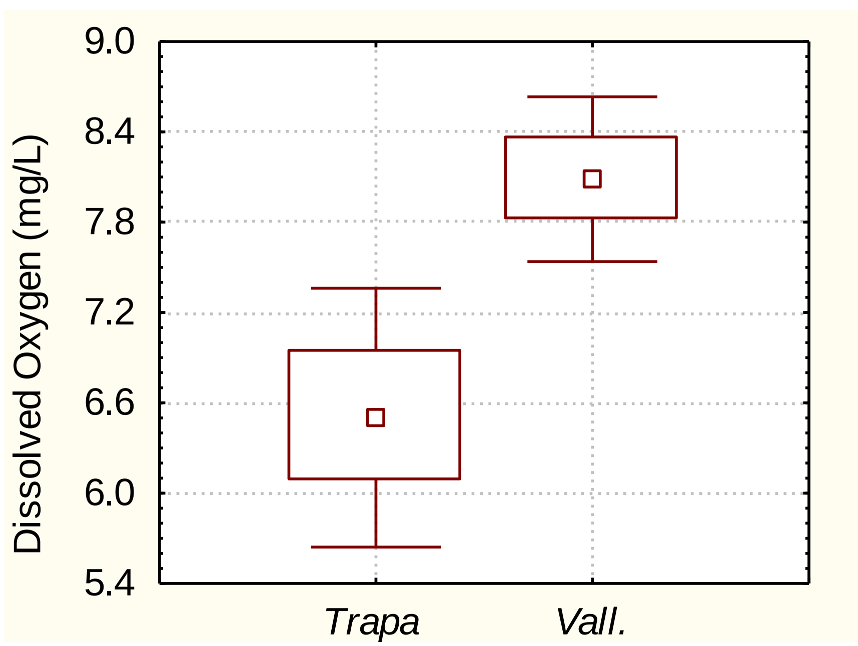

FIGURE 1. Dissolved oxygen in *Trapa* vs. *Vallisneria* experimental beds. Inner box represents the mean; outer box, one standard error; and bars, 1.96 standard error. DO in *Trapa* is significantly lower than that in *Vallisneria* (ANOVA, $p = 0.006$).

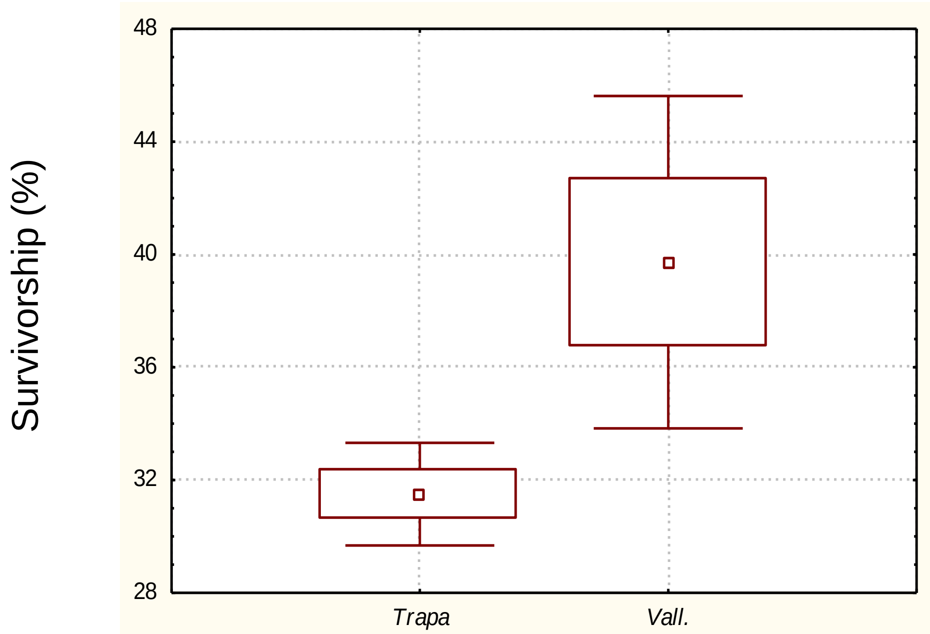

FIGURE 2. Mussel survivorship in *Trapa* vs. *Vallisneria* experimental beds. Inner box represents the mean; outer box, one standard error; and bars, 1.96 standard error. Survivorship in *Trapa* is significantly lower than in *Vallisneria* (ANOVA, p = 0.039).

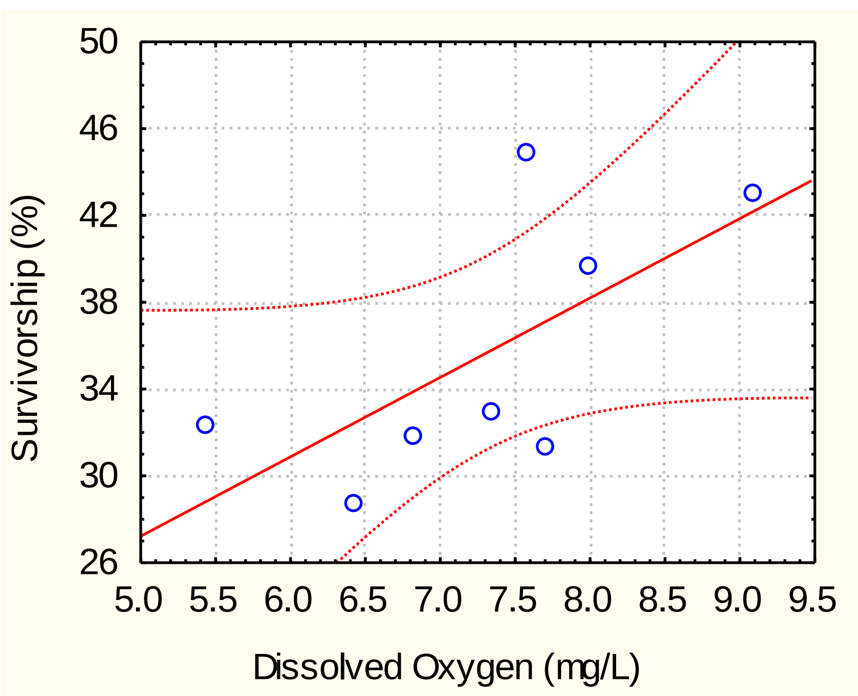

FIGURE 3. Correlation between dissolved oxygen and zebra mussel survivorship. The relationship is not statistically significant (ANOVA, p = 0.072).

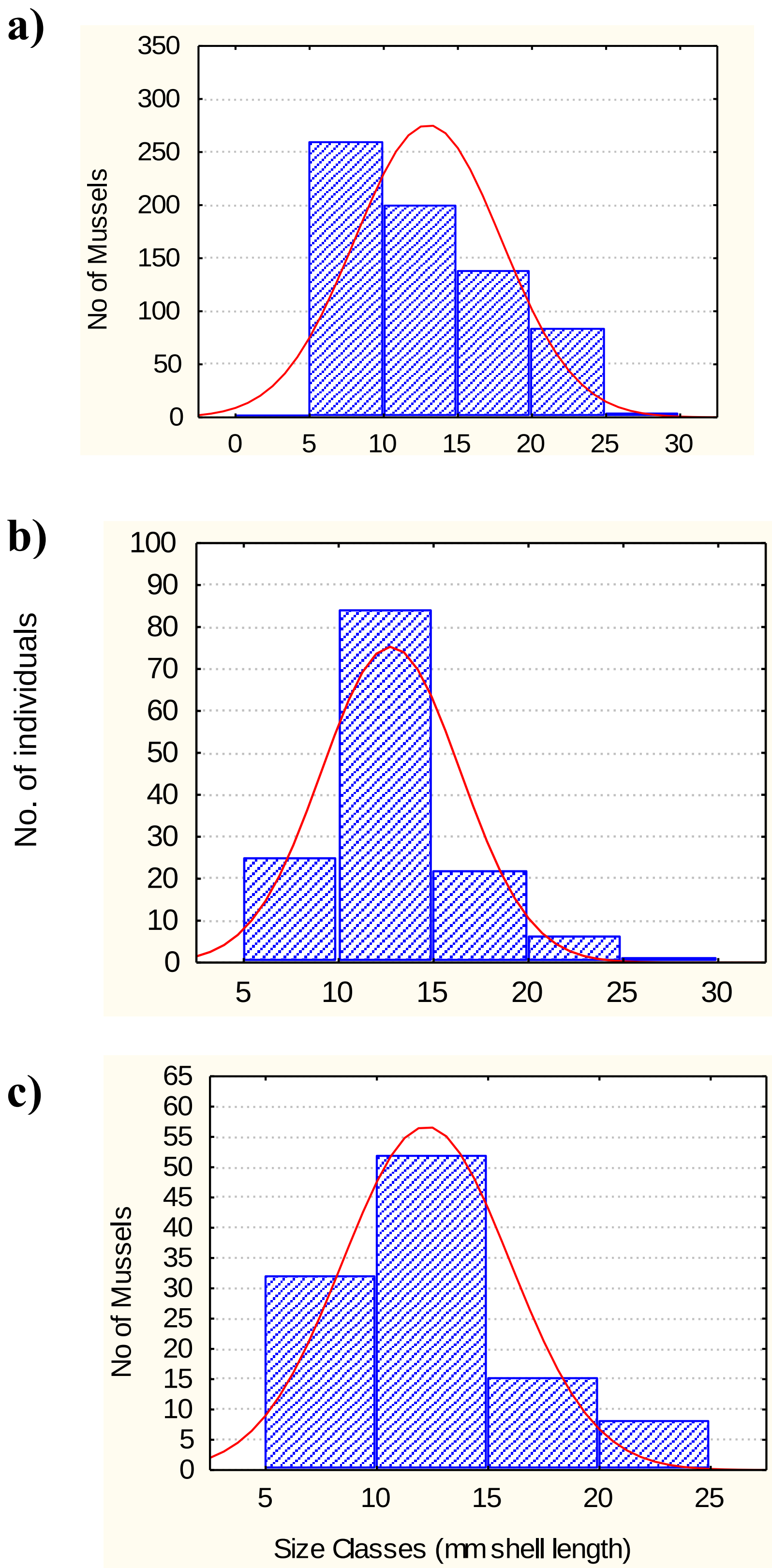

FIGURE 4. Comparison of shell lengths of mussels before and after deployment. a) Shell lengths of all mussels at day zero. b) Shell lengths of live mussels retrieved from *Vallisneria* beds at day 27. c) Shell lengths of live mussels retrieved from *Trapa* beds at day 27. The solid line represents the expected normal curve.