

TOPOGRAPHIC HETEROGENEITY INFLUENCES FISH USE OF AN EXPERIMENTALLY RESTORED TIDAL MARSH

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Abstract. Ecological theory predicts that incorporating habitat heterogeneity into restoration sites should enhance diversity and key functions, yet research is limited on how topographic heterogeneity affects higher trophic levels. Our large (8-ha) southern California restoration experiment tested effects of tidal creek networks and pools on trophic structure of salt marsh habitat and high-tide use by two regionally dominant fish species, California killifish (*Fundulus parvipinnis*) and longjaw mudsucker (*Gillichthys mirabilis*). We expected tidal creeks to function as “conduits” that would enhance connectivity between subtidal and intertidal habitat and pools to serve as microhabitat “oases” for fishes. Pools did provide abundant invertebrate prey and were a preferred microhabitat for *F. parvipinnis*, even when the entire marsh was inundated (catch rates were 61% higher in pools). However, *G. mirabilis* showed no preference for pools. At a larger scale, effects of tidal creek networks were also mixed. Areas containing creeks had 12% higher catch rates of *G. mirabilis*, but lower catch rates and feeding rates of *F. parvipinnis*. Collectively, the results indicate that restoring multiple forms of heterogeneity is required to provide opportunities for multiple target consumers.

Key words: *Fundulus parvipinnis*; *Gillichthys mirabilis*; invertebrates; microtopography; restoration; salt marsh; tidal creeks; Tijuana Estuary; topographic heterogeneity.

INTRODUCTION

Habitat heterogeneity has broad effects on the structure and functioning of ecosystems (Watt 1947, Pickett and Cadenasso 1995, Palmer and Poff 1997), but knowledge from natural systems is not always used in ecological restoration (Larkin et al. 2006). Topographic heterogeneity is especially important in wetlands, where <5 cm of variation in elevation can shift hydrologic conditions and biotic responses (Vivian-Smith 1997). Natural wetlands have tussocks, hummocks, hollows, pools, and creeks, while restored wetlands are often smooth and homogeneous (Barry et al. 1996, Stolt et al. 2000, Bruland and Richardson 2005, Larkin et al. 2006). Without heterogeneous features, restoration sites might not effectively deliver ecosystem functions, such as food web support (e.g., Williams and Zedler 1999, Minello and Rozas 2002, Able et al. 2003).

Tidal wetlands offer unique opportunities to test the effects of topographic heterogeneity on trophic structure, because spatial variations interact strongly and predictably with daily flooding and drainage. Southern

California’s mixed semidiurnal tidal regime has two high and two low tides of differing amplitude per day (Maloney and Chan 1974), plus weekly and seasonal patterns (two sets of greater amplitude [spring] and two sets of lesser amplitude [neap] tides per lunar cycle and greatest tidal amplitudes around the December and June equinoxes). Water level data from San Diego, California (NOAA 2006), indicate that the lower elevation of the intertidal marsh plain (0.7 m National Geodetic Vertical Datum [NGVD]) was inundated for ~63% of the year 2000, while the upper elevation (1.0 m NGVD, just 30 cm higher) was submerged only 41% of that year. The availability of the marsh plain to fishes is not persistent, but varies as tidal regimes and topography interact: Depressions that drain or evaporate during neap tides become pools during spring tides, while tidal creeks function as periodic links between salt marsh and subtidal habitats. Since fish are key components of estuarine food webs and respond rapidly to changing habitat conditions (Kwak and Zedler 1997, Jordan et al. 1998, Able and Ragan 2003, West et al. 2003), their response to site heterogeneity is an important indication of restoration effectiveness.

Topographic heterogeneity is important to fish support and trophic functioning in tidal marshes. Salt marsh pools contain abundant algae and invertebrates and act as refugia for fishes (Daiber 1982, Smith and Able 1994, Stevens et al. 2006). When topographic variability declines, e.g., following *Phragmites australis* invasion of

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U.S. Atlantic marshes, the reduction of standing-water microhabitats results in lowered macroinvertebrate richness and density and reduced feeding functions for fishes (Angradi et al. 2001, Able et al. 2003). Tidal marsh creek networks impart horizontal and vertical heterogeneity and increase connectivity with subtidal waters, enhancing exchanges of nutrients, detritus, and biota between wetlands and estuarine or marine habitats (Zedler et al. 1992, Michener et al. 1997). Creeks increase the length of intertidal–subtidal edge, extend inundation times, make it easier for subtidal fishes to access marsh surfaces, and are associated with higher densities of fishes and invertebrates (Minello et al. 1994, Peterson and Turner 1994, Desmond et al. 2000, Madon et al. 2001, Williams and Desmond 2001). As components of restoration, creeks and pools can increase biotic equivalence with reference sites (Minello and Rozas 2002, Adamowicz and Roman 2005).

Two fishes make substantial use of southern California salt marsh habitat (Talley 2000). *Gillichthys mirabilis* (longjaw mudsucker) tolerates low oxygen concentrations and is associated with soft, muddy bottoms (Williams et al. 2001), while *Fundulus parvipinnis* (California killifish) is an active, school-forming fish that forages across the marsh surface. Both feed predominantly on epibenthic invertebrates, which are primarily supported by algae (Kwak and Zedler 1997, Williams et al. 2001, West et al. 2003). On the marsh plain, *F. parvipinnis* can obtain up to six times as much food as when confined (by low tides) to estuarine channels (West and Zedler 2000). *Fundulus parvipinnis* are largely visual predators, so daytime marsh-plain access is important. Such access is especially limited from March to May. A bioenergetics model predicts that *F. parvipinnis* would lose weight and die without marsh-plain access (Madon et al. 2001).

We tested fish support functions in an 8-ha experimental restoration site (with a semi-diurnal mixed tide) that was designed to test the importance of topographic heterogeneity (replicate areas with and without tidal creek networks; Zedler 2001). We hypothesized that fish would be more abundant in areas with tidal creek networks than without (Minello et al. 1994, Desmond et al. 2000). We also explored the influence of seasonal and interannual effects, including variable water levels, accessibility of the marsh surface to fish, and variable estuary-wide population sizes. Following the bioenergetics model of Madon et al. (2001), we tested the prediction that *F. parvipinnis* uses the marsh in synchrony with seasonal high tides. Finally, we hypothesized that pools would have higher densities of prey items, greater use by fishes, and higher fish feeding rates than non-pools (Angradi et al. 2001, Able et al. 2003).

METHODS

Study approach

We assessed source populations of *G. mirabilis* and *F. parvipinnis* throughout the Tijuana River National

Estuarine Research Reserve, California, USA (hereafter Tijuana Estuary), by analyzing the monitoring record. Within the 8-ha restoration site, we assessed fish use of the salt marsh during high tides over a six-year period, comparing areas with and without tidal creek networks, as well as years, months, pool, and non-pool areas, and areas of different vegetation and with high vs. low plant cover. We conducted in-situ fish-feeding experiments to detect differences based on year, month, creek presence or absence, and pools vs. vegetated areas. We assessed trophic resources as algal chlorophyll and invertebrate abundance among months and in pools vs. vegetated areas.

Study area

Tijuana Estuary (32°35' N, 117°07' W) is located in San Diego County, California, USA, just north of the international border with Mexico. Three-fourths of its 4500-km² watershed lies in Mexico. It is a 1024-ha salt marsh-dominated estuary in the Californian biogeographic region, which has a Mediterranean-type climate characterized by dry summers and cool, wet winters (Zedler et al. 1992).

Although designated a Ramsar Wetland of International Importance in 2005 (Ramsar Convention 2006), Tijuana Estuary is vulnerable to impacts from its rapidly urbanizing watershed. The city of Tijuana, Mexico, upstream of the estuary, has developed steep, sparsely vegetated hillsides (Ward et al. 2003) that discharge sediments following winter storms, leading to short-term (6–9 month) marsh-surface accretion as high as 9.5–12.7 cm (Ward et al. 2003, Wallace et al. 2005).

Estuarine fish populations

The Pacific Estuarine Research Laboratory (PERL) monitored fish populations during the project. PERL sampled quarterly at three third-fourth order tidal channels distributed throughout Tijuana Estuary (West et al. 2002). At each location, two blocking nets spanning the width of the channel were positioned ~10 m apart to confine fishes. A bag seine (13.3 × 2.1 m, 3-mm square mesh) was swept between the blocking nets and across the channel to the opposite bank. Passes were repeated (typically 3–5 times) until the number of fish captured per pass approached zero. Sampling was performed in winter, spring, summer, and fall, during the slack period of low neap tides. Dates and months varied based on tidal conditions. Trapped fish were identified to species and their lengths measured (West et al. 2002).

Densities of fishes (total number of individuals per square meter) were calculated by species. We normalized densities using $\log(x + 1)$ -transformation and analyzed them using linear models in R 2.3.1 (R Development Core Team 2006).

Experimental design

The 8-ha Friendship Marsh was designed as an experiment (areas with and without tidal creek net-

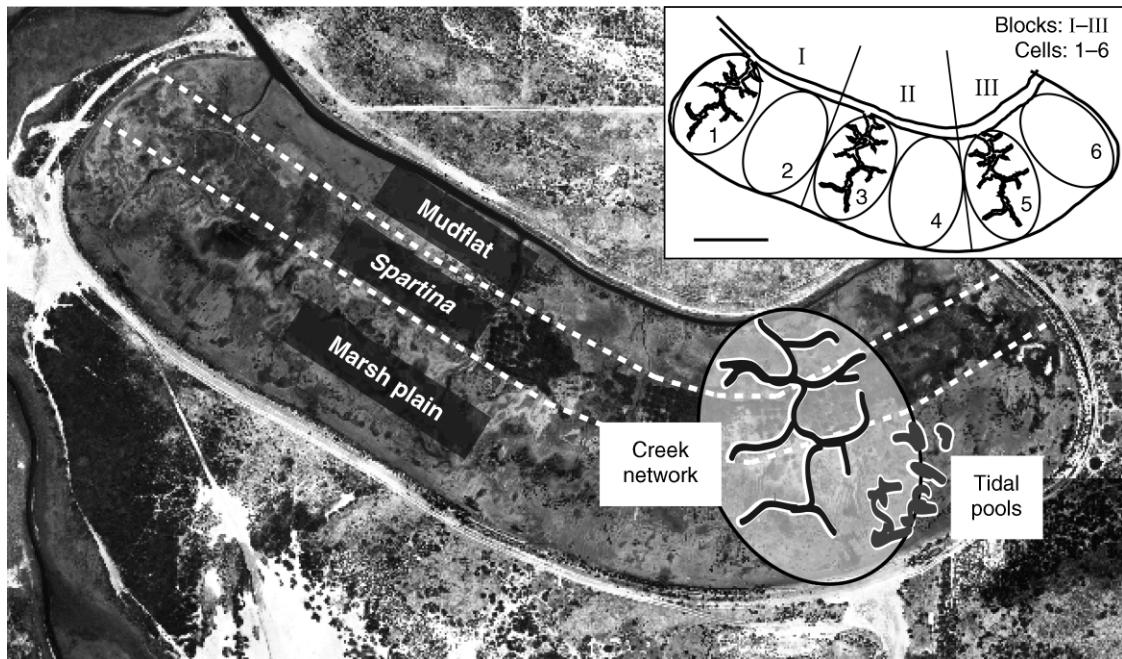


FIG. 1. A 2002 multispectral aerial photo of the Friendship Marsh in Tijuana Estuary, California, USA. The inset shows the experimental design of the site, with three replicate cells containing built tidal creek networks and three replicates without tidal creeks. The site contains three different elevation–vegetation zones: higher marsh plain, intermediate zone dominated by *Spartina foliosa*, and low mudflat adjacent to channel that provides tidal flow. Illustrations highlight one of the tidal creek networks and a subset of tidal pools.

works; Entrix et al. 1991), excavated in 1999 and opened to tidal flushing in February 2000 (Zedler et al. 2003). Tidal creeks were patterned after a third-order tidal creek network elsewhere in the estuary that has a comparable drainage area (Wallace et al. 2005). Three replicate “cells” (~1.3 ha each) have tidal creek networks and three do not; they are paired in a complete block design (Fig. 1). Each cell has unplanted mudflat (initially ~0.3-m elevation [NGVD 29], adjacent to subtidal channel), *Spartina* zone with *Spartina foliosa* (Pacific cordgrass) planted as plugs, and marsh plain (~0.8-m elevation) planted with five halophyte species (Wallace et al. 2005). Plantings and soil preparations were the same in all cells to avoid confounding creek treatments (O’Brien and Zedler 2006).

Geomorphological changes with possible relevance to fish support functions are summarized here (from Wallace et al. 2005). “Volunteer” creeks formed in areas not intended to have creeks, but they covered less than one-fourth the area of constructed creeks and did not extend onto the marsh plain. Constructed creek networks were reduced in depth by sedimentation, but they elongated, increasing their overall drainage areas. Sediment inputs led to marsh surface accretion that averaged 1.3 cm/yr with episodic sedimentation as high as 9.5 cm over 6 months. Resuspension of sediments in summers led to elevation changes as great as –12.8-cm over a six-month period and formation of shallow pools throughout the marsh plain. The largest area of pools

formed in the eastern cells. Sedimentation during the 2004–2005 rainy season eliminated pools throughout much of the marsh. Cells 5 and 6 had the highest area of pools both before (Wallace et al. 2005) and after the 2004–2005 rainy season (D. Larkin, *personal observation*). In 2005, ~42% of the marsh plain was pools (from line transects; A. Varty, *unpublished data*). The bare marsh plain and mudflat (2000–2003) became dominated by *Salicornia virginica* (pickleweed). From April 2004 to September 2005, plant cover increased from 12% to 53% in the mudflat, 76% to 97% in the *Spartina* zone, and 8% to 21% in the marsh plain (based on aerial photos; Zedler and West, *in press*).

Fish trapping

We assessed fish use of the site with steel minnow traps (42 cm long, 23 cm widest diameter, 0.64-cm square mesh, 2.2 cm diameter entrance holes on each end) staked to the marsh surface. Minnow traps cannot be used to estimate fish densities and are prone to species-specific biases (Kneib and Craig 2001, Layman and Smith 2001). However, past research has demonstrated that minnow traps are effective sampling devices for the few species that typically use salt marsh habitat in southern California (Ambrose and Meffert 1999, Talley 2000, West and Zedler 2000). Their low cost and easy deployment make minnow traps efficient sampling devices for achieving high replication with low impacts to sensitive habitats (Rozas and Minello 1997, Layman

and Smith 2001). Precautions we took to limit sampling biases included recording and/or calculating the duration of inundation ("soak time") for each trap and placing traps so that their entrances were readily accessible.

Each trap was baited with two cut anchovies, set prior to high spring tides, and retrieved after the tide had receded. We recorded species identity, numbers of individuals per species, and the total length (TL) of each individual. The amount of time that tide water remained high enough for fish to access each trap was recorded during daytime sampling events. For nighttime trapping events, we set traps out in the late afternoon to early evening and collected them at dawn the following day. We estimated inundation times for nighttime trapping using regressions between daytime inundation data and NOAA-reported tide heights (NOAA 2006).

On each sampling date, we deployed 10 traps in each of the 6 cells. During 2000–2002 sampling events, five traps per cell were in the *Spartina* zone and five were on the marsh plain. In 2003–2004, we changed sampling locations to test the effects of pools and plant cover. We set six traps in the *Spartina* zone of each cell, with three of those traps in areas with low plant cover (25–50%) and three in areas with high plant cover (>50%). We placed four additional traps on the marsh plain in each cell: two in shallow pools, one in low cover (<25%), and one in high cover (>50%). Traps in cells with creeks were generally placed near to creek networks (≤ 5 m), but this varied depending on proximity of appropriate pool and plant cover conditions. In 2005, sampling on the marsh plain followed the 2003–2004 protocol, but we did not deploy traps in the *Spartina* zone due to nesting by an endangered bird, the Light-footed Clapper Rail (*Rallus longirostris levipes*). In all, 2089 traps were deployed during 40 sampling events (19 daytime, 21 nighttime) from 2000 to 2005.

In general, trapping was performed monthly during high spring tides from spring to fall, but there was annual variability in trapping occurrence. In 2001, fish trapping was suspended in July but resumed in September. Intense storms and flooding precluded trapping in October 2004.

We used data from traps to calculate each fish species' catch per unit effort (CPUE, number of fish per species per trap per hour of inundation), a measure of relative abundance. CPUE data were "zero-inflated" (many samples with zero individuals of a given species), as is common in fishery data and counts of rare species (Ye et al. 2001, Cunningham and Lindenmayer 2005). Such data require specialized statistical approaches as they violate distributional assumptions of standard statistical models. We employed a statistical approach from econometrics, a pooled Tobit model, developed for data that are (1) zero-inflated, (2) when positive, come from a continuous distribution, and (3) are collected using a mixed-effects or repeated-measures design (Woolridge 2002). CPUE data for *F. parvipinnis* and *G. mirabilis*

were square-root transformed to increase normality of nonzero values and analyzed using a Tobit regression model for panel data with maximum-likelihood estimation in STATA 9.2 (StataCorp 2007). We verified conclusions from the Tobit model using conventional logistic regression (for frequency of occurrence, i.e., presence/absence) and mixed-effects models (for nonzero CPUE values). The results from these analyses were consistent with the Tobit model, but were more difficult to interpret (two independent analyses) and were dependent upon frequency of occurrence, which does not factor in inundation time.

We used regression tree analyses to identify variables that best explained *F. parvipinnis* and *G. mirabilis* abundance. In regression tree analysis, data are recursively split into increasingly homogeneous groups. The higher in the tree a variable appears, the more variation it explains, while factors unimportant in explaining variation are pruned out of the tree. This nonparametric method is robust against outliers, non-normal distributions, and correlation of variables (Urban 2002). We constructed regression trees using the rpart package in R 2.3.1 (R Development Core Team 2006, Therneau and Atkinson 2006) with data for *G. mirabilis* from 2000 to 2005 and for *F. parvipinnis* from 2003 to 2005 (when pool effects were tested and identified as important for this species). Variables were CPUE (dependent), year, month, predicted high tide, whether trapping occurred during the day or at night, block, creek or non-creek cell, marsh plain or *Spartina* zone, and pool or non-pool (*F. parvipinnis* only).

Fish-feeding experiments

We assessed feeding by *F. parvipinnis* via experiments in which fish were enclosed on the marsh during inundation by a daytime high spring tide (tide height >1.7 m). Enclosures were wooden frames with 0.64-m square galvanized metal hardware cloth walls. They were 1 m² in area with open tops and open, staked bottoms that were sunk several centimeters into the marsh surface.

One to two days prior to each sampling event, we seined tidal creeks within Tijuana Estuary to capture live specimens of *F. parvipinnis*. Captured fish lengths ranged from 27 to 78 mm with a mean TL of 52.7 ± 0.24 mm (mean \pm SE). Fish were held unfed for ~24 h in aquaria containing water collected at capture locations; bubblers were used for oxygenation. During sampling, we placed 5–7 individuals (depending on availability) in each of 24 screened 1-m² enclosures as water began to rise over the marsh surface and kept them there throughout a high-tide feeding opportunity. As tide waters receded, we recovered fish using aquarium nets, anesthetized them with MS-222, and preserved them in 70% ethanol (Nickum 2004). In some cases, some individuals could not be recovered due to escapes from small openings at the bottoms of enclosures or apparent predation by piscivorous birds. In the laboratory, fish were dissected

and their foregut prey contents were identified to lowest possible taxon and weighed wet. We performed feeding experiments on nine dates in 2001–2005. All experiments took place during the fall, the only time of year when high-amplitude daytime spring tides coincided with the availability of mature killifish.

In 2001–2002, we used four enclosures in each cell, two in the *Spartina* zone and two on the marsh plain. In 2004, we changed enclosure locations to assess feeding rates in pool vs. non-pool areas. We placed two enclosures in each cell in pools and two in *S. virginica* vegetation. All enclosures were placed on the marsh plain, because *S. foliosa* density was too high for recovery of fish and the *Spartina* zone was being used by Light-footed Clapper Rails. In 2005, enclosures were again deployed on the marsh plain to test pool vs. plant cover effects, but all 24 enclosures were placed in cells 5 and 6 because of losses of pools elsewhere in the marsh following sedimentation during the 2004–2005 rainy season.

We calculated fish feeding rates (milligrams of food per grams of fish per hour) based on whole-gut wet food weights (as per Madon et al. 2001). The majority of fish did not feed during caging events, resulting, as in the case of fish trapping, in zero-inflated data. We square-root transformed feeding rates to increase the normality of nonzero values and analyzed data using a Tobit regression model based on maximum-likelihood estimation (in STATA 9.2, StataCorp, College Station, Texas, USA). To compare rates at which different prey items were consumed, we calculated Index of Relative Importance (IRI) values for each prey item (as per Pinkas et al. 1971).

Assessment of trophic resources

We assessed trophic resources for fishes (invertebrate prey and their algal foods, based on trophic modules identified in Kwak and Zedler 1997, West et al. 2003) in pool and non-pool areas on the marsh plain in summer–fall 2005. In June 2005, we selected 12 pools on the marsh plain in cells 5 and 6, as there were few persistent pools elsewhere in the marsh due to sedimentation during 2004–2005. The 12 pools comprised a majority of the remaining pools in cells 5 and 6 and were variable in size, depth, and position. We randomly selected one quadrant within each pool for ongoing sampling and a paired “non-pool” location ~2 m from the edge of each pool.

We sampled algae and invertebrates within 0.25-m² plots in the 24 pool and non-pool locations during three periods once every two months in summer–fall 2005. We sampled during low tides in order to assess patch characteristics of pools vs. drained marsh surfaces. We sampled epibenthic algae in June, August, and October 2005 by collecting two 1.5 cm diameter, 1 cm deep cores at sampling points and immediately placing them in plastic containers, wrapping them in aluminum foil, and placing them on ice. We assessed phytoplankton in pools

during the same periods by collecting ~100-mL water samples in plastic containers, which were also wrapped in foil and placed on ice.

We measured chlorophyll concentrations (chl) as an indicator of algal abundance (APHA 1992). All photosynthetic algae and cyanobacteria (blue-green algae) have chl *a*; in addition, chl *b* is found in photosynthetic green algae, and chl *c* in photosynthetic diatoms (Rowan 1989). We processed chlorophyll samples on the same day they were collected. Epibenthic samples were transferred to 15-mL screw-top centrifuge tubes. Water samples were vacuum filtered through 0.45- μ m pore size mixed cellulose ester membranes, which were then transferred to centrifuge tubes. Pigments were extracted with 90% acetone (90 parts acetone, 10 parts saturated magnesium carbonate solution), sonicated, and kept in the dark at 4°C for 12–24 h. Biomasses of chl *a* (with correction for presence of pheophytin *a*, a degradation product of chlorophyll with a similar absorption peak), *b*, and *c* were estimated by placing extracts in 1-cm quartz cuvettes and measuring optical densities with a Beckman spectrophotometer (Fullerton, California, USA) at 750, 664, 647, and 630 nm before acidification, and at 750 and 665 nm following acidification with 1 mol/L HCl (APHA 1992).

We calculated concentrations of chlorophyll samples by area (milligrams per square meter) for epibenthic data and by volume (milligrams per cubic meter) for water samples. We changed negative values that occurred as artifacts of biomass estimation to zeros prior to statistical analyses and normalized data using a $\log(x + 1)$ -transformation. We analyzed transformed chlorophyll data using a linear model in R 2.3.1 (R Development Core Team 2006).

We collected epibenthic invertebrates in June, August, and October 2005 using 3 cm deep, 7.5 cm (Aug, Oct) to 10 cm diameter (Jun) polyvinyl chloride (PVC) cores. We preserved cores in plastic containers by adding 90% ethanol and shaking vigorously. We collected invertebrates in pool water columns during the same periods. We sank a bottomless plastic bucket (28 cm diameter) into the marsh surface to trap nekton, bailed water from the bucket using plastic containers and poured it through a 0.5-mm sieve. Samples were washed with water, rinsed from the sieve into plastic containers, and 90% ethanol was added.

In the laboratory, we rinsed epibenthic and water column samples through a 0.5-mm sieve. We soaked samples in a Rose Bengal-ethanol solution for 30 min to stain organic material, and then separated animals from debris. We counted animals and identified them to the lowest feasible taxon using an Olympus dissecting microscope (10–70 \times ; Model SZH10, Center Valley, Pennsylvania, USA).

We calculated densities of invertebrates for epibenthic and water column samples as total individuals per square meter. We normalized data through $\log(x + 1)$ -transformation and analyzed them using a linear mixed-

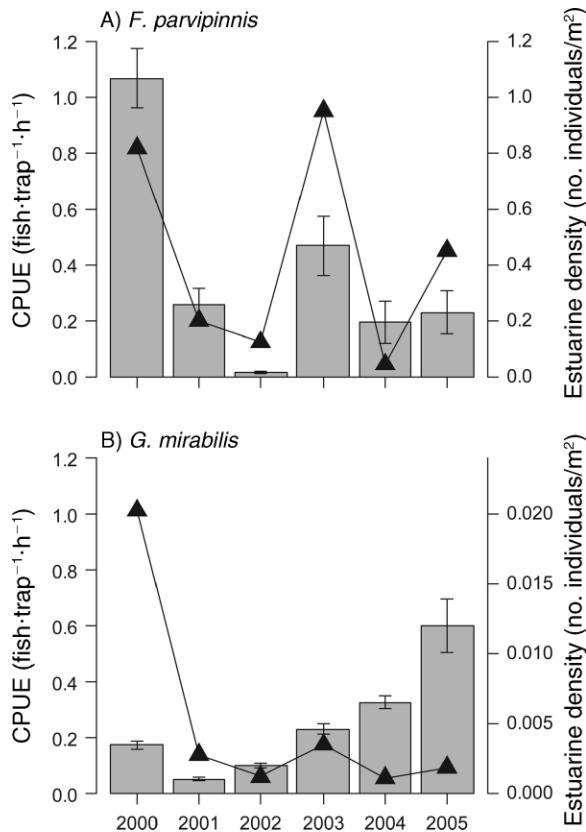


FIG. 2. Catch per unit effort (CPUE) within the Friendship Marsh (bars) and densities in Tijuana Estuary (triangles) for (A) *Fundulus parvipinnis* and (B) *Gillichthys mirabilis* by year, 2000–2005. Estuarine densities are from quarterly sampling conducted by Pacific Estuarine Research Laboratory (PERL) staff at three locations throughout the estuary. Error bars for CPUE data are \pm SE.

effects model in R 2.3.1 (nlme package; Pinheiro et al. 2006, R Development Core Team 2006). We used multivariate methods to address differences in invertebrate composition. Nonmetric multidimensional scaling (NMS) ordination and analysis of similarity (ANOSIM) testing were performed using the vegan package in R

2.3.1 (Oksanen et al. 2006, R Development Core Team 2006). Dissimilarity matrices were calculated from log-transformed invertebrate density data using Sørensen (Bray-Curtis) distances. The appropriate number of NMS axes (dimensions) was determined to be three based on scree-plots. NMS ordinations were created using random starting configurations and iterated until solutions converged. ANOSIM is a nonparametric permutation procedure that tests whether differences in dissimilarity *between* groups exceed differences *within* groups (Clarke 1993, McCune and Grace 2002). We used ANOSIM (with 1000 permutations) to test whether there were significant differences in invertebrate composition between pool vs. non-pool samples and between samples collected during different months.

RESULTS

Source populations

Densities of *Gillichthys mirabilis*, but not *Fundulus parvipinnis*, were highly variable from year to year during quarterly monitoring of channels in Tijuana Estuary ($P=0.047$ and $P=0.19$, respectively; see Fig. 2). Over the six-year study, *G. mirabilis* density was highest in 2000 and lowest in 2004, while *F. parvipinnis* mean density peaked in 2003 and was lowest in 2004. *F. parvipinnis* individuals accounted for 10.8% and *G. mirabilis* for 0.6% of all fishes caught during this period.

Fish use of the marsh

Over the six-year study, we caught eight fish species and a total of 5539 individuals (Table 1). *F. parvipinnis* and *G. mirabilis* were numerically dominant, accounting for >99% of all individuals caught (71% and 28%, respectively), typical for salt marshes in the San Diego region (Zedler et al. 1992, Talley 2000). Other species were typical of the region's estuaries and lagoons (Williams et al. 1998). Regression tree analyses indicated that *F. parvipinnis* and *G. mirabilis* populations varied both spatially and temporally (Fig. 3). For *F. parvipinnis*, seasonal and then pool effects were dominant in

TABLE 1. Summary of fish trapping activity at the Friendship Marsh, California, USA, from 2000 to 2005.

Variable	2000	2001	2002	2003	2004	2005	Total
No. sampling dates	9	8	9	5	3†	6	40
No. traps	457	469	540	300	179	144	2089
Individuals trapped (no./m ²)							
Total	2268	810	379	1186	552	344	5539
<i>Fundulus parvipinnis</i>	1854	668	312	784	195	117	3930
<i>Gillichthys mirabilis</i>	410	136	57	400	342	227	1572
<i>Atherinops affinis</i>	1	0	2	1	15	0	19
<i>Leptocottus armatus</i>	0	6	8	0	0	0	14
<i>Acanthogobius flavimanus</i> ‡	1	0	0	0	0	0	1
<i>Clevelandia ios</i>	1	0	0	0	0	0	1
<i>Girella nigricans</i>	0	0	0	1	0	0	1
Unidentified goby	1	0	0	0	0	0	1

† Planned October and November 2004 sampling events not carried out due to flooding.

‡ Aggressive invasive, which preys on and competes with native species.

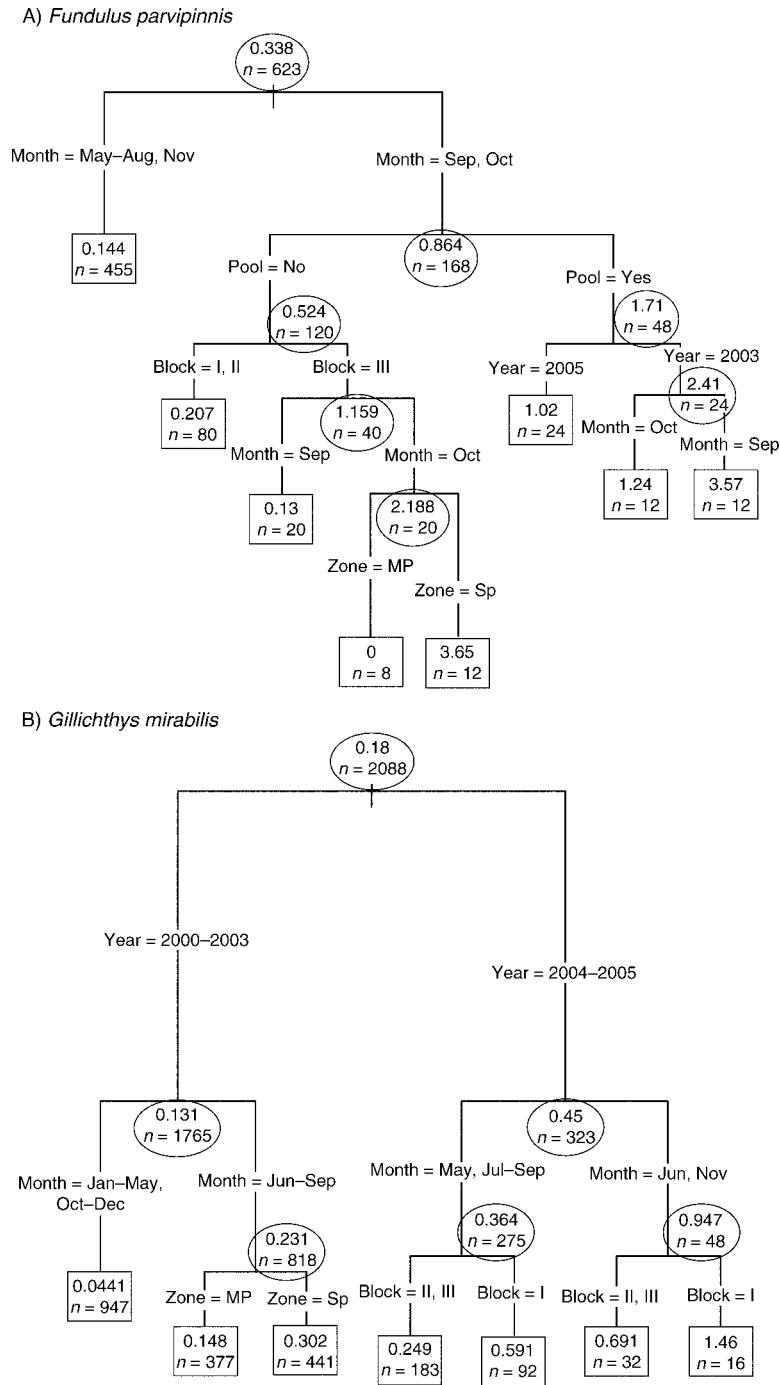


FIG. 3. Regression tree analyses of CPUE data for dominant fish species trapped in the Friendship Marsh. Groups are split at nodes into branches based on homogeneity. Within ellipses at nodes and rectangles at branch terminals are mean CPUE and number of traps for each group. Branch lengths are proportional to the homogeneity of the groups defined by the split. (A) *Fundulus parvipinnis*, years 2003–2005. Tested factors were year, month, predicted high tide, trapping during day or night, block, \pm creek, marsh plain (MP), or *Spartina* (Sp), and pool or non-pool. (B) *Gillichthys mirabilis*. Tested factors were the same as for panel (A) except 2000–2005 data did not include pool effects (see *Methods*).

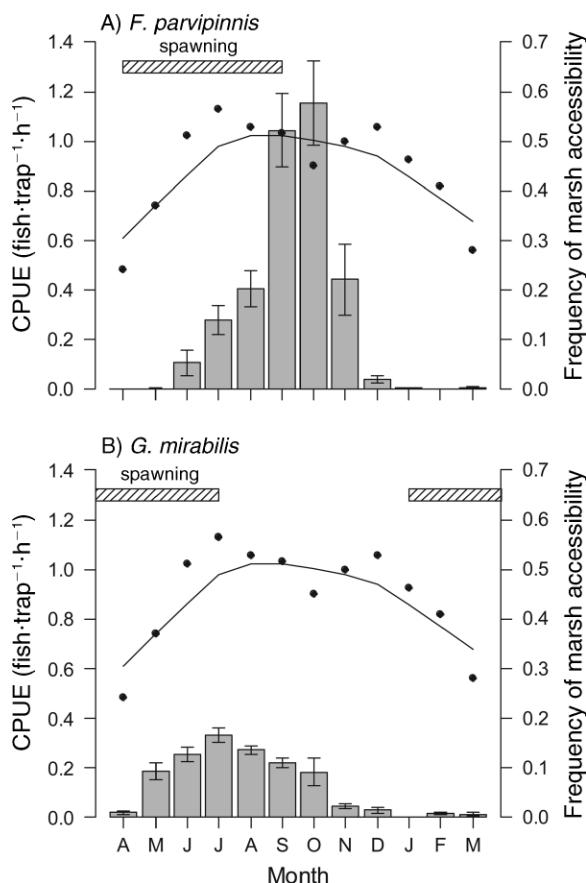


FIG. 4. Monthly mean CPUE data for (A) *F. parvipinnis* and (B) *G. mirabilis* from the Friendship Marsh, 2000–2005. Mean number of days per month that high tides were sufficient to permit fish access to marsh surfaces (>1.76 m, as per Madon et al. 2001) are included as an indicator of marsh availability (dots with loess fit line). Error bars for CPUE data are \pm SE.

predicting abundance, while interannual and then seasonal effects were most important for *G. mirabilis*.

Seasonal effects

Consistent with predictions, CPUE of *F. parvipinnis* differed by month ($P < 0.001$), which emerged as the strongest predictor of abundance in regression tree analysis (Fig. 3). Catch data followed, but lagged, patterns of marsh availability, as indicated by the percentage of days each month (years 2000–2005) when high tides were of sufficient amplitude to permit marsh access (Fig. 4). *F. parvipinnis* CPUE was low in spring, increased through summer, peaked in October at 1.15 ± 0.17 individuals-trap⁻¹·h⁻¹, and declined sharply in winter.

Monthly differences in CPUE were also significant for *G. mirabilis* ($P < 0.001$). Month of sampling strongly influenced regression tree branching of *G. mirabilis* CPUE (Fig. 3) and *G. mirabilis* CPUE was consistent with patterns of marsh availability (Fig. 4). CPUE of *G. mirabilis* was less variable and peaked earlier, in July at

0.33 ± 0.03 individuals-trap⁻¹·h⁻¹, than CPUE of *F. parvipinnis*.

For both *F. parvipinnis* and *G. mirabilis*, total length (TL) differed significantly by month ($P < 0.0001$ for *F. parvipinnis*, $P = 0.0017$ for *G. mirabilis*). Excluding January–May due to low numbers of individuals ($n < 10$), *F. parvipinnis* were largest in November (later peak in marsh availability). *Gillichthys mirabilis* were largest in March, 126.1 ± 3.2 mm, and smallest in June, 106.8 ± 1.5 mm (excluding April, $n = 9$), but showed very little fluctuation and no consistent patterns in size throughout the year.

Annual variability

F. parvipinnis CPUE differed significantly by year ($P < 0.001$), with a low of 0.02 ± 0.004 individuals-trap⁻¹·h⁻¹ in 2002 and a high of 1.07 ± 0.11 individuals-trap⁻¹·h⁻¹ in 2000 (Fig. 2). For *G. mirabilis*, year effects were the strongest factor in regression tree construction (Fig. 3). *G. mirabilis* CPUE was lowest in 2001 at 0.05 ± 0.006 individuals-trap⁻¹·h⁻¹ and highest in 2005 at 0.60 ± 0.10 individuals-trap⁻¹·h⁻¹ ($P < 0.001$).

Catch rates of *F. parvipinnis* in the Friendship Marsh were consistent with estuarine population densities, with both relatively high in 2000 and 2003, moderate in 2001 and 2005, and low in 2002 and 2004 (Fig. 2). *G. mirabilis*, however, showed no apparent relationship between site catches and estuarine density (Fig. 2). Estuarine density of *G. mirabilis* was highest in 2000, a low CPUE year in the Friendship Marsh. Conversely, CPUE of *G. mirabilis* in the Friendship Marsh peaked in 2005, a year when sampled estuarine density was relatively low.

Fish TL differed significantly by year ($P < 0.0001$ for both species). *F. parvipinnis* were largest in 2005 (52.5 ± 0.9 mm) and smallest in 2004 (40.5 ± 0.8 mm). *G. mirabilis* ranged from a low of 97.5 ± 0.9 mm in 2000 to a high of 121.4 ± 0.9 mm in 2004.

Habitat heterogeneity

Fish use varied with habitat (vegetation zones, creeks, and pools). *F. parvipinnis* and *G. mirabilis* CPUE were higher in *Spartina* than on the marsh plain ($P < 0.001$ for both species). *F. parvipinnis* CPUE was 0.48 ± 0.05 individuals-trap⁻¹·h⁻¹ for the *Spartina* zone and 0.32 ± 0.04 individuals-trap⁻¹·h⁻¹ for the marsh plain. *G. mirabilis* CPUE was also higher in *Spartina* traps than in marsh-plain traps; 0.20 ± 0.01 and 0.16 ± 0.02 individuals-trap⁻¹·h⁻¹, respectively. CPUE did not differ by habitat for either species ($P = 0.49$ for *F. parvipinnis* and $P = 0.95$ for *G. mirabilis*). Total lengths did not differ by habitat for *F. parvipinnis* ($P = 0.96$) or *G. mirabilis* ($P = 0.29$).

G. mirabilis followed the predicted creek effect; it was more frequently trapped in cells with creeks (42% of traps) than those without creeks (31% of traps, $P < 0.0001$ by logistic regression; Fig. 5). However, CPUE

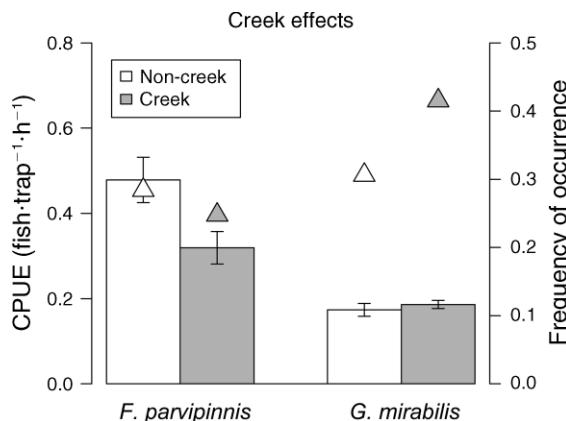


FIG. 5. Fish trap data from the Friendship Marsh for *F. parvipinnis* and *G. mirabilis* in cells with and without built tidal creek networks from 2000 to 2005. Bars represent CPUE, and triangles indicate frequency of occurrence (fraction of traps containing given species). Error bars for CPUE data are ±SE.

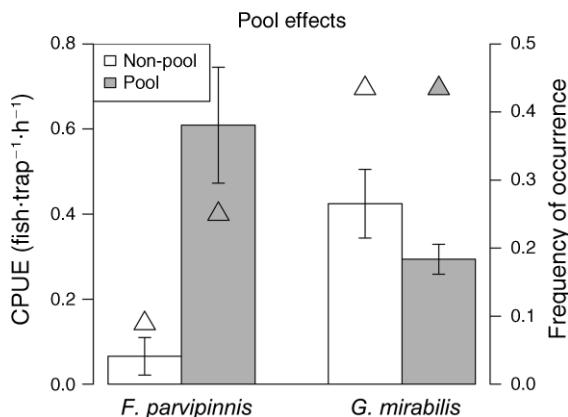


FIG. 6. Fish trap data from the Friendship Marsh for *F. parvipinnis* and *G. mirabilis* in pools and non-pools from 2003 to 2005. Bars represent CPUE, and triangles indicate frequency of occurrence (fraction of traps containing given species). Error bars for CPUE data are ±SE.

differences, though significant, were small: 0.19 ± 0.01 and 0.17 ± 0.02 individuals-trap⁻¹·h⁻¹ in cells with and without creeks, respectively ($P < 0.001$). Unexpectedly, *F. parvipinnis* CPUE was lower in cells with creeks (0.48 ± 0.05 individuals-trap⁻¹·h⁻¹) than those without (0.32 ± 0.04 individuals-trap⁻¹·h⁻¹, $P = 0.031$). This result persisted following removal of data from a non-creek-cell pool trap with elevated *F. parvipinnis* trap rates. Also, it was not explained by pool cover, which was similar for cells with and without creeks (41% and 43% of transects, respectively; A. Varty, unpublished data). Creek effects were not selected as branches of regression trees for either species (Fig. 3). While *F. parvipinnis* sizes were similar in cells with and without creeks ($P = 0.92$), *G. mirabilis* were slightly longer in cells with creeks (mean TL, 114.2 ± 0.7 mm) than those without (110.9 ± 0.7 mm, $P = 0.0023$).

Pools had a strong positive effect on *F. parvipinnis* catches. During 2003–2005 (when pool effects were tested), *F. parvipinnis* CPUE was 0.61 ± 0.14 individuals-trap⁻¹·h⁻¹ in pool traps vs. 0.07 ± 0.04 in non-pool traps ($P < 0.001$; Fig. 6). Pool effects were also a strong factor in regression tree structure for *F. parvipinnis* CPUE. For *G. mirabilis*, CPUE did not significantly differ between pool and non-pool traps (0.29 ± 0.04 and 0.42 ± 0.01 individuals-trap⁻¹·h⁻¹, respectively; $P = 0.53$). Nor did the sizes of *F. parvipinnis* or *G. mirabilis* differ between pool and non-pool habitats ($P = 0.65$ and $P = 0.90$, respectively).

Fish feeding in the marsh

During initial fish-feeding experiments in 2001–2002, only 17% of *F. parvipinnis* specimens consumed food while enclosed on the marsh during high-tide feeding opportunities. Fish fed at lower rates in cells with creeks than in cells without creeks ($3.2 \times 10^{-5} \pm 0.75 \times 10^{-5}$ [mg food]·[g fish]⁻¹·h⁻¹ vs. $1.0 \times 10^{-4} \pm 0.19 \times 10^{-4}$, respectively; $P < 0.001$). There were no significant

differences in feeding rates between fish enclosed in the *Spartina* zone and those enclosed on the marsh plain ($P = 0.54$). Gut contents of fishes were dominated by ostracods, amphipods, insect larvae, and Corixidae (Fig. 7). Prey items consumed were similar to those identified in past studies of *F. parvipinnis* diets (Kwak and Zedler 1997, West and Zedler 2000, West et al. 2003).

After shifting our test of feeding rates in enclosures to compare pools vs. patches of *Salicornia virginica* in 2004, our results were inconclusive. Flooding brought mud and fresh water into the site during our feeding experiment, and subsequent storm events through fall (the only time of year when abundant mature *F. parvipinnis* and high daytime high tides coincide)

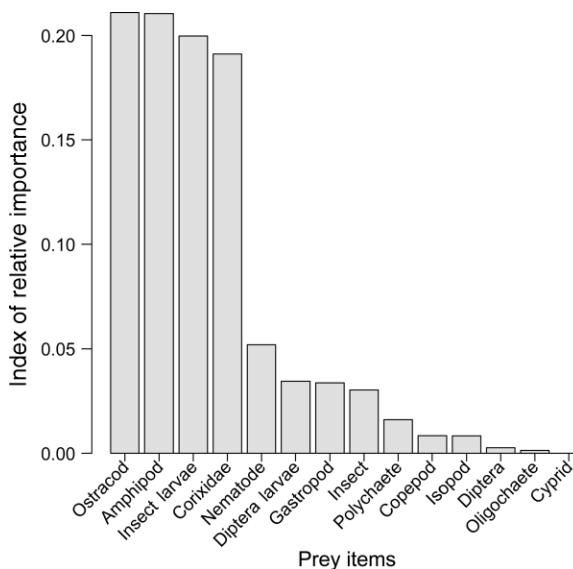


FIG. 7. Index of relative importance (IRI) values for prey items consumed by *F. parvipinnis* specimens during 2001–2002 feeding experiments in the Friendship Marsh.

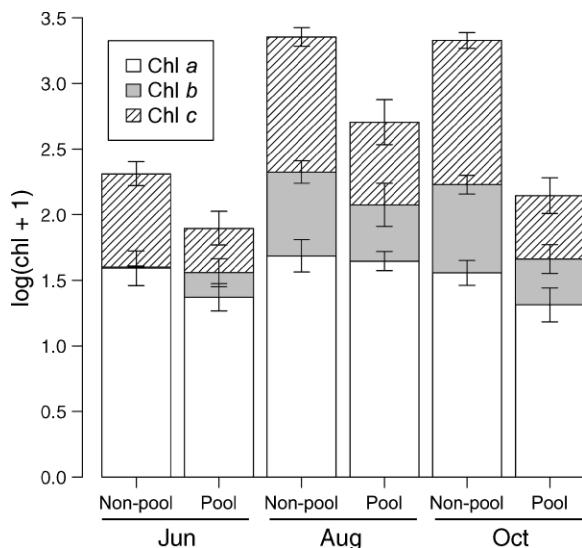


FIG. 8. Epibenthic chlorophyll *a*, *b*, and *c* data by month from paired pool and non-pool areas in the Friendship Marsh, sampled in 2005. Chl *a* data are corrected for presence of pheophytin, and all values were $\log(x + 1)$ -transformed to increase normality. Error bars are \pm SE.

precluded additional attempts. The 2005 experiment had insufficient food consumption to allow pool vs. non-pool comparisons. The *F. parvipinnis* used were primarily large, reproductively active individuals, a group that often had empty guts in previous experiments (J. West, *personal observation*). In our 2001–2002 feeding experiments, there was a weak but significant negative effect of fish weights on feeding rates ($P = 0.031$).

Availability of trophic resources

Epibenthic algal biomass differed by month based on chlorophyll *a*, *b*, and *c* concentrations. Chl *a* concentrations were highest in August ($60.8 \pm 10.5 \text{ mg/m}^2$, $P = 0.061$), as were concentrations of chl *b*, indicative of green algae ($4.2 \pm 1.6 \text{ mg/m}^2$, $P < 0.0001$; Fig. 8). Chl *c*, found in photosynthetic diatoms, differed significantly by month ($P = 0.0025$), but not between August and October, when they were highest (7.2 ± 2.9 and $7.6 \pm 1.7 \text{ mg/m}^2$, respectively; Fisher's test $P = 0.74$).

Mean concentrations of epibenthic chl *a*, *b*, and *c* appeared lower in pools than in non-pools, but differences were significant only for chl *c* ($P = 0.0015$; Fig. 8). At low tide, only pools allowed sampling of phytoplankton. Mean concentration of water column chl *a* was highest in June ($92.1 \pm 30.3 \text{ mg/m}^3$, $P = 0.0003$), while chl *b* and *c* concentrations were highest in August ($16.4 \pm 3.4 \text{ mg/m}^3$, $P < 0.0001$; and $30.7 \pm 5.0 \text{ mg/m}^3$, $P = 0.013$, respectively).

There were no significant differences in invertebrate density by sampling month (June, 447 ± 119 individuals/ m^2 ; August: 974 ± 241 ; October: 1164 ± 295 individuals/ m^2 ; $P = 0.56$). Mean density of invertebrates appeared to be higher in pools (1009 ± 218 individu-

als/ m^2 , epibenthic + water column) than non-pools (707 ± 160 individuals/ m^2 , epibenthic only), but this difference was not significant ($P = 0.16$). Factoring in both density and composition, there were clear differences between pool and non-pool samples (Fig. 9). While numerous taxa were much more abundant in pools or found only in pool samples, only insect larvae had much higher densities in non-pool samples. With insect larvae excluded from density calculations, mean invertebrate densities were significantly higher in pools ($P = 0.009$). NMS ordination and ANOSIM testing of invertebrate abundance and composition showed highly significant differences between pools and non-pools ($P < 0.001$; Fig. 10), but no effect of sampling month ($P = 0.33$).

DISCUSSION

Restoring topographic heterogeneity is considered beneficial in prairies, deserts, and freshwater wetlands (Boeken and Shachak 1994, Vivian-Smith 1997, Ewing 2002, Larkin et al. 2006), and prior research provides support for benefits in salt marsh restoration as well. For example, pools are known to accumulate algae and invertebrates and provide refugia for fishes (Daiber 1982, Smith and Able 1994, Stevens et al. 2006), plus creeks allow exchange of nutrients and detritus, enhance fish access to marsh surfaces, and act as refugia for juvenile fishes (Zedler et al. 1992, Michener et al. 1997, Paterson and Whitfield 2000). We tested the effects of

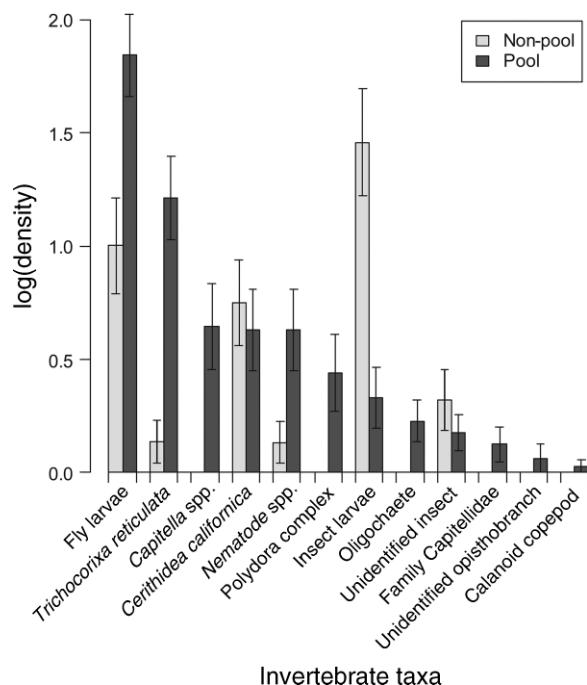


FIG. 9. Invertebrate densities for paired pool and non-pool areas in the Friendship Marsh, sampled in 2005. Epibenthic invertebrates were collected from pool and non-pool areas, and water column invertebrates were collected from pools. Data are no. individuals/ m^2 and normalized by $\log(x + 1)$ -transformation. Error bars are \pm SE.

topographic heterogeneity on fish use and trophic support for fishes in the Friendship Marsh, an 8-ha site designed to provide three-fold replication of a creek network and three areas without creeks. Our test was realistic because the Friendship Marsh is an actual restoration site, with creeks modeled after a natural tidal creek network and pools that formed naturally. In addition, our study spanned six years and drew upon additional study of both the Friendship Marsh and Tijuana Estuary.

Pools and creeks enhanced fish support

Within the Friendship Marsh, pools retained water between high tides and provided conditions suitable for continuous productivity of algae and invertebrates. Even when the entire marsh surface was inundated (i.e., during trapping), pools functioned as oases that attracted fish. Although pools supported different invertebrate assemblages than non-pools, we did not see significantly higher densities of invertebrates. This was due partly to abundant insect larvae in non-pools but also, perhaps, to greater fish feeding in pools. Elsewhere, pools have been identified as nodes of high macroinvertebrate density and richness (Daiber 1982, Angradi et al. 2001).

Creeks enhanced habitat connectivity, supported by findings that creeks accelerated tidal inundation and lengthened the hydroperiod of the Friendship marsh (Wallace et al. 2005). Creeks also increased spatial heterogeneity and the length of edge between marsh and subtidal habitats, which have been associated with greater diversity of nektonic fishes and invertebrates (Kneib 1997, Visintainer et al. 2006). Creeks may also make it easier for fish to access the marsh, lowering energetic costs and elevating returns from marsh-surface foraging (Madon et al. 2001).

Despite these attributes, creeks had mixed effects on fish use of the Friendship Marsh. Schools of *F. parvipinnis* were often observed at the mouths of drained tidal creeks, appearing to wait for rising tides to convey them into the marsh (D. Larkin, *personal observation*), as seen for related species in other systems (Teo and Able 2003). However, catch and feeding rates of *F. parvipinnis* were lower in cells with creeks. *Gillichthys mirabilis* CPUE indicated a small positive effect of creeks on fish use of the marsh. In addition, creeks may have cryptically enhanced overall fish use of the marsh by increasing site tidal prism and inundation (Wallace et al. 2005). Factors that could have weakened differences between cells with and without creeks, and thereby diminished a creek effect, include the formation of “volunteer” creeks, the partial filling of constructed creeks, and the lack of discrete barriers between cells (Wallace et al. 2005).

Limited co-occurrence of *G. mirabilis* and *F. parvipinnis* suggested habitat segregation, with *G. mirabilis* preferring creeks but not pools, and *F. parvipinnis* showing a strong positive response to pools and a

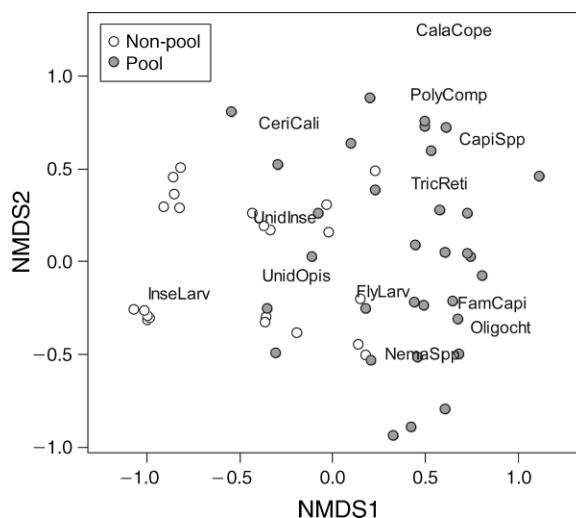


FIG. 10. Nonmetric multidimensional scaling (NMS) ordination of invertebrate data for pools and non-pools. Data consist of $\log(x + 1)$ -transformed density data for 13 taxa. The plot was generated using three dimensions and a dissimilarity matrix based on Sørensen distances between sample units. Abbreviations are: FlyLarv, fly larvae; TricReti, *Trichocorixa reticulata*; CapiSpp, *Capitella* spp.; CeriCali, *Cerithidea californica*; NemaSpp, *Nematode* spp.; PolyComp, *Polydora* complex; InseLarv, insect larvae; Oligocht, *Oligochaete*; Unid-Inse, unidentified insect; FamCapi, family *Capitellidae*; Unid-Opis, unidentified opisthobranch; and CalaCope, *Calanoid copepod*.

negative response to creeks. Differential use of habitat can result from competition between estuarine fishes with similar diets (Allen et al. 1995) or biological and behavioral characteristics. The high activity of *F. parvipinnis* relative to *G. mirabilis* (D. Larkin, *personal observation*) should facilitate discovery of pools and their dense foods. There is also evidence that *G. mirabilis* prey on *F. parvipinnis* (West et al. 2003).

Processes operating at larger spatial and temporal scales also influenced fish use of the marsh. For *G. mirabilis*, year of sampling was the strongest predictor of abundance (by regression tree analysis), while *F. parvipinnis* used the site most when estuarine densities were highest, indicating that spatially extensive changes over longer time periods were factors in site dynamics. Site evolution was also important, with pools forming early and later filling during extreme weather events that elevated the marsh plain (maximum six-month accretion = 9.5 cm; Wallace et al. 2005). If high rates of accretion persist, the site's topographic heterogeneity will likely be compromised, as creeks and pools continue to fill in. The fact that ostracods and amphipods were important fish prey items in 2001–2002, but were not found during 2005 invertebrate sampling may be an early indication of this trend.

Seasonal changes relate to life history pattern

For *F. parvipinnis*, seasonal variability (month of sampling) had primacy over spatial factors, as indicated by regression tree analysis. Temporal patterns were also

found at lower trophic levels. Chlorophyll concentrations were low in June, as summer inundation frequency was increasing, and higher in August, shortly after the summer peak in mean tidal inundation. Invertebrate densities followed a similar pattern, but did not differ significantly by month. Algal abundance was low again in October, a period of low tidal amplitude, when sampled invertebrate density was highest. Thus, in June and August, abundances of algae and invertebrates were increasing concurrently, while invertebrates might have depleted algal biomass by October.

In the bioenergetics model, Madon et al. (2001) posit that the *F. parvipinnis* life cycle exploits the rich marsh food resources by synchronizing juvenile growth and periods of greatest marsh accessibility. If marsh surface foraging accelerates fish growth, high tides should impart a reproductive advantage and select for life history strategies that increase marsh surface access. The model shows that the timing of peak *F. parvipinnis* spawning maximizes early-age marsh-surface foraging opportunities and predicts that killifish grow 20–44% faster if they forage on marsh surfaces (Madon et al. 2001). Behavioral adaptation to temporal patterns of marsh resource availability is also supported by correlations of *F. parvipinnis* feeding activity with tides and association of peak feeding with high tide access to intertidal habitats (Fritz 1975, Madon, *in press*).

Our results are consistent with a relationship between patterns of marsh surface availability and *F. parvipinnis* life history. This species was far less abundant on a per-high-tide basis when tides high enough to access the marsh plain were infrequent (March–May). When marsh inundation increased, so did *F. parvipinnis* abundance and total lengths, with both measures peaking during late summer and early fall, when high-amplitude daytime tides occur. However, abundance of *F. parvipinnis* lagged behind marsh accessibility during late spring through August (Fig. 4). During this period, marsh use by *F. parvipinnis* was likely constrained by biotic factors such as recruitment and development, with marsh surfaces available before young-of-year were large enough to be caught in minnow traps. In December and January, marsh availability was relatively high, but use by *F. parvipinnis* was low, probably because many fish had already died and survivors may have fed less during this period (empty guts observed more in reproductively mature *F. parvipinnis*). The life cycle of *F. parvipinnis* likely constrained this species' use of the marsh within the year, while over evolutionary time, the *F. parvipinnis* life cycle may have been shaped by tidal mediation of marsh-surface foraging opportunities.

Tidal marsh restoration should include creeks and pools

The Friendship Marsh was designed to contrast with typical restoration projects in southern California by including topographic variability in the form of tidal creeks. Other projects in the region have smooth,

vegetated surfaces for birds and plants or wide, deep subtidal channels or large basins for fishes (Zedler et al. 1997, West and Zedler 2000), but no small tidal creeks (Larkin et al. 2006). Homogeneous sites have low patch richness, little connectivity between intertidal and subtidal habitat, and are unlikely to exhibit functional equivalency with reference systems. Like other heavily managed systems, homogeneous restoration sites may lack resilience, so that stresses overwhelm adaptability and cause deterioration (Levin 1998).

Considerations of how heterogeneous topography and temporal dynamics influence system behavior should be a component of planning and design phases in tidal wetland restoration. The biology of target organisms and heterogeneity of natural systems should dictate spatial attributes (Lepori et al. 2005, Visintainer et al. 2006), not the human tendency to neaten and homogenize (Larkin et al. 2006). Where wetlands are intersected with creek networks, dotted with pools, and inhabited by organisms that inhabit these niches, restoration should mimic this structure. Marsh surface heterogeneity in restored sites can serve as a form of “bet hedging” in the face of uncertainty. While incomplete knowledge and site evolution limit our ability to create an “ideal” site, heterogeneity increases the likelihood that an intertidal species' spatiotemporal (elevation × hydroperiod) niche will be present.

In the case of tidal marsh restoration, we recommend: (1) jumpstarting tidal creek formation by excavating entry points or excavating creeks that mimic the morphology of natural creek networks, (2) leaving marsh surfaces topographically heterogeneous rather than evenly graded in order to initiate pool formation, and (3) including enough area and habitat heterogeneity to allow habitat segregation among target species. Not all of the design features will persist, but they are likely to enhance long-term heterogeneity. For example, tidal creek networks in the Friendship Marsh reduced the impacts of sedimentation (Wallace et al. 2005). Facilitating creek and pool formation and adding topographic heterogeneity will enhance benefits of restoration not only to fishes but also plants and invertebrates (Zedler et al. 1999, Angradi et al. 2001, Minello and Rozas 2002).

Restoration projects designed as large field experiments are powerful tools for testing theory and improving the practice of ecological restoration. Over time, small-scale treatments spawned larger salt marsh restoration experiments (e.g., Weinstein et al. 2001, Cornu and Sadro 2002, Levin and Talley 2002), as well as plans for continued experimentation at Tijuana Estuary. While the experimental approach to restoration enhanced the Friendship Marsh's value from both scientific and applied standpoints, it was not easy to fund the excavation, implement construction, or synchronize research funding and site availability. In this case, 12 years lapsed between the experimental design (1988) and the completed project (2000). Still, the effort needed to create such study systems is justified by their

potential to develop “general guiding principles for restoration” (Hobbs and Norton 1996) and contribute to a “clearly articulated conceptual basis” for restoration that recognizes the dynamic nature of ecosystems (Hobbs and Harris 2001).

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