Assessing Functional Equivalency of Nekton Habitat in Enhanced Habitats: Comparison of Terraced and Unterraced Marsh Ponds

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ABSTRACT: A primary goal of many coastal restoration programs is to increase nekton habitat in terms of both quantity and quality. Using shallow water ponds rehabilitated with a technique called marsh terracing, we examined the quality of nekton habitat created, using and comparing several metrics including nekton density and diversity, functional group composition, and weight-length relationships as indirect measures of habitat quality. We examined three paired terraced and unterraced marsh ponds in southwest Louisiana. Nekton, submerged aquatic vegetation (SAV), and soil and water quality variables were sampled bimonthly from April 2004 through April 2005 at four subtidal habitat types: terraced nearshore, terraced open water, unterraced nearshore, and unterraced open water. Results indicate that terraced ponds had increased the habitat value of degrading unterraced ponds over open water areas for estuarine nekton; nekton density and richness were similar between terraced and unterraced nearshore habitat types, but greater at all nearshore as compared to open water sites. Analysis of the distribution of nekton functional groups and weight:length ratios indicates the terraced and unterraced pond habitats were not functioning similarly: distribution of nekton functional groups differed significantly between habitat types with greater percentages of benthic-oriented species at unterraced open water habitats and higher percentage of open water species in terraced ponds as compared to unterraced ponds, and two of the six numerically dominant fish species had greater weight-length relationships in unterraced ponds as compared to terraced ponds. This lack of functional equivalency may be attributed to environmental differences between terraced and unterraced ponds such as water depth or SAV biomass, or the relatively young age of the terraces studied, which may not have allowed for the development of some critical habitat variables, such as soil organic matter that was found to be significantly lower in terraced versus unterraced ponds (p < 0.05). To properly assess the ecological equivalency of restored or rehabilitated sites for nekton requires that we move beyond measures of nekton density, biomass, and diversity and incorporate measures of functional equivalency, including habitat measures.

Introduction

Determining appropriate metrics to evaluate restoration continues to be a major challenge in restoration ecology (Kentula 2000; Lockwood and Pimm 2001). Goals for ecological restoration projects often vary between measures of structural and functional equivalency (Lockwood and Pimm 2001; Peterson and Lipcius 2003). Structural equivalency, defined as the restoration of the original species composition, is most often used to assess success in coastal restoration projects based on the assumption that the function and value of a habitat is derived from its structural integrity and composition (Moy and Levin 1991; Zedler 2000). This assumption guides most restoration monitoring, despite the facts that the rate of return of function may lag years behind structural restoration (i.e., Craft et al. 1999), and little evidence for a relationship between structure and function exists (Naeem

et al. 1994; French McCay et al. 2003), making evaluation of restoration projects still more art than science.

Coastal restoration often has as a primary goal to increase fishery habitat in terms of area and quality. In this regard, most restoration projects have proceeded with the assumption that physical structure represents function, leading to the field of dreams hypothesis for fish, "if you build it they will come" (Palmer et al. 1997, p. 295). A number of studies have explicitly examined the ability of restored marsh habitats to provide equivalent nekton (fish and decapod crustaceans) habitat, as measured by nekton density, biomass, or abundance, with some finding lower density, biomass, or abundance in restored marsh habitats (Minello and Webb 1997; Minello 2000), and others finding comparable density, biomass, or abundance of nekton between restored and reference marsh habitats (Rozas and Minello 2001; Able et al. 2004; Bush Thom et al. 2004). As fish can rapidly colonize new sites, species abundance may not be the most accurate gauge of habitat value; use of these general

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indicators may mask more meaningful measures such as individual species health, nekton assemblage structure, and community ecology (Minello and Webb 1997; Callaway et al. 2001).

To move measurement of restoration success for fisheries beyond some metric of structure, other approaches are necessary. Some potential approaches include the comparison of nekton functional groups or guilds (sensu Root 1967) as an indication of habitat suitability (sensu Callaway et al. 2001; Bush Thom et al. 2004), or the use of population or standing crop estimates as a surrogate for marsh fishery value (Rozas et al. 2005). Other potential measures include fish condition (Vila-Gispert and Moreno-Amich 2000), RNA:DNA ratios (Bulow 1987), calorific values of fish tissues (Booth and Keast 1986), and protein: energy ratios (Bowen 1979), among others as indicators of fitness. While most of these require time-consuming laboratory work, a measure of basic condition requires only raw weight:length ratio data (Vila-Gispert and Moreno-Amich 2000, 2001; Oliva Paterna et al. 2003). Fish condition is considered to be an indicator of the general well-being of a population and has been used to compare condition between different habitat types (Gilliers et al. 2004), examine response to pollution (Burke et al. 1993), and inform management of fish stocks (Ratz and Lloret 2003) or endangered species (Meretsky et al. 2000), but we are aware of no study that has used this approach to assess the functional equivalency of enhanced or restored marsh habitats.

Marsh terracing is a marsh enhancement technique that was first employed in the United States at Sabine National Wildlife Refuge in Cameron Parish, Louisiana, in 1990 (Underwood et al. 1991). Marsh terracing was developed as a means to address marsh degradation occurring through the development of small shallow water ponds within interior marshes. This marsh loss is hypothesized to result from a lack of vertical accretion in the marsh, vegetation decline, and reduction of surface elevation, followed by further plant death and enlargement of these ponds (Delaune et al. 1994). Terraces are ridges or levees of discontinuous marsh that are created in these ponds by excavating subtidal sediments on-site and forming them into narrow ridges that are created at marsh elevation to be flooded at high tide. The ridges are planted with marsh vegetation, usually Spartina alterniflora. Openings are left between terraces to allow for tidal exchange and the movement of nekton throughout the pond.

While marsh terracing can not be considered a true restoration technique as it does not involve recreating a marsh landscape similar to what previously existed, it was developed as a means to enhance or improve shallow water habitat for submerged aquatic vegetation (SAV) growth, allow for potential spread of marsh emergent vegetation through the reduction of erosion, and improve nekton habitat (Underwood et al. 1991). Most terraced ponds contain a mix of emergent vegetated marsh (on terraces and in the marsh surrounding the terraced pond), and a range of nonvegetated mud bottom, to sparsely or densely vegetated (SAV) subtidal pond bottom habitats.

We examined three paired terraced and unterraced reference pond sites in southwest Louisiana. Our objective was to evaluate the quality of the fishery habitat created, using and comparing several different metrics including nekton density and diversity, functional group composition, and nekton condition as measures of habitat quality, suitability, and nekton fitness. We also examined water quality and sediment characteristics of the terraced and unterraced reference ponds. Our null hypothesis was that nekton densities, biomass, diversity, species composition, and condition would not differ between terraced and unterraced ponds.

Methods

STUDY AREA

Three hydrologically separate pairs of terraced and unterraced ponds located at Rockefeller State Wildlife Refuge (RWR; 29°40'30"N, 92°48'45"W) and Sabine National Wildlife Refuge (SWR; 29°54'N, 93°32'W), in Cameron and Vermillion Parishes, Louisiana, were sampled. RWR is a 30,700-ha area managed by the Louisiana Department of Wildlife and Fisheries. Situated between Louisiana Highway 82 to the north and the Gulf of Mexico to the south, the refuge consists of 17 impoundments (units), as well as approximately 11,700 ha of unimpounded, tidally-influenced marsh (Wicker et al. 1983). RWR units are managed using water control structures, such as flap gates, weirs, and gated culverts, to control water levels and salinity, as well as prescribed burning and structural marsh management. Marsh types at RWR range from saline marsh along the Gulf of Mexico to intermediate marsh farther to the north. SWR, a 50,388 ha area, is located between Sabine and Calcasieu Lakes and is managed by the U.S. Fish and Wildlife Service. SWR is divided into management units by a system of canals and levees, some of which are also heavily managed using prescribed burning and water management for salinity control. Marsh types on the refuge range from saline to fresh.

Site 1

Site 1 is located in Unit 4 of RWR, which is a 2,400ha impoundment that is managed via two variablecrest flap-gated structures. The area is a brackish marsh dominated by saltmeadow cordgrass *Spartina patens* (Flynn et al. 1999). The terraced pond at site 1 was located near the western edge of the impoundment and is approximately 32 ha in size. The terraces, constructed in 2002, are arranged in a duck-wing or chevron-shaped pattern and were planted with *S. alterniflora*. The unterraced pond at site 1 is approximately 65 ha in size and is located to the south of the terraced pond. Both ponds formed after 1956 but before 1978 (Barras et al. 1994). Older surveys of these ponds reported the patchy (time and space) presence of *Ruppia maritima*, *Potamogeton pusilus*, and *Myriophyllum spicatum* (Chabreck 1970).

Site 2

Site 2 is located in Unit 5 of RWR, which is a 1,982 ha impoundment directly south of Unit 4. The area is composed of brackish marsh dominated by S. patens. Levees are constructed around 3 sides of the impoundment, while the southern end is a broad beach rim at the Gulf of Mexico. The terraced pond at site 2 is located in the northern portion of Unit 5 west of Deep Lake and is approximately 59 ha in size. The terraces were constructed in 2000 in a linear pattern and were planted with S. alterniflora. Since their construction, the Unit 5 terraces have degraded severely. Only 2 complete terraces along the western border of the pond and several terrace fragments throughout the pond were present at the completion of the study. The unterraced pond at site 2 is located to the west of the terraced pond and is approximately 51 ha in size. The terraced and unterraced ponds formed after 1956 but before 1978 (Barras et al. 1994). Older surveys of these ponds reported the patchy (time and space) presence of R. maritima and P. pusilus (Chabreck 1970).

Site 3

The terraced pond at site 3 is located in Unit 7 of SWR. The area is composed of brackish marsh dominated by *S. patens.* The terraced pond is approximately 482 ha in size. The Unit 7 terraces were constructed in 2001 in a duck-wing pattern and were planted with *S. alterniflora.* The unterraced pond is approximately 1260 ha in size and is located in Unit 5 of SWR to the north of the terraced pond near an area known as Greens Lake. Unlike the ponds at RWR, these ponds formed after 1978 (Barras et al. 2003). This area is also brackish marsh dominated by *S. patens*, but with small patches of common reed *Phragmites australis* interspersed throughout. Older surveys of these ponds reported the patchy (time and space) presence of *M.*

spicatum, Najas guadalupensis, Chara spp., and Nitella spp. (Chabreck 1970).

SAMPLING DESIGN

The three study sites each contained paired terraced and unterraced ponds. Four treatments were identified for sampling: two treatments were subtidal ponds located along the marsh-water interface, defined as the waterward area within 1 m of emergent vegetation (terraced nearshore, unterraced nearshore), and two were subtidal open water, defined as greater than 50 m from any terrace or pond edge (terraced open water, unterraced open water). Due to the temporal and spatial patchiness of SAV, all four treatments included some mudbottom nonvegetated samples as well as samples with SAV. Within each pair of study ponds, two samples were taken from each treatment type identified; each site had eight nekton samples (two each of terraced nearshore, unterraced nearshore, terraced open water, and unterraced open water) per sample period, for a total of 24 samples for the three sites. Sampling began in April 2004 and occurred bimonthly over 12 mo (April, June, August, October, and December 2004 and February and April 2005) for a total of seven sample periods. Due to logistical problems, Site 3 was not sampled in October or December 2004. A total of 152 samples were collected.

Actual sample points were haphazardly selected by overlaying a grid over georeferenced Digital Orthophoto Quarter Quadrangle aerial maps of the study ponds using ArcView 3.2 (ESRI, Redlands, California). A random number generator was used to select numbers corresponding to squares within the grid. GPS coordinates obtained for each sampling point were used to locate points in the field.

ENVIRONMENTAL CHARACTERISTICS

Salinity (g l^{-1}), temperature (°C), and dissolved oxygen (mg l^{-1}) were measured with a YSI model 556 water quality meter (Yellow Springs Instruments, Yellow Springs, Ohio) at each sample point. Turbidity (NTU) was measured with a Turner Designs Aquafluor turbidimeter (Turner Designs, Sunnyvale, California). Water depth was determined by calculating the mean of three random depth measurements (cm) taken within each throw trap sample.

Soil cores were collected in May 2005 for analysis of organic matter content. Eight 5-cm diameter soil cores were collected from the top 5 cm of soil at each sampling point (64 cores per site, 128 cores total). Cores were stored on ice until processing. Upon return to the laboratory, the soil cores from each sampling point were homogenized into one composite sample. Composite samples were placed in crucibles and dried at 60° C to constant weight in a forced air drying oven. The samples were ground with a mortar and pestle and split into five subsamples. The subsamples were weighed to the nearest 0.001 g (initial dry weight), fired in a muffle furnace at 500°C for 4 h, and weighed again (final dry weight). Percent organic matter was calculated as: % organic matter = $[1 - (final dry weight/initial dry weight)] \times 100$.

NEKTON SAMPLING

Nekton was quantitatively sampled at each sample station with a 1-m^2 throw trap. The trap consisted of a $1 \times 1 \times 0.66$ m aluminum frame with 1.6-mm knotless nylon mesh sides. To facilitate sampling in water greater than 0.66 m deep the nylon mesh was extended above the frame to a total height of 1.25 m. A 1-m^2 PVC square was integrated into the top of the extended netting and buoyed by net floats. The interior of the throw trap was swept with a 1-m wide bar seine (1.6-mm mesh) to clear all nekton from the trap. The trap was considered cleared when five consecutive sweeps of the bar seine yielded no organisms. Samples were placed on ice for transport to the laboratory, where they were frozen until processing.

Upon returning to the laboratory, samples were sorted, identified to species or lowest feasible taxon, measured, counted to determine density (individuals m⁻²), and weighed to determine biomass (g m⁻²). Fish and shrimp were measured to the nearest 0.1-mm total length and crabs were measured to the nearest 0.1-mm carapace width. All nekton were weighed to the nearest 0.001 g wetweight using an Ohaus Adventurer model toploading laboratory balance (Ohaus Corp., Pinebrook, New Jersey).

SUBMERGED AQUATIC VEGETATION SAMPLING

All SAV was collected from each throw trap sample. Prior to nekton removal all aboveground SAV was collected by hand. SAV samples were placed on ice for transport to the laboratory where they were sorted according to species, dried in a forced air drying oven at 60° C to constant weight, and weighed to the nearest 0.001 g dry weight to determine SAV biomass (g m⁻²).

STATISTICAL ANALYSES

All statistical analyses were performed using SAS software (SAS Institute 1989) and an alpha level of 0.05 was used to determine significance. All data (nekton, SAV, and environmental) were tested for normality, by examining model residuals, and

homogeneity of variance to satisfy the assumptions of the statistical analyses performed. Subsequent logarithmic [log10(x+1)] transformation was necessary only for nekton density and SAV biomass data and arcsine transformation was used for proportion data. Nekton density was highly correlated with nekton biomass (Prob > |r| = 0.80, p < 0.0001), so only density data are presented.

Data analyses were based on a randomized block design, blocking by site. Two-way analysis of variance (ANOVA, Proc MIXED) was used to examine differences in nekton density, diversity (H'; Magurran 1998), species number, and environmental variables among treatments. The treatments selected for analyses were habitat type (terraced nearshore, unterraced nearshore, terraced open water, and unterraced open water) and sampling date (April, June, August, October, and December 2004 and February and April 2005), blocked on site, followed by least square (LS) means for significant results. All results presented are mean \pm standard error.

A χ^2 test was used to examine differences in nekton species composition by functional group (open-water species: Anchoa mitchilli, Archosargus probatocephalus, Brevoortia patronus, Alosa chrysochloris; marsh or SAV-oriented species: Cyprinodon variegatus, Syngnathus scovelli, Lucania parva, Menidia beryllina, Poecelia latipinna, Lagodon rhomboides, Bairdeilla chrysoura, Gobiosoma bosc, Gambusia affinis; benthic-oriented species: Microgobius gulosus, Micropogonias undulatus, Fundulus pulverous, Prionotus rubio, Lepomis spp.; crustaceans: Callinectes sapidus, Farfantepenaeus aztecus, Litopenaeus setiferous, Palaemonetes pugio, family Xanthidae) at each of the four habitat types sampled. Groupings were based on species use of estuarine habitats and draw largely on findings reported in the literature from the northern Gulf coast of Mexico (i.e., Minello et al. 1994; Peterson and Turner 1994; Minello 1999; Rozas and Zimmerman 2000).

Simple linear regression (SLR, Proc REG) was used to examine the potential relationship between SAV biomass (independent predictor variable) and nekton biomass (dependent response variable).

FISH CONDITION

A measure of fish condition was calculated for the six numerically dominant fish species found in both terraced and unterraced ponds (*G. bosc, G. affinis, M. gulosus, L. parva, P. latipinna, M. beryllina*), following the methods of Vila-Gispert and Moreno-Amich (2000, 2001) and Oliva-Paterna et al. (2003). With this approach, univariate analysis of covariance (ANCOVA) was conducted with weight as the dependent variable and length as the covariate. Length and weight data were log transformed to

TABLE 1. Mean (± SE) values for environmental variables for the four habitat types. p values are results of a two-fact	or ANOVA (habitat
type and month) for data collected at three paired terraced and unterraced ponds ($n = 3$). Significant results ($p < 0.0$	are in bold type.
Superscript letters adjacent to means denote differences identified by least squares means for habitat type.	

	Terraced		Unterraced			
Variable	Nearshore	Open water	Nearshore	Open water	р	
Depth (cm)	35.7 (2.4) ^{AB}	43.1 (3.5) ^A	32.9 (2.6) ^B	48.6 (2.9) ^c	< 0.001	
Salinity (%)	$4.6 (0.5)^{4}$	$4.4 (0.6)^{4}$	$5.4 (0.7)^{B}$	5.5 (0.7) ^B	0.006	
Temperature (°C)	21.8(1.0)	22.0 (1.0)	24.1(1.0)	23.0(1.0)	0.243	
Dissolved oxygen (mg l ⁻¹)	8.3 (0.6)	9.0 (0.5)	8.0 (0.6)	8.6 (0.6)	0.711	
Turbidity (NTU)	27.9 (3.6)	23.5 (3.2)	27.5 (4.0)	28.9 (5.6)	0.352	
SAV biomass (g m^{-2} dry weight)	22.4 (9.4)*	$16.9 (5.5)^{\text{A}}$	$1.9 (0.5)^{B}$	$0.7 (0.5)^{B}$	0.020	
Soil organic matter (%)	$11.9 \ (1.7)^{\text{A}}$	21.1 (1.5) ^B	35.6 (2.1) ^c	25.2 (2.6) ^B	< 0.0001	

ensure a linear relationship. Homogeneity of slopes for dependent-covariate relationships were tested using an ANCOVA model that included the pooled covariate-factor interaction. If the slopes were homogeneous, a standard ANCOVA model was used to test for differences in the y-intercept between treatments. In cases where slopes were heterogeneous, equality of mean weights was compared at the overall mean value of the covariate.

In order to minimize differences due to potential seasonal effects (differential cohort use), only data from the August 2004 sampling period were used for the fish condition analysis. Environmental variables (salinity, temperature, dissolved oxygen, turbidity, conductivity, organic matter, SAV biomass) associated with the August 2004 samples were analyzed using a one-factor ANOVA to examine differences among pond types, blocked on site, followed by LS means for significant results. Stepwise regression (p < 0.15) examined the explanatory value of environmental variables for log transformed weight:length ratios, for each individual species and the associated August 2004 environmental variables.

Results

ENVIRONMENTAL CHARACTERISTICS

Water quality characteristics were typical of brackish marsh environments (Table 1). No significant differences were found among the four habitat types for temperature, dissolved oxygen, or turbidity. Water depth and salinity were significantly different among habitat types with salinity differing between terraced (4.5 ± 0.4 g l⁻¹) and unterraced sites (5.4 ± 0.5 g l⁻¹) and depth differing between all four habitat types, with the exception of terraced and unterraced nearshore habitats. Soil organic matter content was significantly lower at terraced nearshore as compared to unterraced nearshore habitat.

Presence of SAV was detected in 68% of terraced pond samples and 68% of unterraced pond samples (Table 2). Analysis of SAV data found SAV biomass to be significantly higher at both site 3 terraced habitat types (nearshore and open water), in spring samples (February, April), as compared to all other site and habitat type and pond combinations; these samples accounted for $68\overline{\%}$ of the total SAV biomass collected during this project (555 of 816.2 g). M. spicatum accounted for 94% of total SAV biomass collected during this project, despite being present in only 20% of samples (only in site 3 samples). R. maritima and P. pusilus were present in 26% and 34% of samples, respectively, but each accounted for only 4% of the total SAV biomass collected. Other species collected include Vallisneria americana, N. guadalupensis, Nitella spp., Eleocharis spp., Chara spp., and Ceratophyllum demersum. Filamentous algae were also present in many samples and patterns of filamentous algae presence and absence matched those of SAV presence and biomass, although they were not included in the analysis.

TABLE 2. Comparison of mean submerged aquatic vegetation biomass (g m⁻² [\pm SE]) and percent presence of SAV of all samples collected over a 1-yr time frame (n = 152) presented by site. ANOVA for biomass (habitat type and month, by site) found a significant interaction; February and April 2005 terraced nearshore and terraced open water samples from site 3 had significantly greater SAV biomass as compared to all other habitat type by month combinations. Site 3 spring samples accounted for 68% of total biomass collected during the study. Ninety-four percent of SAV biomass (816.2 g total) consisted of *Myriophyllum spicatum* (Eurasian milfoil).

Terraced				Unterraced				
	Nearsh	iore	Open w	vater	Nears	hore	Oper	n water
Site	Biomass (g)	Presence (%)	Biomass (g)	Presence (%)	Biomass (g)	Presence (%)	Biomass (g)	Presence (%)
1	0.22 (0.12)	71	0.81 (0.66)	71	0.34 (0.17)	100	0	57
2	0.04(0.02)	50	0.02(0.01)	31	1.13 (0.67)	64	0.03 (0.02)	57
3	47.16 (15.76)	100	30.33 (14.96)	100	0.66 (0.29)	100	0	22

TABLE 3. Mean density (\pm SE) of crustacean and fish species collected during the study period by pond and habitat type (n = 3). Nekton were collected using a 1-m² throw trap at nearshore subtidal (< 1 m from emergent vegetation edge) and open water subtidal (> 50 m from emergent vegetation edge) habitats at three paired terraced and unterraced ponds bimonthly from April 2004 through April 2005. Species with total catch less than 3 organisms total are not included in the summary.

			Terraced			Unterraced		
Common name	Scientific name	Study total	Total	Nearshore	Open water	Total	Nearshore	Open water
Crustaceans								
Daggerblade grass shrimp	Palaemonetes pugio	7.0 (1.5)	5.1(1.3)	8.8 (2.4)	1.4(0.4)	8.8 (2.7)	15.3 (5.2)	2.5(1.0)
Blue crab	Callinectes sapıdus	0.9 (0.2)	0.8(0.2)	1.1 (0.4)	0.4(0.3)	1.0(0.4)	1.7(0.7)	0.3 (0.2)
White shrimp	Litopenaeus setiferous	0.6(0.2)	0.3(0.1)	0.4(0.2)	0.3(0.1)	0.8(0.3)	1.3(0.7)	0.3(0.1)
Mud crab	Xanthidae spp.	0.7 (0.3)	0.6(0.3)	1.2 (0.6)	0	0.8(0.5)	1.5(1.0)	0.02 (0.02)
Brown shrimp	Farfantepenaeus aztecus	0.04 (0.02)	0.05 (0.04)	0.1(0.1)	0	0.04 (0.02)	0.05 (0.03)	0.02 (0.02)
Fishes								
Rainwater killifish	Lucania parva	2.9 (0.5)	4.1 (1.0)	4.6 (1.4)	3.6 (1.4)	1.6(0.5)	2.5(0.8)	0.7(0.5)
Sailfin molly	Poecilia latipinna	2.4(1.4)	1.6(0.8)	1.6(1.1)	1.5(1.2)	3.1(2.6)	0.7(0.4)	5.5(5.2)
Inland silverside	Menidia beryllina	2.3(0.9)	2.0(0.8)	2.6(1.4)	1.4(0.5)	2.5(1.6)	3.7 (3.2)	1.4(0.9)
Naked goby	Gobiosoma bosc	1.7(0.4)	1.5(0.4)	2.7 (0.8)	0.3 (0.1)	1.9 (0.6)	1.9(0.5)	1.9(1.2)
Western mosquitofish	Gambusıa affinıs	0.7(0.3)	0.2(0.1)	0.2(0.2)	0.1(0.1)	1.2(0.6)	1.4(0.9)	1.0 (0.8)
Clown goby	Microgobius gulosus	0.5(0.1)	0.6(0.2)	0.6(0.3)	0.6(0.2)	0.5(0.2)	0.4(0.2)	0.4(0.3)
Sheepshead minnow	Cyprinodon variegatus	0.5(0.1)	0.5(0.2)	0.3(0.1)	0.6 (0.3)	0.4(0.2)	0.8(0.5)	0.1(0.1)
Sunfish	Lepomis spp.	0.4(0.3)	0.9(0.7)	1.6(1.4)	0.1(0.1)	0	0	0
Gulf pipefish	Syngnathus scovelli	0.4(0.1)	0.7(0.2)	1.1 (0.4)	0.4(0.2)	0.1 (0.05)	0.2(0.1)	0.02(0.02)
Bay anchovy	Ánchoa mitchilli	0.2(0.1)	0.2(0.1)	0.3(0.1)	0.1(0.1)	0.2(0.1)	0.3(0.3)	0.1(0.1)
Silver perch	Bairdiella chrysoura	0.1(0.1)	0.1(0.1)	0	0.3(0.3)	0.01 (0.01)	0	0.02 (0.02)
Bluegill	Lepomis macrochirus	0.1 (0.04)	0.1(0.1)	0.2(0.1)	0.1 (0.04)	0	0	0
Gulf menhaden	Brevoortia patronus	0.06 (0.05)	0.1(0.1)	0.2(0.2)	0	0	0	0
Atlantic croaker	Micropogonias undulatus	0.1 (0.1)	0.2(0.1)	0.3 (0.3)	0	0.1 (0.04)	1	0.1 (0.1)

NEKTON

A total of 3,544 organisms were collected representing 25 taxa (Table 3; unpublished data available from the author). Total catch consisted of 57% fish (2,033 individuals, 20 species) and 43% crustaceans (1,511 individuals, 5 species). The most frequently collected fish species were rainwater killifish *L. parva* (n = 465), sailfin molly *P. latipinna* (n = 392), and inland silverside *M. beryllina* (n = 387). The most frequently collected crustacean species were daggerblade grass shrimp *P. pugio* (n = 1,171), blue crab *C. sapidus* (n = 150), and white shrimp *L. setiferous* (n = 93).

The composition of total catch differed between terraced and unterraced ponds. In terraced ponds, total catch consisted of 65% fishes (1,061 individuals, 17 species) and 35% crustaceans (562 individuals, 5 species). In unterraced ponds, total catch consisted of 51% fishes (972 individuals, 14 species) and 49% crustaceans (949 individuals, 5 species).

Distribution of nekton functional groups differed significantly among the four habitat types (χ^2 : p < 0.0001; Fig. 1). Percent of total catch of benthicoriented species was highest in unterraced open water habitats (46%) as compared to other habitat types. Percent total catch of open water species was higher in terraced (> 4%) as compared to unterraced ponds (< 4%), and highest at terraced open water habitats (5%). Percent total catch of marsh-SAV oriented species was highest in terraced ponds (> 42%) as compared to unterraced ponds



Fig. 1. Total percent catch composition at terraced edge, unterraced edge, terrace open water, and unterraced open water habitat sites. Percent of each functional group was significantly different by habitat for (1) open water species: Anchoa mutchilu, Archosargus probatocephalus, Brevoortia patronus, Alosa chrysochloris, (2) marsh or SAV-oriented species: Cyprinodon vanegatus, Lucania paroa. Syngnathus scovelli, Menidia beryllina, Poecelia latipinna, Lagodon rhomboides, Bairdeilla chrysoura, Gobiosoma bosc, Gambusia affinis, (3) benthic-oriented species: Microgobius gulosus, Micropogonias undulatus, Fundulus pulverous, Prionotus rubio, Lepomis spp.; and (4) crustaceans: Callinectes sapidus, Farfantepenaeus aztecus, Litopenaeus setiferous, Palaemonetes pugio, Family Xanthidae (Chisquare for overall model: p < 0.0001; n = 3, 544). Catch data are based on bimonthly throw trap sampling.

TABLE 4. Comparison of mean (\pm SE) values of nekton density, number of species, and diversity (H') by habitat type for three paired terraced and unterraced ponds. A two-factor ANOVA (habitat type, period) blocked on pond found significant habitat type effects with terraced and unterraced nearshore habitats, supporting higher nekton densities as compared to terraced and unterraced open water sites. Similar analysis of species number found a significant habitat type effect with terraced and unterraced nearshore sites supporting greater numbers of species as compared to unterraced open water sites. Diversity was not found to differ significantly by habitat type or month. Superscript letters adjacent to means denote differences identified by least squares means for habitat type.

	Terrace	Terraced pond		Unterraced pond		
	Nearshore	Open water	Nearshore	Open water		
Density (individuals m ⁻²)	30.3 (6.0) ^A	12.4 (2.9) ^B	34.5 (7.4) ^A	 16.0 (9.7) ^в		
Number of species (m ²)	3.6 (0.3) ^A	2.5 (0.3) ^{AB}	3.3 (0.3)*	$1.4 (0.3)^{B}$		
Diversity (H')	0.9 (0.1)	0.8 (0.1)	0.7 (0.1)	0.6 (0.2)		

(< 35%). Crustaceans were higher at nearshore habitats as compared to open water habitats, and highest at unterraced nearshore habitats (62%) as compared to terraced nearshore habitats (42%).

Nekton density and species number differed significantly between habitat types (p < 0.05; Table 4). Nekton density was significantly higher at both terraced and unterraced nearshore habitats as compared to terraced and unterraced open water sites. Species number was significantly higher at both terraced and unterraced nearshore sites as compared to unterraced open water sites. Diversity did not differ significantly by habitat types or month (p = 0.07).

Nekton density was positively related to SAV biomass (p < 0.0001). This relationship can be described by the following regression equation: log nekton density = $1.92 + 0.44(\log SAV \text{ biomass})$. The explained variance (r^2) for the model was 10%.

FISH CONDITION

For the August 2004 sample period, there was a significant degree of homogeneity of slopes of the weight-length relationship between ponds for *G. bosc* and *G. affinis*, so the y-intercept was used to determine condition. Slopes of the weight-length relationship for *M. gulosus*, *L. parva*, *P. latipinna*, and *M. beryllina* were not homogeneous between pond types, so LS means were used to test for differences in condition at the mean length value for each of these species.

For *M. gulosus* and *P. latipinna*, condition was significantly lower for fish collected in terraced ponds as compared to those collected in unterraced ponds. There was no significant difference in condition between terraced and unterraced ponds for *L. parva*, *G. affinis*, *G. bosc*, or *M. beryllina* (Table 5).

In the August 2004 data, significant differences were found among ponds for water depth, salinity, temperature, turbidity, SAV, biomass and percent organic matter with greater water depth and SAV biomass in terraced ponds, and lower organic matter, salinity, turbidity, and temperature in terraced ponds as compared to unterraced ponds (Table 6). Stepwise regression analysis of the log of the weight:length ratios by species with environmental variables indicated a significant relationship only for *L. parva* for organic matter ($r^2 = 0.05$; p = 0.0750).

Discussion

A recent study assessing estuarine habitat value suggests that multiple measures are required to fully assess habitat value: nekton density, assessment of the functional significance of habitat, and temporal

TABLE 5. Weight-length ANCOVA regressions of the six dominant species collected in three paired terraced and unterraced subtidal ponds in August 2004. ANCOVA p values for differences between treatments for the six most frequently collected fish species by pond type (T = terraced, U = unterraced).

Species	Pond Type	Regression	ANCOVA p	
Gambusia affinis	T	$y=3.3325x-4.58 r^2=0.97$	0.74	
55	U	$y=3.1164x-4.39 r^2=0.95$		
Microgobius gulosus	Т	$y=2.5522x-4.262 r^2=0.98$	0.05	
0 0	U	$y=2.7328x-4.3661 r^{2}=0.98$		
Menidia beryllina	Т	$y=2.8361x-4.7652 r^{2}=0.99$	0.18	
-	U	$y=2.8182x-4.7302 r^{2}=0.96$		
Gobiosoma bosc	Т	$y=3.0677x-4.3381 r^{2}=0.99$	0.90	
	U	$y=2.9545-4.26 r^2=0.94$		
Poecilia latıpınna	Т	$y=2.9489x-4.0112 r^{2}=0.98$	0.03	
-	U	$y=3.0707x-4.1887 r^{2}=0.96$		
Lucania parva	Т	$y=2.9167x-4.3492 r^{2}=0.95$	0.23	
-	U	$y=2.9847x-4.3602 r^{2}=0.97$		

TABLE 6. Mean (\pm SE) values for environmental variables by pond type for August 2004 samples of the six dominant species used for ANCOVA, for three paired terraced and unterraced pond sites. p values are results of a one-factor ANOVA (pond type). Significant results (p < 0.05) are in bold type.

Variable	Terraced pond	Unterraced pond	р
Depth (cm)	29.9 (0.7)	13.4 (0.2)	< 0.0001
Salinity (%)	0.6 (0)	1.1(0.1)	< 0.0001
Temperature (°C)	25.9 (0.1)	28.7(0.1)	< 0.0001
Turbidity (NTU)	17.7 (0.6)	25.4 (3.6)	< 0.0123
SAV biomass (g m ⁻² dry weight)	12.2 (0.7)	0.04 (0.0)	< 0.0001
Soil organic matter (%)	15.5 (0.6)	30.4 (0.2)	< 0.0001

and spatial measures of habitat diversity (Meng et al. 2004). In this study, we assessed and compared the results of three different metrics for valuing restored nekton habitat. Based on comparisons of basic structural measures (i.e., nekton density, diversity, and biomass), our results indicate that terracing improves the habitat value of degrading marsh ponds for estuarine nekton; nekton density, biomass, and diversity are all increased through the conversion of shallow open water habitat to nearshore habitats. Our other two lines of evidence suggest that the terraced ponds still lack functional equivalency with comparable unterraced ponds: nekton community composition differed between terraced and unterraced subtidal pond habitats, and two out of six fish species were found to be in poorer condition as measured by weight-length relationships in terraced ponds as compared to unterraced ponds. The three metrics results do not contradict one another; each one provides a different piece of the picture in assessing the functional equivalency of two habitats (in this case terraced and unterraced ponds). This lack of functional equivalency between terraced and unterraced ponds, highlighted by differences in fitness (i.e., condition) and habitat suitability (i.e., species composition), may simply reflect nekton response to site specific environmental differences such as water depth and SAV biomass in the studied ponds, or may be partially attributable to the relatively young age of the terraces studied, which may not have allowed for the long-term development of some environmental variables, such as soil organic matter.

Because marsh terracing converts areas of open water to marsh edge, comparisons of these two habitat types (open water, terraced marsh edge) have been used to evaluate the success of past terracing projects (i.e., Rozas and Minello 2001, In press; Bush Thom et al. 2004). Findings from these two studies, comparable to our findings that nekton densities are greater at terraced nearshore habitats in comparison to open water habitat, also reflect nonrestoration specific studies that document the value of marsh edge as habitat for nekton (Minello et al. 1994; Peterson and Turner 1994). Marsh terracing does appear to enhance habitat value for nekton by converting areas of lower quality open water habitat to higher quality nearshore habitat. These findings support the conclusions of Rozas and Minello (2001) that to maximize the effect of a marsh terracing project on nekton habitat, the amount of marsh edge created should be maximized.

In previous studies of nekton in terraced marsh ponds in the same region, actual nekton densities have varied considerably. Bush Thom et al. (2004) reported mean nekton densities of 3.3 individuals m^{-2} along the terrace edge and 1.3 individuals m^{-2} in open water. Rozas and Minello (2001) found much higher densities of up to 110.3 individuals m^{-2} (107.2 crustaceans, 3.1 fish) along the terrace edge and 14.7 individuals m⁻² (10.9 crustaceans, 3.8 fish) in reference pond open water. While the mean density value for open water was similar in our study to that of Rozas and Minello (2001; 16.0 individuals m^{-2}), the mean density values for terraced edge $(30.2 \text{ individuals } m^{-2})$ fell between the densities reported in the two previous site specific studies. The higher number for Rozas and Minello's (2001) study likely reflects their sampling of the emergent marsh surface as opposed to the nearshore subtidal pond bottoms sampled by Bush Thom et al. (2004) and in this study. A review using data from 22 studies in estuarine areas of the northern Gulf of Mexico reported mean nekton densities ranging from 36.0 to 83.5 crustaceans m^{-2} and 7.7 to 14.9 fish m⁻² at marsh edge habitats, depending on the type of emergent vegetation present, and 5.5 crustaceans m^{-2} and 10.5 fish m^{-2} at shallow unvegetated bottom habitats (Minello 1999). In another study from a Louisiana estuary, nekton densities ranged from 12.4 to 32.4 individuals m⁻² at the marsh edge (Baltz et al. 1993). As indicated by the above literature, nekton densities can vary greatly, which may be attributable to specific properties of the sites, sampling gear, time of day, time of year, or different definitions of marsh edge or nearshore habitat.

While the nekton density numbers indicate an increase in habitat value between open water and terraced nearshore habitats, nekton community composition, compared between terraced and unterraced nearshore habitats, differed significantly in our study, indicating some underlying habitat differences. The greatest proportion of total catch at nearshore habitats consisted of crustaceans, with a greater proportion at unterraced edge (62%) as compared to terraced edge (42%). These findings are similar to previous studies of restored terraced

edges and open water habitat (Rozas and Minello 2001; Bush Thom et al. 2004). Differences in abundance of crustacean species at terraced and unterraced edge habitats could be caused by differences in the availability of suitable benthic prey, although this was not quantified in our study. Decapod crustaceans are known to feed on benthic infauna and epifauna (Hunter and Feller 1987). Minello and Zimmerman (1992) found a positive correlation between density of benthic infauna and density of decapod crustaceans, and found that diversity of infauna was significantly greater in natural as compared to created salt marshes. Terraced sites had more marsh-SAV oriented species, possibly a reflection of the greater SAV biomass found in terraced ponds, and the increased marsh habitat created by the terraces themselves.

We examined the weight-length relationship of dominant fish species as a third indicator of habitat value. Fish condition (length:weight ratios) has been shown to be influenced by fish density and environmental conditions such as food supply, oxygen concentration, and water temperature and has been used as an integrative measure of environmental conditions (Gilliers et al. 2004). Of the six species examined, condition was lower in terraced ponds for two species (M. gulosus, P. latipinna) and similar between pond types for the four remaining species (L. parva, G. affinis, M. beryllina, G. bosc). The lower condition of M. gulosus and P. latipinna from terraced ponds could be attributed to a number of causes including both abiotic or biotic factors. In this study, we were only able to quantify environmental differences, but none were significant factors in regressions explaining the weight: length ratios of these two species. Temperature and salinity were both lower in the terraced pond as compared to the unterraced pond and could affect fish condition, although species specific data are needed to identify the significance of the actual differences detected (i.e., terraced pond temperature $25.9^{\circ}C \pm 0.1$; unterraced pond temperature $28.7^{\circ}C \pm 0.1$).

SAV biomass, one habitat characteristic often valued as it may provide both refuge from predators and a rich food source for nekton (Rozas and Odum 1988; Heck et al. 2003), was in this study associated with greater nekton densities, but was also higher in terraced ponds where the two fish had lower condition. While there was a significant relationship between SAV and nekton density and biomass for the entire study, SAV biomass was not related to fish condition for any of the six species tested in the August samples. This lack of a significant relationship may be due to the minimal amount of SAV found in the majority of our August samples; Heck and Orth (1980) argued that minimal vegetation, in terms of biomass or percent cover, offers poor refuge. Recent studies in the northeast and in Louisiana provide data supporting this contention (Raposa and Oviatt 2000; Kanouse et al. 2006).

A second environmental factor that was significantly greater in terraced ponds was water depth; water depth has been found to affect the size class distributions of nekton in shallow water areas with smaller fish finding reduced predation risk from predators in shallower waters (Ruiz et al. 1993). This depth difference could potentially have resulted in smaller size classes locating in the shallower unterraced ponds, and the larger size classes locating in the deeper terraced ponds, although our data fail to support this hypothesis (Table 5).

Terraced ponds were also found to have significantly lower organic matter. Differences in soil organic matter between natural and constructed marshes have been positively linked to differences in benthic infaunal communities (Moy and Levin 1991; Sacco et al. 1994; Levin et al. 1996). In gut content analysis of mummichogs Fundulus heteroclitus collected in North Carolina, major differences were observed in the diets of fish collected in natural and constructed marshes (Moy and Levin 1991). There were differences in the composition of meiofauna and macrofauna consumed by F. heteroclitus as well as plant detritus; fish from the natural marshes consumed more plant detritus than fish from the constructed marsh. It is possible that the differences we detected reflect differences in infauna and plant productivity between the terraced and unterraced ponds, although this was not examined. Located at the base of the estuarine food web, marsh infauna are an important component linking the primary production of the marsh to surrounding waters and are needed for a marsh to reach full functional equivalency (Sacco et al. 1994; Craft et al. 2003).

Several recent quantitative studies have examined aspects of restored wetlands in order to determine functional equivalency trajectories of restored wetlands (Zedler and Callaway 1999; Morgan and Short 2002). This trajectory research indicates that various ecological processes linked to soil characteristics and vegetative productivity may develop at different rates. Aboveground and belowground biomass of Spartina has been found to be similar between restored and reference marshes within 3-5 yr of construction (Craft et al. 1999); benthic invertebrate communities of restored marshes may take 10-15 yr to reach equivalency with reference sites (Craft et al. 1999); while soil properties such as organic carbon and nitrogen, may take more than 30 yr to develop (Craft et al. 1999). In a study of constructed marshes ranging from 1 to 28 years of age, Craft et al. (2003) found that ecological attributes linked to heterotrophic processes (invertebrate density, carbon mineralization) were strongly tied to levels of organic carbon in the top 10 cm of soil. Most ecological processes reached equivalence to natural marshes after 5–15 yr when carbon and nitrogen reached critical levels in the soil.

The three terraced ponds investigated were all 3-4 yr of age at the time of the study. Although nekton density, biomass, species number, and diversity were similar between terraced and unterraced ponds, the composition of the nekton communities differed, and condition of two numerically dominant fish was found to be lower in terraced ponds as compared to unterraced ponds. These findings indicate that, for assessment of ecological equivalency of rehabilitated or restored sites for nekton, it is essential that we move beyond measures of nekton density, biomass, and diversity and incorporate measures of functional equivalency; this may include nekton community (i.e., structure, diversity) and species condition, as well as habitat measures. Quantifying more precisely the development trajectory of key ecosystem functions linked to soil characteristics and vegetative productivity, and the most important characteristics influencing nekton habitat use is important for better informing our rehabilitation efforts of coastal habitats and identifying the necessary order of ecosystem assembly.

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