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LONG-TERM FISH ASSEMBLAGE DYNAMICS OF THE ALVARADO LAGOON ESTUARY, VERACRUZ, MEXICO

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ABSTRACT The fish assemblages of Alvarado Lagoon Estuary (a complex of coastal lagoons in the state of Veracruz, Mexico) have been surveyed intermittently by different researchers over the last 40 years. Assessing long-term trends in fish assemblage composition for this ecosystem is problematic due to differences in sampling efforts among the survey periods (1966–1968, 1987–1988, 1989, 1989–1990, 1990–1991 and 2000–2001) and by the inherent ecological variability of estuaries. To overcome these data limitations and better understand fish assemblage change over time, we used robust, simulation-based analyses to compare collections from the different surveys. The 107 fish species collected from the Alvarado Lagoon Estuary in these surveys represent 4 ecological guilds: marine stenohaline, marine euryhaline, estuarine, and freshwater fishes. The occurrence frequency of fish species representing each guild did not change significantly among the survey periods: the chi-square deviation statistic ($\chi^2 = 8.53$) was not significantly larger than the average value for 1000 simulated matrices ($\chi^2 = 138.64$; $P = 1.00$). A non-metric multidimensional scaling (MDS) based on Bray-Curtis similarities of fish species presence-absence data showed that the 1966–1968 survey period was the least similar to the other survey periods. For the 1966–1968 survey, the range of Bray-Curtis inter-survey similarities was 40.4–58.6 ($n = 5$). By comparison, the remaining range of inter-survey similarities was 61.5–81.7 ($n = 10$). Average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+), two sample size-independent measures of diversity, were calculated for all survey periods. Although Δ^+ and Λ^+ for all survey periods were within the simulated 95% confidence limits for expected values, these values for the 2000–2001 survey period were less than the average Δ^+ and Λ^+ values for the entire species pool. This suggests that the fish assemblage collected during the latest survey reflects a loss of both widespread higher taxa (reduced Δ^+) and that the higher taxa lost are those with only a few representative species in the assemblage (reduced Λ^+). These assemblage data show that fish assemblages of Alvarado Lagoon Estuary have not experienced significant changes over 40 years, but differences among the earliest (1966–1968), the latest (2000–2001), and the remaining survey periods indicate a recent decline in diversity.

RESUMEN Los ensamblajes de peces del sistema lagunar de Alvarado (un complejo de lagunas costeras del Estado de Veracruz, México) han sido investigados intermitentemente por diferentes grupos durante los últimos 40 años. La determinación de las tendencias a largo plazo de estos ensamblajes ha sido problemática debido a las diferencias en los esfuerzos de muestreo empleados entre los períodos de investigación (1966–1968, 1987–1988, 1989, 1989–1990, 1990–1991 y 2000–2001) y por la variación ecológica inherente a los estuarios. Para evitar estas limitaciones de los datos y presentar una explicación apropiada de los cambios de los ensamblajes de peces respecto al tiempo, se usó un análisis de simulación para comparar las colectas de los diferentes períodos de trabajo. Las 107 especies colectadas en el sistema lagunar de Alvarado representan 4 gremios ecológicos: marino estenohalino, marino eurihalino, estuarino y dulceacuícolas. La frecuencia de ocurrencia de las especies de peces que representan cada gremio no cambió significativamente entre los períodos de investigación: El estadístico de desviación chi cuadrada ($\chi^2 = 8.53$) no fue significativamente mas grande que el valor promedio para las 1000 matrices simuladas ($\chi^2 = 138.64$; $P = 1.00$). La prueba de escalamiento múltiple dimensional no-métrico (MDS) se ejecutó considerando los datos de presencia-ausencia y las similitudes calculadas por el índice de Bray-Curtis, esta prueba mostró que el período 1966–1968 fue menos similar a los otros períodos de colecta. Para el período 1966–1968, el rango de similitudes Bray-Curtis entre investigaciones fue de 40.4–58.6 ($n = 5$). En comparación, el rango de similitudes restante entre investigaciones fue de 61.5–80.7 ($n = 10$). La distinción taxonómica promedio (Δ^+) y la variación de la distinción taxonómica (Λ^+), dos medidas de la diversidad independientes del tamaño de muestra, fueron calculadas para todos los períodos de investigación. Aunque los valores de Δ^+ y Λ^+ para todos los períodos de investigación estuvieron dentro de los límites de confianza de 95% para los valores esperados, estos valores fueron menores para el período 2000–2001 respecto a los valores promedio de Δ^+ y Λ^+ para el conjunto completo de especies. Esto sugiere que el ensamblaje de especies colectado en el último período de investigación refleja una pérdida de taxa superiores (Δ^+ reducida) y que los taxa superiores perdidos son aquellos con pocas especies representativas en el ensamblaje (Λ^+ reducida). Estos datos muestran que los ensamblajes de especies del sistema lagunar de Alvarado no han sufrido cambios significantes durante los últimos 40 años, pero las diferencias entre el primer y último período de investigación y los otros períodos indican una declinación reciente en la diversidad.

INTRODUCTION

Coastal lagoons are interface ecosystems that have a rich biodiversity of organisms due to their position between river drainages and the continental shelf. The environmental gradients within coastal lagoons typically allow for numerous species with various life cycles, resulting in the formation of communities whose structures are influenced by physical and chemical factors. These ecosystems are dynamic and vary seasonally, which influences the presence of organisms from marine or freshwater origin and creates an environment that is critical for commercially important species such as molluscs, crustaceans, and fishes (Beck et al. 2001, Blaber 2002).

The Alvarado Lagoon Estuary is a complex of coastal lagoons located in southern Veracruz, Mexico. The Papaloapan, Blanco, and Acula rivers drain into the estuary, which in turn drains north into the Gulf of Mexico near Alvarado Port. The largest of these river basins, the Papaloapan River Basin, is more than 500 km long, covers an area of 46,517 km², and has an annual discharge of 47 million m³. The combination of numerous freshwater sources and multiple connected lagoon complexes forms a rich coastal ecosystem in the Alvarado Lagoon Estuary (Chávez-López 1998). However, environmental and ecological changes due to anthropogenic factors such as over-exploitation of the resources, industrial contamination, and construction of dams have contributed to the progressive decrease in the quality and ecological value of estuaries (Whitfield and Elliot 2002). This increasing alteration of environmental quality and quantity contrasts with the recent classification of lagoonal systems as strategic areas for the conservation of biodiversity (CONABIO 1998, Zárate-Lomelí et al. 1999). If the biodiversity of the Alvarado Lagoon Estuary is to be protected, it is necessary to determine which organisms are consistently present in the ecosystem and which appear to be declining in response to increased anthropogenic impacts.

Although the fish assemblages of the Alvarado Lagoon Estuary have been surveyed intermittently over the last 40 years by various researchers, these data have never been analyzed as an entirety to assess possible changes in fish biodiversity over that period. We compared fish collection data for 6 surveys (1966–1968, 1987–1988, 1989, 1989–1990, 1990–1991 and 2000–2001) to determine if the fish assemblages had changed among the survey periods. More specifically we addressed the following questions: 1) Did the frequency of marine stenohaline, marine euryhaline, estuarine, and freshwater fishes change significantly among surveys?, 2) Did assemblages remain similar throughout the 40 year period as determined by Bray-

Curtis similarity indices?, and 3) Did biodiversity decline significantly over the same period as determined by comparisons of average taxonomic distinctness and variation in taxonomic distinctness (two sample size-independent measures of biodiversity)?

Study Area

The Alvarado Lagoon Estuary is comprised of the Alvarado, Buen Pais, and Camaronera lagoons and the estuarine zone of the Papaloapan River (Figure 1). This estuarine system has a total surface area of 6,200 ha, with a mean depth of 2.5 m in the central zone of the lagoon and 14 m in the channel of the Papaloapan River. Water temperatures from April to September range between 27–33 °C, while during winter months (December to February) water temperatures reach as low as 22 °C. The salinity varies from 0–10 psu between July and October (rainy season), although during this period salinities are higher at the artificial inlet in Camaronera Lagoon. From November through June (nortes and dry seasons) salinities average 16 psu in Camaronera Lagoon and 22 psu at the mouth of the Papaloapan River, whereas the rest of Alvarado and Buen Pais lagoons have salinities ranging from 0–8 psu.

MATERIALS AND METHODS

We compiled fish assemblage data for the Alvarado Lagoon Estuary from previous research reports that described past fish surveys (Reséndez 1973, Chávez-López 1998). Reséndez (1973) provided a list of species collected between 1966 and 1968 using various fishing gear but did not provide precise information on capture methods, abundance, biomass, or physico-chemical variables. Chávez-López (1998) included a list of species as well as abundance, biomass, and ecological variables of the assemblage from November 1987 to August 1991. Our own monthly collections from June 2000 to August 2001 provided the latest data from the Estuary. We sampled fishes at 12 stations which included various habitat types: submersed aquatic vegetation (*Ruppia maritima*) (stations 2, 3, 4, and 6), old oyster reefs (station 5), river mouths (stations 7 and 10), the estuarine zone of the Papaloapan River (stations 11 and 12), a station near the artificial inlet that did not have submersed aquatic vegetation (station 1), and 2 stations located near Alvarado Port with urban influence (stations 8 and 9; Figure 1). Our fish sampling method consisted of a single seine haul with a 30 m long x 2 m high seine with 19 mm mesh, resulting in an effective collection area of 27.5 x 27.5 m (756.2 m²). Seines were operated perpendicular to shore at all stations except 11, where

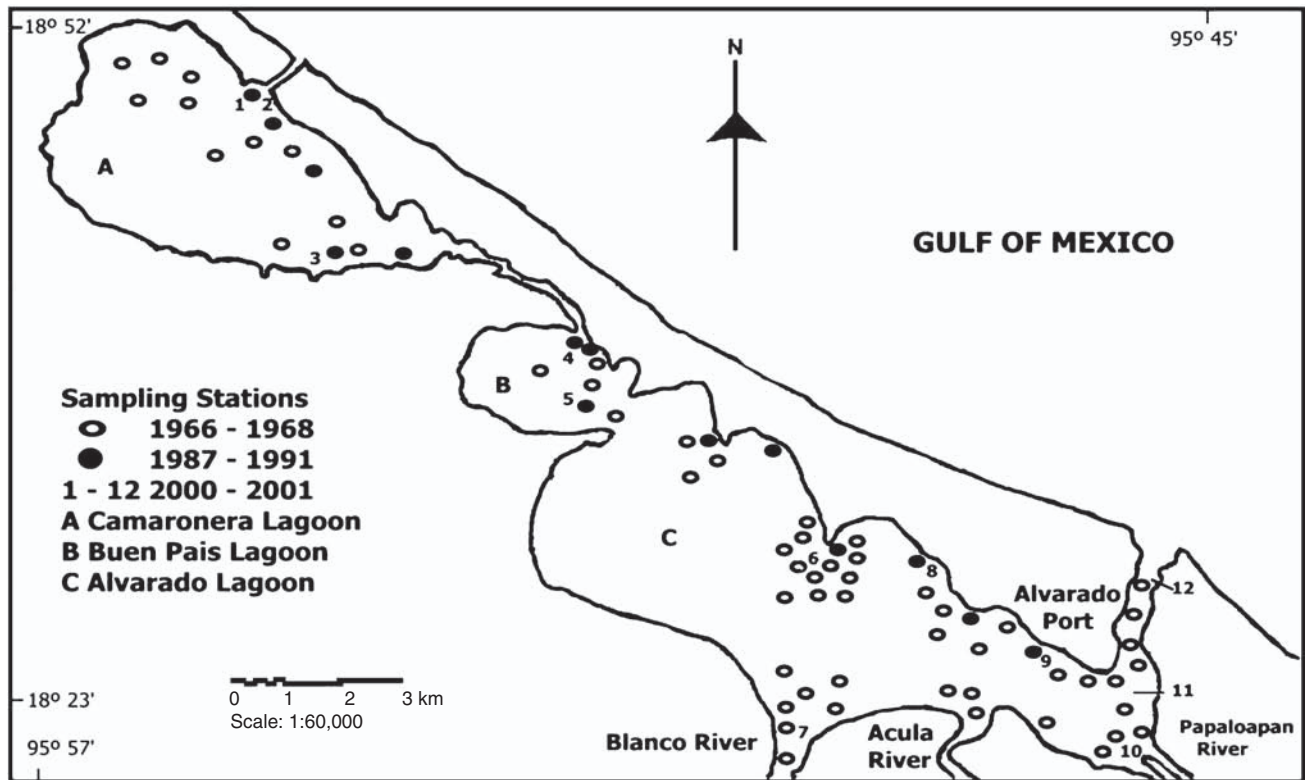


Figure 1. Map of the Alvarado Lagoon Estuary showing sampling stations for 6 fish surveys conducted during the following periods: 1966–1968, 1987–1988, 1989, 1989–1990, 1990–1991 and 2000–2001.

the same area was sampled in a circular pattern. The mean depth of all stations was 0.98 m. All organisms were fixed in 10% formalin and later washed in tap water and preserved in 70% ethanol. Species identification and common names were verified based on Reséndez (1973, 1981, 1983), Fischer (1978), Arredondo and Guzmán (1987), Hubbs et al. (1991), Hoese and Moore (1998), and Nelson et al. (2004).

From the lists of fishes, we constructed a presence-absence matrix of species based on the 6 collection periods: 1966–1968, November 1987–September 1988, February–September 1989, November 1989 to June 1990, November 1990 to August 1991, and June 2000 to June 2001 (Table 1). All seasons are represented in each collection period except 1989 when no collections were made during the nortes season (November through February). We classified fishes of the Alvarado Lagoon Estuary into 4 ecological guilds: marine stenohaline (M), marine euryhaline (ME), estuarine (E), and freshwater (F). These guilds were based on descriptions in Castro-Aguirre et al. (1978), Chávez-Lopez (1998), and Ross et al. (2001). If a fish specimen could not be identified to species level, it was recognized as “sp.” under its genus epithet and included in the list as a separate species. We used EcoSim software (v. 7.58) to determine if the occurrence frequency of marine

stenohaline, marine euryhaline, estuarine, and freshwater fishes differed significantly among surveys. A matrix representing the number of species from each guild collected from each survey was compared to a matrix representing expected values. For this comparison, expected frequencies were represented as the mean frequencies of each guild across all surveys. A chi-square statistic was generated to quantify the level of deviation between the observed and expected matrices. Once this statistic was calculated, EcoSim was used to create 1000 simulated matrices based on a randomization of the observed matrix. For this case, randomization of frequencies was designated to operate across surveys but not across guilds. In other words, if Guild A consistently had roughly twice as many species as Guild B for all 6 surveys, then all simulated matrices reflected this reality. A chi-square deviation statistic was calculated for the comparison of each of these 1000 simulated matrices to the expected mean frequencies. The resulting 1000 chi-square statistics were plotted as a frequency diagram and compared with the original observed-expected chi-square statistic. If the observed frequencies of species in guilds deviated significantly from random, the original observed-expected chi-square statistic should be greater than at least 950 chi-square statistics generated by the simulated matrices ($P = 0.05$).

TABLE 1

Fish species collected from the Alvarado Lagoon Estuary during 6 separate surveys from 1966 to 2001. Each species was assigned to one of 4 ecological guilds: marine stenohaline (MS), marine euryhaline (ME), estuarine (E), or freshwater (F). Species occurrence in a collection is denoted by an X with non-occurrences denoted by an 0.

Species	Ecological Guild	1966–1968	1987–1988	1989	1989–1990	1990–1991	2000–2001
<i>Dasyatis sabina</i>	ME	X	X	X	X	X	X
<i>Elops saurus</i>	ME	X	X	0	X	X	X
<i>Myrophis punctatus</i>	MS	X	0	0	0	0	0
<i>Harengula jaguana</i>	MS	X	0	0	0	0	0
<i>Opisthonema oglinum</i>	ME	0	X	X	X	X	X
<i>Brevoortia gunteri</i>	ME	X	0	0	X	0	0
<i>Brevoortia patronus</i>	ME	0	0	0	X	0	0
<i>Dorosoma cepedianum</i>	F	0	X	X	X	X	0
<i>Dorosoma petenense</i>	F	X	0	X	X	X	0
<i>Anchoa hepsetus</i>	MS	0	X	0	0	0	0
<i>Anchoa mitchilli</i>	ME	X	0	X	X	X	X
<i>Cetengraulis edentulus</i>	MS	0	X	0	0	X	0
<i>Synodus foetens</i>	MS	0	0	0	X	0	0
<i>Astyanax fasciatus</i>	F	0	0	0	0	0	X
<i>Ictiobus meridionalis</i>	F	X	0	0	0	0	0
<i>Arius felis</i>	ME	X	X	X	X	X	X
<i>Cathoropus melanopus</i>	E	X	X	X	X	X	X
<i>Bagre</i> sp.	ME	0	0	0	X	0	0
<i>Bagre marinus</i>	ME	X	X	0	X	X	X
<i>Rhamdia guatemalensis</i>	F	0	0	0	0	0	X
<i>Opsanus beta</i>	ME	X	X	0	X	X	X
<i>Gobiesox strumosus</i>	ME	X	0	0	0	0	0
<i>Hemirhamphus brasiliensis</i>	ME	0	0	X	0	0	0
<i>Hyporhamphus roberti</i>	ME	0	X	X	X	X	X
<i>Strongylura marina</i>	ME	X	X	X	X	X	X
<i>Strongylura notata</i>	ME	0	X	X	X	X	X
<i>Strongylura timucu</i>	MS	0	0	0	0	0	X
<i>Poecilia mexicana</i>	F	X	X	X	X	X	X
<i>Belonesox belizanus</i>	F	X	0	0	0	0	X
<i>Menidia beryllina</i>	ME	0	0	0	0	X	X
<i>Membras vagrans</i>	MS	0	X	0	0	0	0
<i>Thyrinops</i> sp.	F	X	0	0	0	0	0
<i>Syngnathus louisianae</i>	ME	0	X	0	0	X	0
<i>Syngnathus scovelli</i>	ME	X	0	0	0	X	X
<i>Microphis brachyurus</i>	ME	X	0	0	0	0	X
<i>Ophisternon aenigmaticum</i>	F	X	0	0	0	0	0
<i>Prionotus punctatus</i>	MS	0	X	0	X	X	0
<i>Centropomus undecimalis</i>	ME	X	X	0	X	X	X
<i>Centropomus parallelus</i>	ME	X	X	X	X	X	X
<i>Centropomus poeyi</i>	ME	X	0	0	0	0	0
<i>Centropomus ensiferus</i>	ME	0	0	X	0	0	X
<i>Centropomus pectinatus</i>	ME	0	X	X	X	X	X
<i>Caranx latus</i>	MS	X	0	0	X	X	X

Table 1 (continued)

Species	Ecological	1966–1968	1987–1988	1989	1989–1990	1990–1991	2000–2001
	Guild						
<i>Caranx hippos</i>	MS	X	X	0	0	X	X
<i>Caranx crysos</i>	MS	0	0	0	0	0	X
<i>Selene vomer</i>	MS	X	0	X	X	X	X
<i>Caranx bartholomei</i>	MS	X	0	0	0	0	0
<i>Hemicaranx amblyrhynchus</i>	MS	0	X	X	0	X	0
<i>Trachinotus carolinus</i>	ME	0	X	X	X	X	0
<i>Trachinotus falcatus</i>	ME	0	0	X	X	X	X
<i>Oligoplites saurus</i>	ME	0	X	X	X	X	X
<i>Lutjanus synagris</i>	MS	0	0	0	0	0	X
<i>Lutjanus apodus</i>	MS	X	X	0	0	0	0
<i>Lutjanus griseus</i>	MS	X	X	X	X	X	0
<i>Lutjanus jocu</i>	MS	0	X	0	X	X	0
<i>Eucinostomus gula</i>	MS	0	X	0	0	0	0
<i>Eucinostomus melanopterus</i>	ME	X	X	X	X	X	X
<i>Diapterus rhombeus</i>	ME	X	X	X	X	X	X
<i>Diapterus auratus</i>	ME	X	X	X	X	X	X
<i>Gerres cinereus</i>	MS	0	X	X	0	0	0
<i>Eugerres plumieri</i>	MS	X	X	X	X	X	X
<i>Haemulon plumieri</i>	MS	0	0	0	0	X	0
<i>Conodon nobilis</i>	MS	X	0	0	0	0	0
<i>Pomadasys croco</i>	MS	X	0	0	0	X	X
<i>Archosargus rhomboidalis</i>	MS	0	X	0	X	X	0
<i>Archosargus probathocephalus</i>	ME	X	X	0	X	X	0
<i>Lagodon rhomboides</i>	MS	X	X	0	X	X	0
<i>Cynoscion nothus</i>	MS	X	0	0	0	0	0
<i>Cynoscion nebulosus</i>	MS	X	0	0	0	0	0
<i>Bairdiella ronchus</i>	ME	X	0	0	X	X	0
<i>Bairdiella chrysoura</i>	ME	X	X	X	X	X	X
<i>Stellifer lanceolatus</i>	ME	0	X	X	X	X	X
<i>Micropogonias furnieri</i>	ME	X	X	X	X	X	X
<i>Chaetodipterus faber</i>	MS	0	0	0	X	0	0
<i>Cichlasoma octofasciatum</i>	F	X	0	0	0	0	0
<i>Cichlasoma salvini</i>	F	0	0	0	0	0	X
<i>Vieja fenestrata</i>	F	X	0	0	0	0	0
<i>Cichlasoma urophthalmus</i>	F	0	X	X	X	X	X
<i>Cichlasoma synspillum</i>	F	0	0	0	X	0	X
<i>Cichlasoma champotonis</i>	F	0	0	0	0	0	X
<i>Cichlasoma helleri</i>	F	0	X	X	X	X	0
<i>Cichlasoma sp.</i>	F	0	0	0	0	0	X
<i>Petenia splendida</i>	F	0	X	X	X	X	X
<i>Oreochromis aureus</i>	F	0	X	X	X	X	X
<i>Oreochromis niloticus</i>	F	0	X	X	X	X	X
<i>Mugil curema</i>	ME	X	X	X	X	X	X
<i>Mugil cephalus</i>	ME	X	X	X	X	0	X
<i>Mugil gaimardianus</i>	MS	0	0	X	0	0	0
<i>Agonostomus monticola</i>	F	0	0	0	0	0	X
<i>Sphyraena barracuda</i>	MS	0	X	0	0	X	X
<i>Polydactylus octenemus</i>	MS	X	X	X	X	0	0

Table 1 (continued)

Species	Ecological						
	Guild	1966–1968	1987–1988	1989	1989–1990	1990–1991	2000–2001
<i>Lupinoblennius nicholsi</i>	E	X	0	0	0	0	0
<i>Gobionellus oceanicus</i>	E	0	X	X	X	X	X
<i>Gobioides broussonetii</i>	E	X	0	0	X	X	X
<i>Lophogobius cyprinoides</i>	E	0	0	0	0	0	X
<i>Bathygobius soporator</i>	E	X	X	0	0	0	X
<i>Guavina guavina</i>	E	0	X	X	X	0	0
<i>Evorthodus lyricus</i>	E	X	X	0	0	0	0
<i>Lythripnus</i> sp.	E	0	0	X	0	0	0
<i>Gobiomorus dormitor</i>	E	X	0	0	0	X	X
<i>Dormitator maculatus</i>	E	X	0	0	X	X	X
<i>Eleotris pisonis</i>	E	0	0	0	0	0	X
<i>Erotelis smaragdus</i>	E	0	X	0	X	X	X
<i>Trichiurus lepturus</i>	MS	X	0	0	X	X	0
<i>Citharichthys spilopterus</i>	ME	X	X	X	X	X	X
<i>Achirus lineatus</i>	ME	X	X	X	X	X	X
<i>Trinectes maculatus</i>	ME	X	0	0	0	0	0

To determine if the species composition of assemblages changed over time, we used PRIMER (v. 5) software to generate a non-metric multidimensional scaling (MDS) diagram. This diagram shows the relative similarity of fish assemblages in ordinate space based on pair-wise Bray-Curtis similarities of presence-absence data. Fish assemblages that are more similar appear closer together in the diagram.

We also used PRIMER to calculate average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) for all survey periods. These 2 statistics are sample size-independent measures of diversity where the taxonomic distance between every pair of species in a given assemblage is the basis for determining relative diversity (Warwick and Clarke 1995). More specifically, average taxonomic distinctness (Δ^+) is the mean taxonomic distance apart of all species pairs in an assemblage, and variation in taxonomic distinctness (Λ^+) is the variance of the taxonomic distances between each species pair about their mean (Clarke and Warwick 2001). A detailed description of the properties that make these 2 statistics sample-size independent, and therefore useful for extracting meaningful information from simple presence-absence data, is provided in Clarke and Warwick (2001). To calculate these statistics for each survey, the total list of species collected for all surveys was used. Based on classification from Nelson (1994), we identified the following taxonomic categories for each species: species, genus, family, order, superorder, subdivision, division, subclass, class, and grade. Each of these categories represents a “node” in determining taxonomic distances between species pairs.

We used this taxonomic species list in combination with the original presence-absence species data to run a TAXDTEST analysis in PRIMER. This analysis produces “funnel plots” where Δ^+ and Λ^+ for each survey are plotted in comparison with the mean and 95% confidence limits of Δ^+ and Λ^+ calculated for 1000 simulated matrices of presence-absence species data. Values of Δ^+ and Λ^+ for observed data that fall outside of the 95% confidence limits represent significant differences in diversity from expected. For this TAXDTEST analysis, the weighting option of using taxonomic richness was chosen. For this option, the weighting of inter-category distances is calculated using the species richness information from the original presence-absence species data.

RESULTS

A total of 107 fish species was collected during the 6 analyzed surveys (Table 1). Of these, 15 species occurred in every survey: Atlantic stingray (*Dasyatis sabina*), hard-head catfish (*Arius felis*), dark sea catfish (*Cathoropus melanopus*), Atlantic needlefish (*Strongylura marina*), shortfin molly (*Poecilia mexicana*), fat snook (*Centropomus parallelus*), flagfin mojarra (*Eucinostomus melanopterus*), rhombic mojarra (*Diapterus rhombeus*), Irish pompano (*Diapterus auratus*), striped mojarra (*Eugerres plumieri*), silver perch (*Bairdiella chrysoura*), whitemouth croaker (*Micropogonias furnieri*), white mullet (*Mugil curema*), bay whiff (*Citharichthys spilopterus*), and lined sole (*Achirus lineatus*; Table 1). A total of 37 species were collected in only a single survey over the 6

TABLE 2

Frequency of species representing 4 ecological guilds (marine stenohaline, marine euryhaline, estuarine, and freshwater) collected from the Alvarado Lagoon Estuary during 6 surveys conducted over 33 years (1968–2001).

Survey Period	Marine Stenohaline	Marine Euryhaline	Estuarine	Freshwater
1966–1968	16	26	8	7
1987–1988	16	26	7	6
1989	7	24	8	4
1989–1990	12	31	9	6
1990–1991	15	30	8	6
2000–2001	9	29	13	9

survey periods. Of these, 15 species occurred only in the 1966–1968 survey and may have since become extirpated from the estuary: speckled worm eel (*Myrophis punctatus*), scaled sardine (*Harengula jaguana*), southern buffalo (*Ictiobus meridionalis*), skilletfish (*Gobiesox strumosus*), an unidentified silverside (*Thyrinops* [*Atherinella*] sp.), obscure swamp eel (*Ophisternon aenigmaticum*), Mexican snook (*Centropomus poeyi*), yellow jack (*Caranx bartholomei*), barred grunt (*Conodon nobilis*), silver seatrout (*Cynoscion nothus*), spotted seatrout (*Cynoscion nebulosus*), Jack Dempsey (*Cichlasoma octofasciatum*), blackstripe cichlid (*Vieja fenestrata*), highfin blenny (*Lupinoblennius nicholsi*), and hogchoker (*Trinectes maculatus*) (Table 1).

When these species were divided into ecological guilds, marine euryhaline species dominated the Alvarado Lagoon Estuary during all survey periods (Table 2). The mean number of marine euryhaline species collected across the 6 surveys was 27.67 species (range = 24–31),

whereas marine stenohaline, estuarine, and freshwater species averaged 12.50 (7–16), 8.83 (7–13), and 6.33 (4–9) species, respectively (Table 2). The occurrence frequency of fish species representing each ecological guild, though, did not change significantly among the survey periods. The chi-square deviation statistic calculated for the observed matrix ($\chi^2 = 8.53$) was not significantly larger than the mean value for 1000 simulated matrices ($\chi^2 = 138.64$; $P = 1.00$). The number of species representing each guild did not differ significantly from average over the 6 survey periods.

A non-metric multidimensional scaling (MDS) diagram based on Bray-Curtis similarities of fish species presence-absence data showed that the 1966 survey period was the least similar to the other survey periods (Figure 2). The assemblage representing the 2000–2001 survey period was somewhat separated from the 1987–1988, 1989–1990, and 1990–1991 surveys, but this separation was similar to the degree of separation from these surveys exhibited by the 1989 survey period (Figure 2). For the 1966–1968 survey, the range of Bray-Curtis inter-survey similarities was 40.4–58.6 ($n = 5$; Table 3). By comparison, the remaining range of inter-survey similarities was 61.5–81.7 ($n = 10$; Table 3).

Average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) for all survey periods were within the simulated 95% confidence limits for expected values (Figures 3 and 4). Both the Δ^+ and Λ^+ values for the 2000–2001 survey period, though, were less than the mean Δ^+ and Λ^+ values for the entire species pool (Figures 3 and 4). The only other values that were less than average (and only slightly) were the Δ^+ values for the 1987–1988, 1989, and 1990–1991 survey periods (Figure 3).

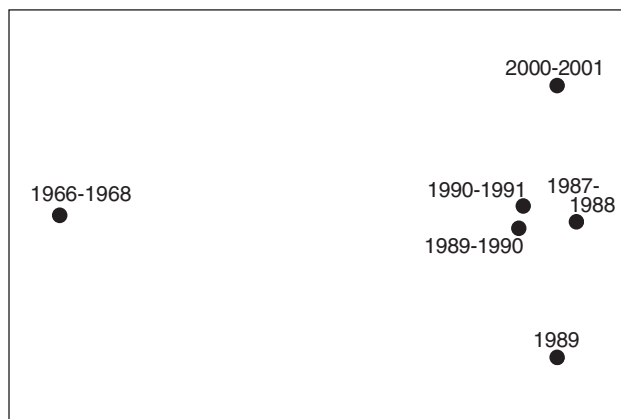


Figure 2. Non-metric multidimensional scaling (MDS) diagram of fish species assemblage differences among the 6 fish surveys. Distances in diagram represent relative Bray-Curtis similarity values. Assemblages closer to each other are more similar. Representation of assemblage relationships is at the highest level of accuracy (stress = 0.01).

DISCUSSION

Fish assemblages in the Alvarado Lagoon Estuary have not changed significantly over the last 40 years. This

TABLE 3

Bray-Curtis inter-survey similarities for fish assemblages collected during 6 survey periods from the Alvarado Lagoon Estuary. Bray-Curtis indices typically range from 0–100 with higher values representing greater similarity between assemblage pairs.

Survey Period	1966–1968	1987–1988	1989	1989–1990	1990–1991	2000–2001
1966–1968	–	–	–	–	–	–
1987–1988	50.0	–	–	–	–	–
1989	40.4	70.1	–	–	–	–
1989–1990	56.6	73.9	69.4	–	–	–
1990–1991	58.6	78.9	67.3	81.7	–	–
2000–2001	55.5	61.5	61.5	64.4	72.7	–

conclusion, though, needs to be considered in context of the loss of several species since 1966–1968 and an apparent more recent (since 1991) overall decline in biodiversity in this ecosystem. Unfortunately, the highly variable nature of estuarine ecosystems precludes simple diagnoses of significant changes in fish assemblages (O’Connell et al. 2004). In these ecosystems, inter-habitat movement, especially by migrating estuarine fishes, creates temporally dynamic fish faunas that are difficult to accurately assess without complete long-term data (Thompson and Fitzhugh 1985; Peterson and Ross 1991; Poff and Allan 1995). While the data and analyses presented here cannot definitively show a statistically significant change in fish-

es relative to ecological guilds or assemblages, the results suggest past and potentially future ecological changes in the fishes of this estuary.

The consistent occurrence of marine euryhaline fishes in collections over time reflects the salinity-tolerant nature of this ecological guild. Of the group of 15 species that were collected from all 6 surveys, 12 were marine euryhaline. The remaining 3 species consistently collected were *C. melanopus* (estuarine/freshwater), *P. mexicana* (freshwater), and *E. plumieri* (marine stenohaline). Marine euryhaline fishes were the most suited to withstand the variety of events that have influenced the hydrological dynamics of Alvarado Lagoon Estuary since 1966. An artificial inlet

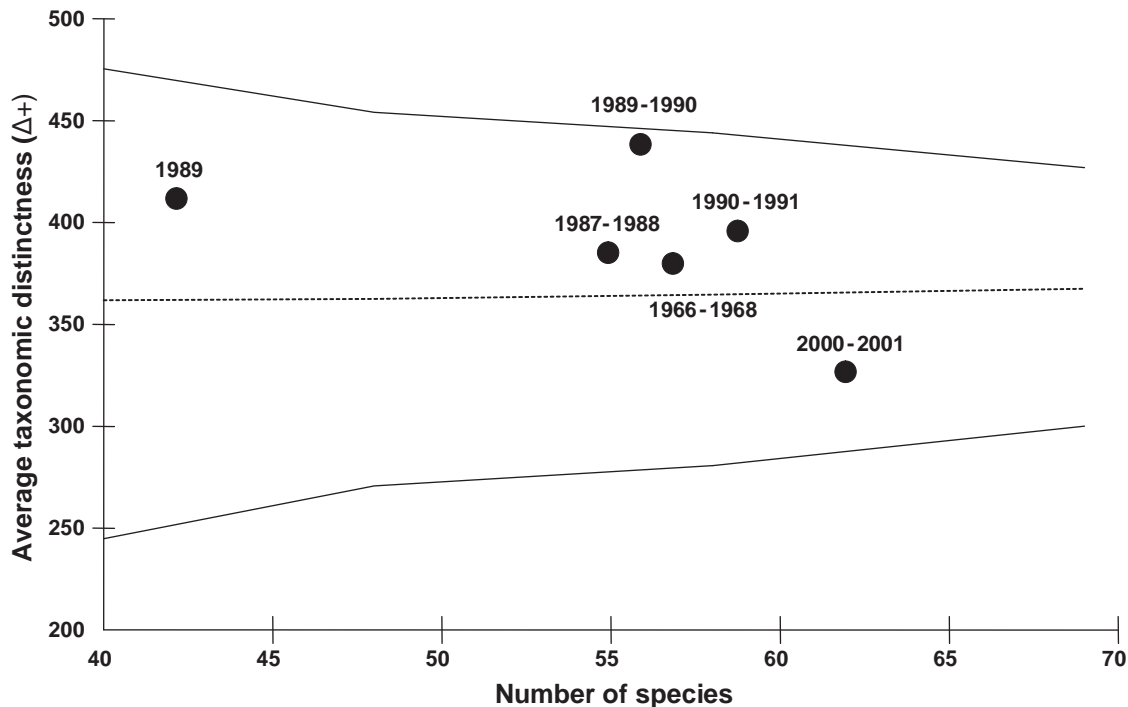


Figure 3. Average taxonomic distinctness (Δ^+) of fish assemblages collected during the 6 surveys relative to the mean Δ^+ (dotted line) and the 95% confidence intervals (solid lines) for 1000 simulated fish assemblages. Simulated fish assemblages were generated from a total species list representing all fishes collected over all surveys.

was opened in Camaronera Lagoon in 1979 with hopes of increasing the salinity in this area of the system to increase shrimp production. Rosales-Hoz et al. (1986) reported a change from 4 to 25 psu in Camaronera Lagoon after the opening of the artificial inlet. Villalobos et al. (1975) found that discharge from the rivers was the principal influence on the hydrological and salinity patterns in the 1960s. Stratification of the system occurred from the estuarine zone of the Papaloapan River to the central region of the Alvarado Lagoon. The lagoon was almost entirely oligohaline in the 1960's, with slight salinity increases provided by the tides during the dry season. In contrast, during the 1980s, the majority of Camaronera Lagoon was mesohaline (Raz-Guzmán et al. 1992). The artificial inlet at Camaronera Lagoon was dredged in 1990, but by 1996 excessive sedimentation began, greatly restricting the circulation of marine waters into the lagoon. An El Niño event in 1998 resulted in increased freshwater inflow into the lagoonal ecosystem, as was reported for other coastal lagoons (García et al. 2001, Kupschus and Tremain 2001, Mol et al. 2001). Thus, during this time period a large part of the lagoonal ecosystem had oligohaline and freshwater characteristics, with mesohaline conditions only found in the dry season near the inlets. These conditions were similar to those reported in the 1960s (Reséndez 1973; Villalobos et al. 1975). Given this variability, marine eury-

haline fishes have a considerable advantage over fishes in the other 3 ecological guilds. Neither freshwater nor marine stenohaline fishes could consistently withstand such changes in salinity. Estuarine fishes, though capable of tolerating a wide range of salinities, would be more prone than marine euryhaline species to local anthropogenic disturbances such as the opening of the artificial inlet and subsequent dredging. The entirety of their life cycles occurs in closer proximity to these impacts than marine euryhaline fishes. A similar response was seen in the Lake Pontchartrain Estuary, another degraded Gulf of Mexico ecosystem. Atlantic croaker (*Micropogonias undulatus*), an estuarine species, experienced relatively greater declines than other fishes during a period of increased local shell dredging. More transient marine species that used the estuary less frequently, though, were not as impacted (O'Connell et al. 2004).

The 15 fish species that were never collected after the 1966–1968 survey reflect the extent to which Alvarado Lagoon Estuary has changed over nearly 3 decades of multiple anthropogenic impacts. By comparison, the degraded Lake Pontchartrain Estuary lost only 3 species between 1954 and 2000 (O'Connell et al. 2004). While some of these “lost” species may be fishes that under normal conditions rarely occur in the estuary (e.g., there was a total of 37 species that were collected in only a single survey), it is

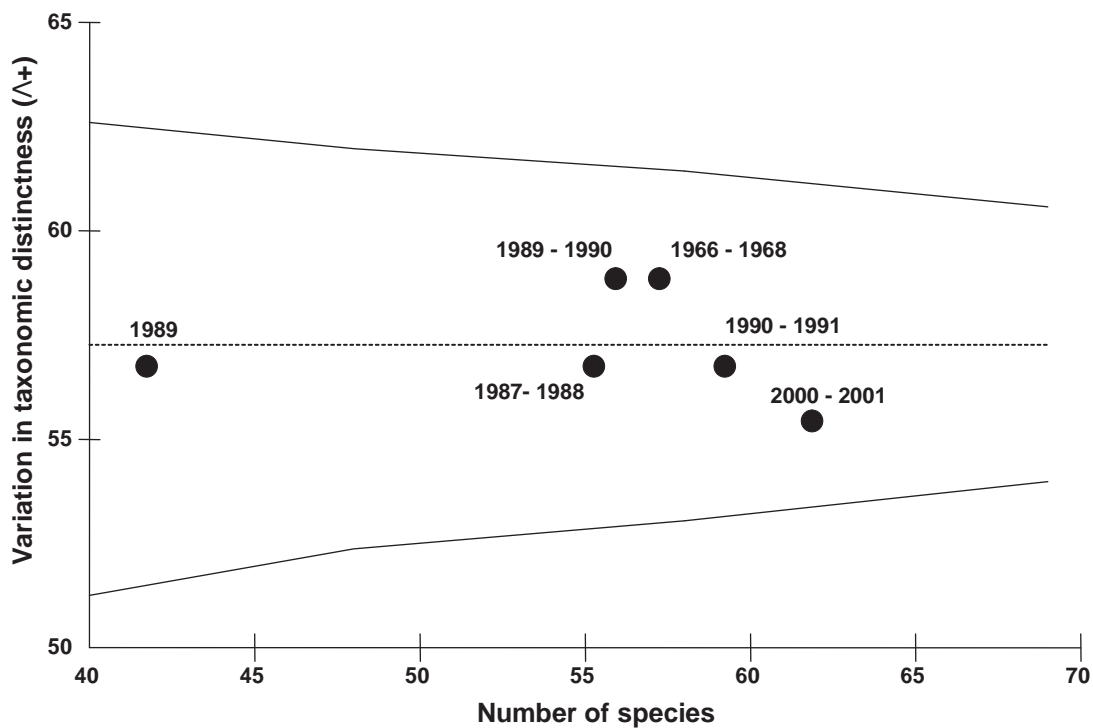


Figure 4. Variation in taxonomic distinctness (Λ^+) of fish assemblages collected during the 6 surveys relative to the mean Λ^+ (dotted line) and the 95% confidence intervals (solid lines) for 1000 simulated fish assemblages. Simulated fish assemblages were generated from a total species list representing all fishes collected over all surveys.

noteworthy that the survey with the most of these single occurrences was 1966–1968 (Table 1). The fact that this group of 15 single-occurrence species contains members of all 4 ecological guilds (6 marine stenohaline, 3 marine euryhaline, one estuarine, and 5 freshwater) suggests no single cause can explain the possible extirpations. For example, the loss of the freshwater cichlid species *C. octofasciatum* and *V. fenestrata* would more likely be related to habitat alteration in nearby rivers, while the absence of marine stenohaline species such as *H. jaguana* and *C. bartholomei* in later surveys may reflect responses to local salinity changes.

This loss of species over time was not enough to significantly change the occurrence frequency of species in each of the 4 guilds. The marine euryhaline guild consistently had the greatest species representation in the Estuary while the number of species for the remaining 3 guilds fluctuated at lower species numbers; the highest number of non-marine euryhaline species in any one survey period was 16 (marine stenohaline in 1966–1968 and 1987–1988) while the lowest number of marine euryhaline species in any one period was 24 in 1989. A lack of significant change over time in the numbers of species in these guilds reflects the stability and tolerance of the dominant group, the marine euryhaline species. Whether natural or anthropogenic factors are influencing fish assemblages, the ecological guilds that will respond most closely to the impacts in this estuary happen to possess fewer species. Thus, if and when degradation starts to affect fishes, we should not expect to notice a significant change by examining the system using a broad-scale approach such as comparing ecological guilds. Had we discovered significant changes at this level of analysis, we could assume a much more severe impact had affected this ecosystem.

Using the more precise approach of MDS, though, we developed a clearer understanding of how similar the surveys were to each other and how this loss of species affected the assemblages. In the MDS diagram (Figure 2), the 1966–1968 survey clearly stands apart from the other 5 surveys and this is supported by the Bray-Curtis similarity index data (Table 3). The long horizontal “leap” from the single survey on the left of the diagram to the clump of surveys on the right indicates the largest assemblage change occurred between the 1966–1968 and 1987–1988 survey periods (Clarke and Warwick 2001). For the 5 more recent surveys, it appears that the estuarine assemblages have reached a new compositional “mean” and any assemblage changes since 1987 seem centered about this mode. This “cyclicality” (Matthews 1998) in later surveys implies 2 situations: 1) recent assemblages have stabilized at a species compositional mode that is different from 1966–1968 and

2) recovery to an assemblage like that collected in the 1966–1968 survey is unlikely without massive restoration efforts. It should also be noted that within the cyclicality of the later 5 surveys, the 1989 and 2000–2001 surveys appear the furthest from the implied mode (in the diagram, 1989 is below the mode, 2000–2001 is above). While these positions might only reflect annual differences in species composition (e.g., a low rainfall year attracting more marine stenohaline fishes into the estuary), the position of the 2000–2001 assemblage may reflect the beginning of yet another compositional shift as occurred between 1966–1968 and 1987–1988. Further surveys could confirm whether the estuarine fish assemblage has stabilized (i.e., exhibits cyclicality) or is changing again (i.e., moving away from the recent compositional mode).

When compared with the other 5 surveys, the Δ^+ and Λ^+ values for the 2000–2001 period indicate that assemblage diversity is decreasing, though the change is not yet significant (Figures 3 and 4). In the funnel plot diagrams this latest survey is the only period where both Δ^+ and Λ^+ values are less than the calculated overall mean values (Figures 3 and 4). The implication is that the estuarine assemblage is at the beginning stages of yet another compositional change that involves the loss of species diversity. The relatively (though not significantly) depressed Δ^+ value for the 2000–2001 period translates into an assemblage that is less taxonomically diverse than the other assemblages (e.g., fewer species per genus, fewer genera per family, etc.). Measuring and comparing Λ^+ (which is the variation of Δ^+) allows for an even finer analysis of relative diversity. It is possible that 2 assemblages will have similar Δ^+ values even when one has mostly species-rich genera while the other has many higher taxa (e.g., families, orders, etc.) represented by only one or a few species (Clarke and Warwick 2001). Therefore, when both Δ^+ and Λ^+ values are relatively low (as for the 2000–2001 period) it suggests a reduction in both the normal array of higher taxa (reduced Δ^+) and a loss of those higher taxa with only a few representative species in the assemblage (reduced Λ^+). As with the MDS results, the fact that this latest survey reflects a unique situation of lowered diversity relative to previous surveys should raise concerns that the fish assemblage in Alvarado Lagoon Estuary may once again be irreversibly transforming to another compositional mode.

This work represents one of relatively few published studies on fish assemblages from the southern Gulf of Mexico (Castañeda and Contreras 1994). Information on species composition from other coastal lagoons and estuaries in Mexico shows that the Alvarado Lagoon Estuary is typical, with only 3 other lagoon systems possessing high-

er fish diversity (Castañeda and Contreras 1994; Pérez-Hernández and Torres-Orozco 2000; Raz-Guzmán and Huidobro 2002). In general, the Gulf of Mexico in this region is subjected to a variety of impacts, particularly the region in south-central Veracruz. Oil and gas exploration began on the continental shelf off Alvarado in 2000 and has since moved steadily closer to the lagoon ecosystem. Population growth, changes in land use practices, an increase in the cattle industry, and unregulated fishing have negatively impacted the lagoon ecosystem, which has resulted in the disappearance of valuable habitats for fishes. Furthermore, large-scale climatic phenomena like El Niño effects and Global Warming (Blaber 2002, Whitfield and Elliot 2002) have influenced the hydrological characteristics of the system as well. The combination of these effects will no doubt continue to result in the deterioration of the integrity of the habitats of the lagoon system and the species that occupy them. Thus, this study documenting changes in assemblage composition of fishes over a 40-year period may be an important baseline data for future comparisons documenting additional anthropogenic changes in the Alvarado Lagoon Estuary.

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