Eurasian milfoil invasion in estuaries: physical disturbance can reduce the proliferation of an aquatic nuisance species

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ABSTRACT: Biological invasions are among the most pervasive yet least understood of the consequences of the urbanization of estuarine ecosystems. In Mobile Bay, Alabama (USA), the construction of a transportation corridor, locally known as the Mobile Bay Causeway, has been hypothesized to have modified natural disturbance regimes to the point that numerous invasive species now persist in oligohaline reaches of this estuary. Here, we provide the results of field surveys and experiments designed to determine if the causeway facilitated the proliferation of the dominant invasive species, Eurasian milfoil *Myriophyllum spicatum* Linnaeus, 1753, throughout the Mobile-Tensaw Delta (MTD). Field surveys showed that the composition of submerged aquatic vegetation (SAV) varies greatly with location in the MTD; SAV south of the causeway is dominated by a single native species, wild celery *Vallisneria americana* Michaux, 1803, while milfoil and canopy-forming native species dominate areas north of the causeway. We found no evidence that the differences in species composition were related to differences in salinity, sediment grain size composition along the causeway, or competitive exclusion of the dominant native species by milfoil. We did, however, find a strong negative relationship between milfoil bio-mass and maximum wave force. These results suggest the causeway functions as a breakwater, reducing the penetration of large, wind-driven waves into oligohaline embayments north of the causeway. Counter to current thinking, these findings suggest that reductions in the intensity of physical disturbances will create opportunities for invasive milfoil to proliferate in the estuarine waters of the northern Gulf of Mexico.

KEY WORDS: Gulf of Mexico · Mobile Bay · Salinity · Competition · *Myriophyllum*

INTRODUCTION

Biological invasions are major threats to global bio-diversity (Lubchenco et al. 1991, Lodge 1993, Cohen & Carlton 1998, Carlton 2001, Grosholz 2005) and the ecosystem services inherent to species-rich native eco-systems (Mack et al. 2000, Zedler & Kercher 2004). Surprisingly, however, recent studies focusing on large spatial scales have found that plant invasions can add to species richness in at least some invaded ecosystems (Cleland et al. 2004, Smith et al. 2004, Capers et al. 2007). While invasions are known to occur across mul-tiple trophic levels in a variety of ecosystems, most studies report the effects of plant invasions on freshwa-ter and terrestrial ecosystems (Carlton & Geller 1993, Pyšek et al. 2008). Comparatively less is known about the effects of invasions in estuaries (but see Silliman & Bertness 2004), although we do know that invasions are numerous and widespread in these ecosystems (e.g. Duffy & Baltz 1998, Hicks et al. 2001, Peterson et al. 2005, Martin & Valentine 2011). Furthermore, the mechanisms by which some invasive species gain footholds in dynamic estuarine environments remain uncertain (Cohen & Carlton 1998, Ruiz et al. 1999).

Estuaries in the northern Gulf of Mexico exist in close proximity to sites of intense commercial activity (e.g. Valentine et al. 2009). The cumulative effects of the increasing globalization of the region's economy have created opportunities for cross-ecosystem delivery of non-native propagules and plant fragments (for example, through increased ballast water discharge, aquarium trade, poorly managed aquaculture, etc.) (Mack et al. 2000). This, along with increasing population densities and anthropogenic disturbances around these coastlines, is thought to have resulted in increasing rates of invasions in estuarine ecosystems (Ruiz et al. 1999).

Still, not all invasions are successful (sensu the 'roulette hypothesis'—Carlton & Geller 1993, Vitousek et al. 1996), and among the many hypotheses that have been advanced to explain this variability in invasion success has been the prediction that exotic species are more likely to gain footholds in environments that are highly disturbed by humans than in naturally disturbed environments. This typically occurs in areas of extensive habitat alteration that are presumed to result in the creation of 'vacant niches' (Elton 1958, Hobbs & Huenneke 1992, Wiser et al. 1998, Mack et al. 2000). Estuaries, by their very nature, are physically and physiologically challenging environments for native flora and fauna to persist in. As such, their proximity to a probable abundance of invasive propagules and intense, persistent, anthropogenic disturbances suggests estuaries are at greater risk of invasion than other marine systems (Cohen & Carlton 1998, Grosholz 2002). The uptake and subsequent release of both adult and larval stages of marine species that have evolved a tolerance of natural environmental fluctuations (i.e. temperature, salinity, etc.) through ballast water exchange is thus more likely as most shipping ports are located in nearshore bays, harbors, and estuaries (MacIsaac et al. 2002). Conversely, natural disturbance regimes, such as wave action, may preclude invasion by resisting initial establishment or thwarting the growth and proliferation of exotics, thus preventing the competitive exclusion of native species by the dominant competitor (Gross et al. 2005). A growing body of research now suggests that both invasive and native species may respond similarly to environmental conditions, and that the mere presence of higher species richness does not automatically infer increased invasion resistance (Levine & D'Antonio 1999, Lonsdale 1999, Cleland et al. 2004, Smith et al. 2004, Capers et al. 2007).

Anthropogenic modifications to the landscape of estuaries can take many different forms. Shoreline stabilization devices and earthen causeways, as well as ship channel excavations, are common hydrological modifications in urbanized estuaries that may facilitate the spread of introduced species as these modifications open new routes for transfer as well as creating disturbed habitats. Such construction projects dampen the intensity of many ecologically important disturbances (i.e. natural disturbances such as salinity and wave action) known to regulate estuarine ecosystem structure. Specifically, we hypothesized that reductions in the severity of natural, episodic disturbances may allow non-native species to colonize and then proliferate throughout the oligohaline waters of the northern Gulf of Mexico.

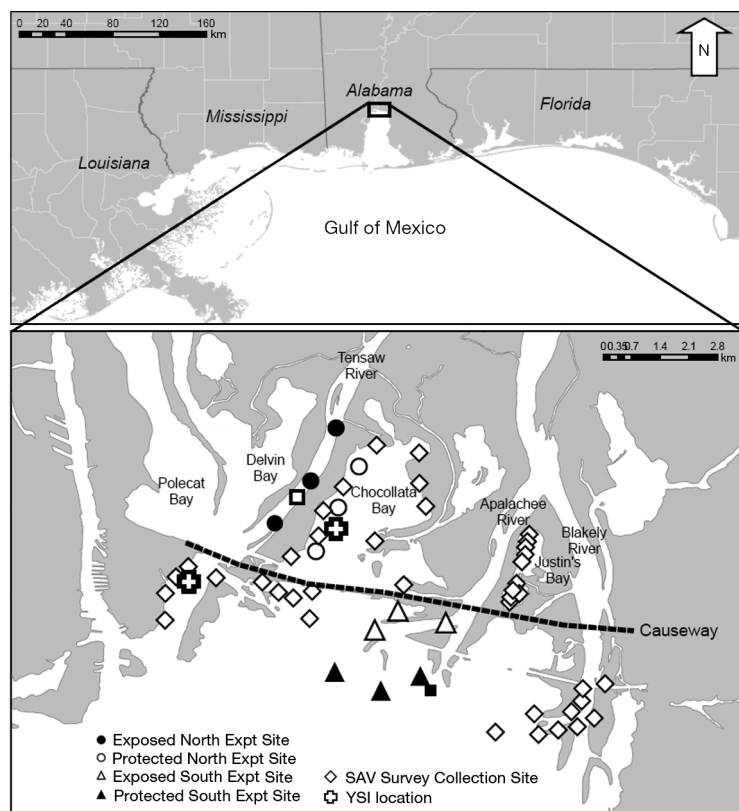In Mobile Bay, Alabama, the construction of an earthen causeway (hereafter referred to as the

Fig. 1. Submerged aquatic vegetation (SAV) study sites in the Mobile-Tensaw Delta and Mobile Bay for surveys, environmental measurements, and wave energy experiment

causeway; Fig. 1) in the early 1920s physically separates the northern reaches of Mobile Bay from the deltaic rivers and embayments of the Mobile-Tensaw Delta (MTD). This causeway effectively limits tidal exchange (as well as freshwater discharge) to passes below bridges constructed over 4 river channels, thus creating a salinity gradient over a relatively small area (Berrell 2002). The causeway also disturbs natural physical processes as a breakwater, blocking the penetration of larger wind-generated waves into the MTD (Schroeder & Wiseman 1985). The presence of the causeway thus represents an unintended opportunity to gain new insights into the role of natural disturbance and habitat alteration in facilitating the persistence of a single dominant invasive species, Eurasian milfoil *Myriophyllum spicatum*, in the estuary.

Although the coverage of submerged aquatic vegetation (SAV) has varied among seasons and surveys, Eurasian milfoil, first recorded in the MTD in the 1950s, is one of the most abundant species found in the area. Milfoil has been found to cover up to 80% of surveyed areas, and has been hypothesized to competitively displace other SAV, such as the most abundant native species, wild celery *Vallisneria americana* (Beshears 1982, Vittor and Associates 2004).

A number of factors could influence the distribution and proliferation of milfoil in the area. Because the estuaries of the northern Gulf of Mexico are located at the base of some of the nation's largest watersheds, they are also exposed to extensive seasonal and annual variation in salinity. Salinity peaks in the MTD during fall, when freshwater inflow declines and the salt wedge encroaches to its furthest northward point along river banks (Berrell 2002). Therefore, during low watershed input, the cumulative effects of oligotrophic, higher salinity waters may retard milfoil growth and reduce its areal coverage via the disruption of cellular processes (Haller et al. 1974). Previous studies, conducted elsewhere, found that Eurasian milfoil biomass is negatively correlated with salinity (Haller et al. 1974, Frazer et al. 2006), suggesting that salinity could be a key determinant of milfoil distribution in the MTD. Specifically, Haller et al. (1974) found toxicity to occur at 13.32 psu. Moreover, milfoil is hypothesized to disperse primarily following plant fragmentation (Kimbel 1982, Madsen et al. 1988) caused by either episodic physical disturbances (e.g. storm-induced wave action or boat propellers) or autofragmentation (Madsen et al. 1988, Valley & Newman 1998) and as such could be limited by physical forces. Therefore, changes to the physical disturbance regime may rep-

resent an alternative mechanism to facilitate the introduction and subsequent spread of milfoil in the MTD.

Here, we present the findings of a study conducted in the lower MTD and upper Mobile Bay, Alabama, that was designed to evaluate the effects of changes in disturbance intensity on the distribution of invasive Eurasian milfoil. Specifically, we (1) documented SAV distributional patterns and hydrographical conditions on each side of the causeway and (2) experimentally tested the influence of variation in salinity, interspecific competition, and physical wave action on the success of invasive Eurasian milfoil.

MATERIALS AND METHODS

Distribution patterns of submerged aquatic vegetation (SAV)

The ecosystem-scale distribution of the SAV in this river delta (which comprises ~110 000 ha) was mapped in 2002 by Barry A. Vittor and Associates with the aid of aerial photography, ground truthing, and geographic information systems (GIS) (Vittor & Associates 2004). We utilized these data and new analyses to compare and contrast the distributional patterns of the 2 most abundant SAV species found in the area, invasive Eurasian milfoil *Myriophyllum spicatum* and native wild celery *Vallisneria americana*. SAV beds containing milfoil and wild celery represented 41.5 and 40.2%, respectively, of the total acreage surveyed.

The estimated total areal coverage (m^2) of each SAV species was compared to total water surface area (m^2). Then, comparisons of the relative areal coverage of both milfoil and wild celery were made north versus south, as well as in rivers versus embayments north of the causeway. Because both SAV species colonize similar depths (Titus & Stephens 1983) and the available area was so much greater south of the causeway, a ratio of the areal coverage of the 2 species on each side of the causeway was also calculated.

To determine if differences in the relative abundances of native and non-native species existed among sites on a much finer spatial and temporal scale than was mapped in the Vittor survey, we conducted a second, more intensive mapping effort on both sides of the causeway. Samples were taken every 2 mo during the growing season (May to September 2007) at 40 preselected sites (20 sites located north and the remaining sites located south). Repli-

cate 10 cm diameter cores were taken at 5 locations within each site (n = 200 cores). Cores penetrated ~5 cm into the sediment, enclosing above- and belowground plant material. Extruded cores were transferred to pre-labeled individual Ziploc bags placed on ice and returned to Dauphin Island Sea Lab (DISL) for processing. Upon return, SAV contained in samples were sorted by species, then placed in pre-weighed aluminum pans and dried to constant weight (±0.001 g) at 60°C.

Mesocosm experiments

Salinity tolerance

To document the extent to which salinity varied with causeway location and to document the range of physiological conditions that the SAV species are exposed to, salinity was continuously measured from May to September. To accomplish this, a YSI6600 was deployed north and south of the causeway and programmed to measure salinity at 15 min intervals throughout the SAV growing season.

We further hypothesized that documented differences in sediment type (Valentine & Sklenar 2004) observed on each side of the causeway may have a contributing effect on milfoil growth since sediment composition varies greatly between areas and may affect plant growth. Sediments in areas north of the causeway (hereafter referred to as 'mud') contain less sand (34.62%) than do areas to the south (53.02%). As a result, a second factor (sediment type) was added to the experimental design. This factor consisted of 2 treatments (sediments collected from both sides of the causeway).

To test the influence of spatial variation in salinity and sediment on milfoil growth and survival, a 3 × 2 factorial analysis of variance (ANOVA)-designed laboratory experiment, consisting of 3 salinity treatments (0, 5, or 15 psu) that bracketed the range observed during the growing season in the MTD, and 2 sediment treatments (sand or mud from each side of the causeway) was conducted in 18 replicated 98 l tanks (n = 3 per unique treatment) in the wet laboratory at DISL.

SAV were collected from the north side of the causeway, and epiphytes, algae, dead tissue, and potential herbivores (primarily gastropods and amphipods) were gently removed from the SAV by hand prior to the experiment. Cleansed plants were placed in a salad spinner, turned for 1 min (~100 turns) to remove water before weighing (wet

weight, WW; ±0.01 g), and placed in tanks. Ten plants were randomly stocked in each tank, and nutrient conditions were kept consistent with current field conditions throughout the trials. Salinities in the experimental tanks were gradually increased at a rate of 1 psu d^{-1} until the desired salinity level was reached. Once the assigned salinity was reached, treatments were held constant throughout the remainder of the experiment. Lighting (held constant between 150 and 250 µmol m^{-2} s^{-1} during day) was set on a 12 h light:12 h dark cycle to mimic natural conditions during summer. At Day 70 (end of the experiment), plants were removed from the tanks, returned to the salad spinner to remove water, and reweighed. Final WWs were used to calculate milfoil growth as percent change in biomass.

Competitive exclusion

To determine if the seeming dominance of Eurasian milfoil was the result of milfoil competitively displacing native SAV, as would be generally suggested by the fundamental principles of invasion theory (sensu Elton 1958), we performed an interspecific competition experiment using milfoil and wild celery (August to October 2006).

Because salinity may alter the strength of competitive interactions, we included variation in salinity as a factor in these experiments. The same 3 salinity treatments used in the salinity tolerance experiments (0, 5, and 15 psu) constituted 1 main effect. The second main effect consisted of treatments comprised of either wild celery grown in monoculture or wild celery grown in combination with milfoil. The influence of these main effects on wild celery growth were evaluated using a 3 × 2 factorial ANOVA design replicated 3 times per unique treatment in randomly assigned 98 l tanks in the DISL's recirculating wet laboratory facility.

Ten plants (either 10 wild celery or a mix of 5 milfoil and 5 wild celery) harvested from monospecific beds in Chocolatta Bay were transplanted to randomly assigned tanks. These experimental densities mimic the natural densities found in the SAV survey described above. Small wild celery plants (<25 g) and milfoil fragments (<5 g) were selected for this experiment, as we expected growth rates to be highest for younger plants. Also, because milfoil's main mode of reproduction is thought to be through fragmentation (Kimbel 1982, Madsen et al. 1988), this interaction of small milfoil fragments and established adult wild celery plants mimics the natural first step

for an introduction of milfoil to the area south of the causeway. Procedures for herbivore and epiphyte or algae removal, lighting, light–dark cycle, sediment type (mud from Chocolatta Bay), and maintenance of tanks were identical to those described above. Comparisons of wild celery WWs were made at the end of the experiment (70 d).

Breaking strength, wave action, and shear forces

Winds are predominantly from the south in the study area (Schroeder & Wiseman 1985) during the SAV growing season, so we hypothesized that differences in maximum wave heights (and forces they place on SAV) or tidal current velocities on each side of the causeway may determine the distributional patterns of milfoil and wild celery in our study area.

To determine the force needed to break milfoil stems and wild celery leaves, we used a Lyman® trigger pull gauge, an inexpensive tool used in the gunsmithing industry to set the amount of force necessary to initiate the trigger group on a firearm. The ends of a nylon line were attached to the instrument and 2 wooden blocks, which securely held plant stems in place via 2 bolts and wing nuts (to prevent pinching plants). Force was exerted until the plant fragmented, and the maximum force (g) was recorded. We made these measurements in established milfoil and wild celery beds in Chocolatta Bay.

To further test the hypothesis that the distribution of milfoil could be controlled by physical forces, we performed a field tethering experiment. Field sites (n = 3 per treatment) were chosen based on anticipated variances in maximum wave height: 'protected' sites included enclosed embayments with limited fetch north of the causeway and on the northern side of emergent vegetation islands located south of the causeway and 'exposed' sites on river banks (where channeling should result in increased shear forces) north of the causeway and south of emergent vegetation islands south of the causeway (Fig. 1). Milfoil fragments were harvested from the MTD and stem lengths were measured (±0.1 cm); the fragments were then returned to preselected field sites and tethered to a polypropylene line using a clothespin anchored to the bottom with wire stakes. After 72 h, plants were retrieved and returned to the DISL, stem lengths were remeasured, and the percent loss was calculated. A laboratory pilot study verified that the clothespin did not result in milfoil fragmentation over the 72 h time frame studied here.

Concurrent with this field experiment, we quantified current velocities and maximum wave heights at each site to document treatment effects. We utilized a combination of approaches to document differences in wave height and current among sites. Gypsum disks were used to provide a comparative measure of water flow by documenting the weight loss of gypsum casts during deployment (D'Amours & Scheibling 2007, Hepburn et al. 2007). Disks were constructed of a gypsum ($CaSO_4 \cdot 2H_2O$):water mixture of 1:1.75 (v:v), poured into a mold such that the resulting cylinder was ~5 cm wide × 5 cm deep and allowed to dry for 1 wk (Reidenbach et al. 2006). Gypsum disks were attached to PVC frames placed ~0.5 m above the sediment surface at each site.

Maximum wave energy was measured at the sites using a dynamometer (cf. Bell & Denny 1994). These dynamometers estimate maximum wave height by documenting the stretch of a precalibrated spring attached to a float. All springs were calibrated by hanging 5 known masses from the instrument and measuring the distance the spring stretched (simple linear regression of spring stretch on mass; p < 0.001; $r^2 \geq 0.95$). Each dynamometer was attached to a cinder block and fitted with identical floats ~0.3 m above the sediment surface.

Statistical analyses

One-way ANOVA and *t*-tests were used to compare and contrast the distributional patterns of milfoil and wild celery qualitatively reported in the Vittor and Associates (2004) survey. In the second, more detailed survey, comparisons of plant species composition (percent biomass of the total found at each site) were made using the non-parametric multivariate analysis of similarity (ANOSIM; square root transformed, Bray-Curtis similarity) technique (Warwick & Clarke 1991). Biomass of each species was compared using a Kruskal-Wallis test after assumptions of parametric statistics were not satisfied. Salinity was calculated as the weekly means from observations recorded on YSI instruments. Both laboratory experiments were analyzed using a 2-way ANOVA to determine if the dependent variable (salinity: change in milfoil biomass; interspecific competition: change in wild celery biomass) varied significantly among treatments (salinity: salinity, sediment type, and interaction; interspecific competition: presence/absence of milfoil, salinity, and interaction). A 2-sample unpaired *t*-test was also used to compare the breaking strength of milfoil and wild celery. Wave

action measurements (mean velocity and maximum energy) and milfoil loss were compared among sites using a regression. All results were considered significant at p < 0.05 and moderately significant at p < 0.10.

RESULTS

Milfoil distributional patterns

The areal coverage of milfoil *Myriophyllum spicatum* was ~1.5-fold greater than that of wild celery *Vallisneria americana* north of the causeway (Fig. 2a). Conversely, the areal coverage of wild celery was ~6-fold that of milfoil to the south. Although the areal coverage of both milfoil and wild celery appears to be greater north of the causeway, this is an artifact resulting from large differences in the total area of water (2.65×10^7 m^2 north of the causeway versus 8.52×10^8 m^2 south of the causeway). To standardize for this difference in survey size, the ratio of the 2 species was calculated for each side of the causeway. A subsequent analysis of the area just north of the causeway indicated moderately significantly more milfoil occurred within embayments than along river banks, which suggests the importance of high-energy water flow in hindering the ability of milfoil to attach in areas of higher

Fig. 3. Comparisons of submerged aquatic vegetation (SAV) species (dry weight in g m^{-2}, means +1 SE, n = 20) north and south of the causeway

physical disturbance (negative inverse transformed; $F_{1,10}$ = 4.65; p = 0.056; Fig. 2b).

Results from the ANOSIM of plant community composition conducted on samples collected during the second SAV survey found significant differences in the relative abundances on each side of the causeway (Global R = 0.098; p = 0.001; Fig. 3). SAV species richness was greater north of the causeway (*Myriophyllum spicatum*, *Vallisneria americana*, *Heteranthera dubia* [Jacquin, 1768], *Zannichellia palustris* [Linnaeus, 1753], *Najas guadalupensis* [Sprengel, 1870], and *Ceratophyllum demersum* [Linnaeus, 1753]) than to the south (*Ruppia maritima* [Linnaeus, 1753] and *V. americana* were the only species in abundance). Kruskal-Wallis analysis showed that wild celery biomass (g m^{-2}, means ±1 SE) was significantly greater in cores taken south of the causeway (n = 40, K_1 = 18.131, p = 0.0001), and milfoil biomass was moderately greater north of the causeway (n = 40, K_1 = 3.563, p = 0.059).

Mesocosm experiments

Salinity experiments

Salinity was significantly higher south of the causeway during our surveys [$t(59)$ = −4.57, p < 0.001]. Our laboratory experiment, however, failed to detect significant effects of variation in salinity ($F_{2,12}$ = 1.18, p = 0.34), sediment type ($F_{1,12}$ = 2.90, p = 0.114), or the interaction between these 2 factors ($F_{2,12}$ = 0.36, p = 0.703) on milfoil growth (Fig. 4).
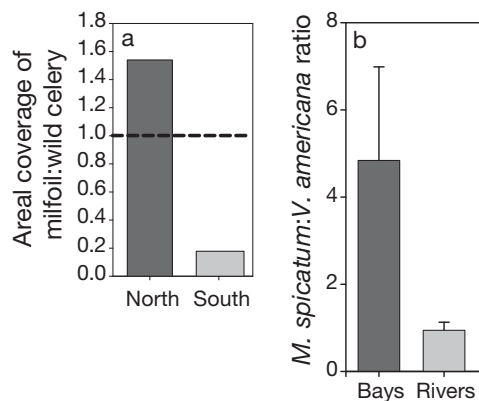

Fig. 2. *Myriophyllum spicatum*, *Vallisneria americana*. Distribution of submerged aquatic vegetation within the lower Mobile-Tensow Delta plotted from the reanalysis of data from Vittor and Associates (2004), with comparisons of the ratio of milfoil to wild celery made (a) north and south of the causeway (dashed line indicating equal areal coverage of each species) and (b) in embayments and rivers only north of the causeway (mean +1 SE, n = 11)
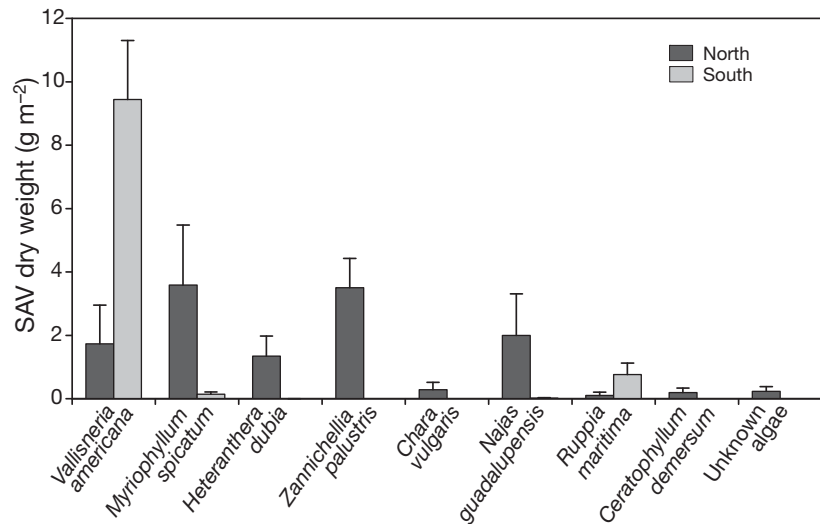
Interspecific competition

A 2-way ANOVA showed that while salinity had a significant, negative effect on wild celery growth ($F_{2,12} = 15.82$, p < 0.001), the presence of milfoil did not ($F_{1,12} = 0.06$, p = 0.810) (Fig. 5). A significant interaction between these 2 main effects was not detected either ($F_{2,12} = 0.481$, p = 0.778).

Wave action and shear forces

Trigger gauge measurements indicated that significantly more force is required to fragment wild celery than milfoil stems [log transformed: $t(18) = -4.094$, p < 0.001].

Gypsum dissolution varied significantly among sites (Fig. 6a; negative inverse square transformed: $F_{3,44} = 7.711$, p < 0.001). Subsequent post hoc tests indicated that currents in designated exposed sites north and south of the causeway are areas of greater dissolution than are protected sites (Fig. 6a). Maximum wave forces also varied significantly among sites, again with greater forces detected at exposed sites, especially south of the causeway (log transformed: $F_{3,44} = 5.741$, p = 0.006; Fig. 6b).

Results from the tethering experiment indicated that milfoil is susceptible to wave energy. Specifically, maximum wave force explained a significant amount of the recorded variability in milfoil loss, while mean current velocity did not (all data arcsine square root transformed, mean current velocity: $F_{1,6} = 0.03$, p = 0.861, R^2 adj. = 0.0%; Fig. 7a; maximum wave force: $F_{1,6} = 66.70$, R^2 adj. = 90.4%, p > 0.001; Fig. 7b).

DISCUSSION

Our observational and experimental study aimed to combine a number of environmental and biological variables to help explain the observed distribu-

Fig. 5. *Vallisneria americana*. Growth as change in wet weight (WW, percent increase plant^{-1} tank^{-1}, means +1 SD, n = 3) of wild celery grown in the absence and presence of *Myriophyllum spicatum* at 0, 5, or 15 psu. Different letters indicate significant differences

Fig. 6. Comparisons of (a) the dissolution of gypsum (loss min^{-1}, means + 1 SE, n = 12) and (b) maximum wave force (g, means +1 SE, n = 15) among study sites. Different letters indicate significant differences among treatments (p < 0.05)
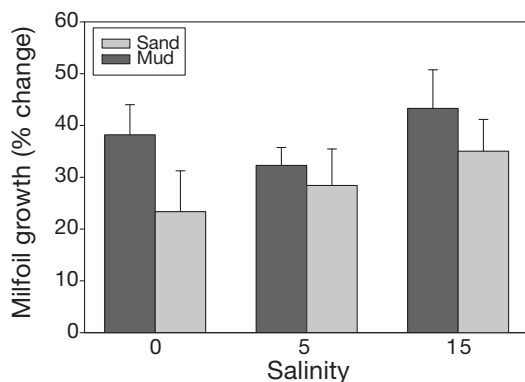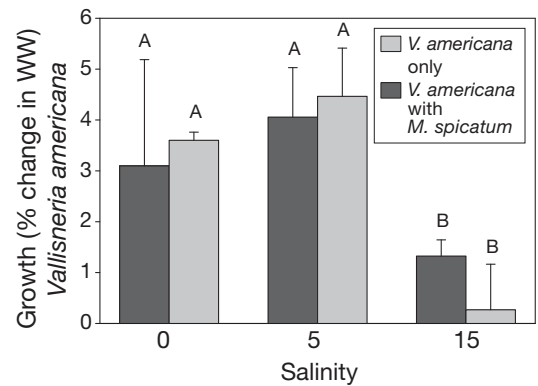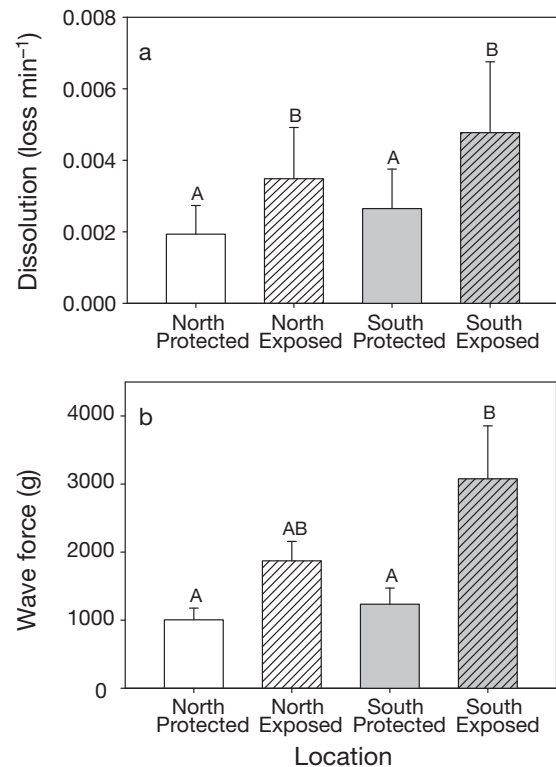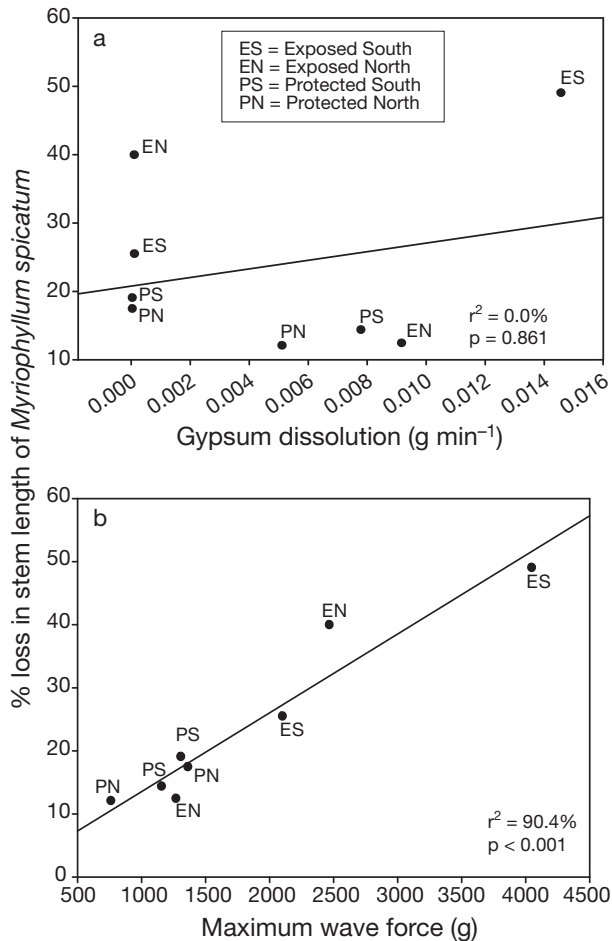

Fig. 4. *Myriophyllum spicatum*. Results of milfoil growth experiments (percent increase in wet weight, means +1 SD, n = 3) considering three salinities and two sediment compositions

Fig. 7. Linear regressions of (a) mean weight loss (g min^{-1}) gypsum blocks and (b) maximum wave force (*g*) on *Myriophyllum spicatum* loss (stem length) in embayments located on each side of the causeway

tions of an introduced and native species of SAV in the MTD. Invasive Eurasian milfoil *Myriophyllum spicatum* dominated the submerged landscape north of the causeway, while wild celery *Vallisneria americana* was more abundant than milfoil to the south. The apparent segregation of invasive milfoil and native wild celery in the MTD could be due to a number of environmental or biological variables that we found to vary with causeway location such as physiological response to salinity (Haller et al. 1974, Frazer et al. 2006), sediment composition, interspecific competition with native species, or physical wave action. Results presented here provide insight into the nature by which anthropogenic and natural disturbance regimes affect milfoil's proliferation into estuaries of the northern Gulf of Mexico and, as such, contains inherent value for environmental managers and scientists alike.

Although salinity was significantly higher south of the causeway, laboratory experiments failed to indicate any effect of salinity treatments on milfoil growth (Fig. 4). One possible explanation for this apparent contradiction between our findings and those of Haller et al. (1974) is that we gradually acclimated plants to treatment salinities. This is most likely what milfoil experiences as salinity increases slowly on a seasonal basis, except in the case of extreme episodic events such as hurricanes (Park et al. 2007).

Because estuaries are located at the interface between aquatic and marine ecosystems, estuarine plants are exposed to an extraordinary number of physiological and physical challenges, which, based on the founding principles of invasion theory, may be less resilient to invasion (Elton 1958). As such, it is reasonable to predict that estuaries are at great risk of invasion. Most estuaries of the northern Gulf of Mexico are in close proximity to urban centers, and by extension sources of invasive propagules, and should be characterized by an abundance of invasive species (i.e. Duffy & Baltz 1998, Hicks et al. 2001, Peterson et al. 2005, Martin & Valentine 2011). As these invaders spread, the prevailing view among ecologists predicts that their competitive dominance will lead to significant reductions of native diversity through competitive displacement (Elton 1958). Contrary to this paradigm (Mooney & Cleland 2001, Didham et al. 2005), we did not find that the presence of milfoil negatively affected wild celery growth at any of the treatment salinities. In fact, at lower salinities (0 and 5 psu), wild celery grew better in the presence of milfoil, although not significantly so, than in the absence of milfoil, indicating facilitation may occur. Wild celery weight was lower in the 15 psu treatment and is known to be negatively affected by higher salinities (Kraemer et al. 1999). Based on the results of our competition experiment, higher salinity in experimental tanks, not the presence of milfoil, affected wild celery growth. Still, some caution should be exhibited in examining these results as only milfoil fragments and young wild celery plants were tested and it is possible that competitive exclusion may occur between other life stages of the plants. Milfoil fragments were chosen because they are the main mode of reproduction and dispersal (Kimbel 1982, Madsen et al. 1988), and younger wild celery plants that have yet to reach their maximum growth would be more likely to demonstrate changes in growth rates. Future studies should be directed at testing the competitive interactions between the various life stages of the plants.

Recent studies in aquatic environments suggest that introduced plants may not always competitively

exclude native species and decrease local species richness (Levine & D'Antonio 1999, Lonsdale 1999, Cleland et al. 2004, Smith et al. 2004, Capers et al. 2007). In fact, Capers et al. (2007) found that invasive SAV in Rhode Island lakes increased local diversity, and the abundance of these invaders was positively correlated with native SAV species. Results of these studies suggest that both invasive and native plants may respond in similar manners to environmental challenges, and that the mere presence of higher species richness does not automatically infer increased invasion resistance. The findings of the present study echo these conclusions. We found no evidence that the areas dominated by milfoil (north of the causeway) in the MTD were the result of competitive exclusion by this non-native species. In fact, areas where milfoil was most abundant were also areas with greater overall SAV species richness (Fig. 3).

Physical disturbance is known to prevent the process of competitive exclusion from becoming a structuring force in many communities (Grime 1973, Connell 1978), and may be an important factor influencing the success of an introduced species. Physical processes, such as waves or ice scour, have been shown to continually reset the successional trajectory of invaded communities (Stachowicz et al. 1999, Seabloom et al. 2003, Gilbert & Lechowicz 2005, Klein et al. 2005, Gross et al. 2005). The exposed waters south of the causeway were areas of greater physical disturbance (greater wave height and energy) than protected areas north of the causeway. Although only 500 g of force is needed to break milfoil (compared to nearly 1700 g for wild celery), our tethering experiment conducted in areas of differing wave force and current velocities indicated that mean current velocity explained very little of the observed variability in the loss of tethered milfoil. In contrast, >90% of the variability in tethered milfoil loss was explained by maximum wave force. As milfoil exhibits characteristics favorable for low-energy environments north of the causeway (i.e. low underground biomass, absence of a root system, high above-ground biomass) with episodic high-energy events that increase reproduction via fragmentation, this introduced species may not be able to survive south of the causeway due to physical forces alone.

Reexamination of the data compiled in the fine-scale SAV survey provides further indirect support for this conclusion: there were more species with broad canopies and fine root structures present north of the causeway (such as *Heteranthera dubia*, *Zannichellia palustris*, *Najas guadalupensis*, and *Ceratophyllum demersum dubia*) than to the south (Fig. 3).

This suggests that physical forces could be controlling the distribution patterns of these canopy-forming native species in the MTD as well. While some of these species could certainly be limited by salinity (i.e. Kraemer et al. 1999) or other factors, their presence and morphological characteristics suggest they are also susceptible to damage from large, forceful waves.

It remains possible that other biotic and abiotic factors could play a contributory role in facilitating the proliferation of milfoil in the MTD (sensu Underwood 1997). We think this is unlikely, however, due to several lines of strong evidence that physical forces limit milfoil's proliferation to areas north of the causeway: (1) similarity in morphological characteristics of plants north of the causeway, (2) differences in the breaking strength of the 2 dominant SAV in the area, (3) the field experiment that showed milfoil fragmentation increased with maximum wave forces, and (4) increased milfoil areal coverage in quiescent embayments relative to open rivers.

Intense disturbances are known to play a determining role in the establishment and proliferation of foundation species in virtually every ecosystem on earth (Connell 1978). We suggest that the reduction of one form of natural disturbance (i.e. physical wave action) facilitated the persistence and proliferation of invasive Eurasian milfoil. Several other introduced species have been shown to be affected by changes in the disturbance regime, including low recruitment of invasive rainbow trout during natural flood regimes (Fausch et al. 2001), successful establishment of introduced fish and bivalve species in highly polluted and affected estuaries such as San Francisco Bay (Nichols et al. 1990, Meng et al. 1994, Cohen & Carlton 1998), and increased invasion success of invasive mussels in fragmented seagrass beds (Reusch & Williams 1999).

Predicting where invasive species will occur in space and time is one of the foremost goals in invasion ecology (Elton 1958, Carey et al. 1996), and this work adds valuable insight into the nature by which canopy-forming SAV species, both native and exotic, are able to develop persistent populations in the Mobile Bay estuary. Natural disturbances have long been hypothesized to be more capable of resisting invasions (Lodge 1993, Moyle & Light 1996), but few studies have documented how natural disturbance processes may actually facilitate the introduction and spread of an introduced species to date (Bennett 1990, Fausch et al. 2001). As such, our study represents an important contribution towards the development of invasion theory among the myriad of complex ecological interactions occurring at a regional scale.

LITERATURE CITED

Bell EC, Denny MW (1994) Quantifying 'wave exposure': a simple device for recording maximum velocity and results of its use at several field sites. J Exp Mar Biol Ecol 181:9–29

Bennett WA (1990) Scale of investigation and the detection of competition: an example from the house sparrow and house finch introductions in North America. Am Nat 135: 725–747

Berrell TA (2002) Variability in bottom-up enrichment in Mobile Bay and its effects on growth rates of *Rangia cuneata*. Masters thesis, University of South Alabama, Mobile, AL

Beshears WWJ (1982) Mobile Delta vegetative survey. Alabama Department of Conservation and Natural Resources, Mobile, AL

Capers RS, Selsky R, Bugbee GJ, White JC (2007) Aquatic plant community invisibility and scale-dependent patterns in native and invasive species richness. Ecology 88: 3135–3143

Carey JR, Moyle P, Rejma'nek M, Vermeij G (eds) (1996) Special issue: invasion biology. Biol Conserv 78:1

Carlton JT (2001) Introduced species in US coastal waters: environmental impacts and management priorities. Pew Oceans Commission, Arlington, VA

Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science 261:78–82

Cleland EE, Smith MD, Andelman SJ, Bowles C and others (2004) Invasion in space and time: non-native species richness and relative abundance respond to interannual variation in productivity and diversity. Ecol Lett 7: 947–957

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

D'Amours O, Scheibling RE (2007) Effect of wave exposure on morphology, attachment strength and survival of the invasive green alga *Codium fragile* ssp. *tomentosoides.* J Exp Mar Biol Ecol 351:129–142

Didham RK, Tylianakis JM, Hutchison MA (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474

Duffy KC, Baltz DM (1998) Comparison of fish assemblages associated with native and exotic submerged macrophytes in the Lake Pontchartrain estuary, USA. J Exp Mar Biol Ecol 223:199–221

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago, IL

Fausch KD, Taniguchi Y, Nakano S, Grossman GD, Townsend CR (2001) Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecol Appl 11:1438–1455

Frazer TK, Notestein SK, Jacoby CA, Littles CJ, Keller SR, Swett RA (2006) Effects of storm-induced salinity changes on submersed aquatic vegetation in Kings Bay, Florida. Estuaries Coasts 29(6A):943–953

Gilbert B, Lechowicz MJ (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology 86:1848–1855

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242:344–347

Grosholz ED (2002) Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17:22–27

Grosholz ED (2005) Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proc Natl Acad Sci USA 102:1088–1091

Gross KL, Mittelbach GG, Reynolds HL (2005) Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. Ecology 86:476–486

Haller WT, Sutton DL, Barlow WC (1974) Effects of salinity on growth of several aquatic macrophytes. Ecology 55: 891–894

Hepburn CD, Holborow JD, Wing SR, Frew RD, Hurd CL (2007) Exposure to waves enhances the growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera.* Mar Ecol Prog Ser 339:99–108

Hicks DW, Tunnell JW, McMahon RF (2001) Population dynamics of the non-indigenous brown mussel *Perna perna* in the Gulf of Mexico compared to other worldwide populations. Mar Ecol Prog Ser 211:181–192

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. Conserv Biol 6: 324–337

Kimbel JC (1982) Factors influencing potential intralake colonization by *Myriophyllum spicatum* L. Aquat Bot 14: 295–307

Klein J, Ruiton S, Verlaque M, Boudouresque CF (2005) Species introductions, diversity and disturbances in marine macrophyte assemblages of the northwestern Mediterranean Sea. Mar Ecol Prog Ser 290:79–88

Kraemer GP, Chamberlain RH, Doering PH, Steinman AD, Hanisak MD (1999) Physiological responses of transplants of the freshwater angiosperm *Vallisneria americana* along a salinity gradient in the Caloosahatchee estuary (southwest Florida). Estuaries 22:138–148

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8:133–137

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

Lubchenco J, Olson AM, Brubaker LB, Carpenter SR and others (1991) The Sustainable Biosphere Initiative: an ecological research agenda. Ecology 72:371–412

MacIsaac HJ, Robbins TC, Lewis MA (2002) Modeling ships' ballast water as invasion threats to the Great Lakes. Can J Fish Aquat Sci 59:1245–1256

Mack RN, Simberloff D, Lonsdale MW, Evans H, Clout M, Bazzaz F (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Madsen JD, Eichler LW, Boylen CW (1988) Vegetative spread of Eurasian watermilfoil in Lake George, New York. J Aquat Plant Manag 26:47–50

Martin CW, Valentine JF (2011) Impacts of a habitat-forming exotic species on estuarine structure and function: an experimental assessment of Eurasian milfoil. Estuaries Coasts 34:364–372

Meng L, Moyle PB, Herbold B (1994) Changes in abundance and distribution of native and introduced fishes in Suisun Marsh. Trans Am Fish Soc 123:498–507

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. Proc Natl Acad Sci USA 98:5446–5451

Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. Biol Conserv 78: 149–161

Nichols FH, Thompson JK, Schemel LE (1990) Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. Mar Ecol Prog Ser 66:95–101

Park K, Valentine JF, Sklenar SA, Weis KR, Dardeau MR (2007) The effects of Hurricane Ivan in the inner part of Mobile Bay, Alabama. J Coast Res 23:1332–1336

Peterson MS, Slack WT, Woodley CM (2005) The occurrence of non-indigenous Nile tilapia, *Oreochromis niloticus* (Linnaeus) in coastal Mississippi: ties to aquaculture and thermal effluent. Wetlands 25:112–121

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23:237–244

Reidenbach MA, Koseff JR, Monismith SG, Steinbuck JV, Genin A (2006) The effects of waves and morphology on mass transfer within branched reef corals. Limnol Oceanogr 51:1134–1141

Reusch TBH, Williams SL (1999) Macrophyte canopy structure and the success of an invasive marine bivalve. Oikos 84:398–416

Ruiz GM, Fofonoff P, Hines AH, Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnol Oceanogr 44:950–972

Schroeder WW, Wiseman WJ (1985) An analysis of the winds (1974–1984) and sea level elevations (1973–1983) in coastal Alabama. Publication No. MASGP-84-024, Mississippi–Alabama Seagrant Consortium, Ocean Springs, MS

Seabloom EW, Harpole SW, Reichman OJ, Tilman D (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proc Natl Acad Sci 100:13384–13389

Silliman B, Bertness M (2004) Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. Conserv Biol 18: 1424–1434

Smith MD, Wilcox JC, Kelly T, Knapp AK (2004) Dominance not richness determines invasibility of tallgrass prairie. Oikos 106:253–262

Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286(5444):1577–1579

Titus JE, Stephens MD (1983) Neighbor influences and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake. Oecologia 56:23–29

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge

Valentine JF, Sklenar SA (2004) Mobile-Tensaw Delta hydrological modifications impact study. Mobile Bay National Estuary Program, Mobile, AL

Valentine JF, Heck KL, Dardeau M, Burch H (2009) Ecosystem-based management of Mobile Bay, Alabama. In: Day J, Yanez-Arancibia A (eds) The Gulf of Mexico: its origins, waters, biota amd human impacts, Vol V. The Gulf of Mexico: Ecosystem-Based Management. Texas A and M University Press, College Station, TX

Valley RD, Newman RM (1998) Competitive interactions between Eurasian watermilfoil and northern watermilfoil in experimental tanks. J Aquat Plant Manag 36:121–126

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:468–478

Vittor BA and Associates (2004) Benthic mapping of submerged aquatic vegetation in Mobile Bay and adjacent waters of coastal Alabama. Mobile Bay National Estuary Program, Mobile, AL

Warwick RM, Clarke KR (1991) A comparison of some methods for analysing changes in benthic community structure. J Mar Biol Assoc UK 71:225–244

Wiser SK, Allen RB, Clinton PW, Platt KH (1998) Community structure and forest invasion by an exotic herb over 23 years. Ecology 79:2071–2081

Zedler J, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Crit Rev Plant Sci 23:431–452