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Fish Assemblage Stability Over Fifty Years in the Lake Pontchartrain Estuary; Comparisons Among Habitats Using Canonical Correspondence Analysis

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ABSTRACT: We assessed fish assemblage stability over the last half century in Lake Pontchartrain, an environmentally degraded oligohaline estuary in southeastern Louisiana. Because assemblage instability over time has been consistently associated with severe habitat degradation, we attempted to determine whether fish assemblages in demersal, nearshore, and pelagic habitats exhibited change that was unrelated to natural fluctuations in environmental variables (e.g., assemblage changes between wet and dry periods). Collection data from three gear types (trawl, beach seine, and gill nets) and monthly environmental data (salinity, temperature, and Secchi depth) were compared for four collecting periods: 1954 (dry period), 1978 (wet period), 1996–1998 (wet period), and 1998–2000 (dry period). Canonical correspondence analysis (CCA) revealed that although the three environmental variables were significantly associated with the distribution and abundance patterns of fish assemblages in all habitats (with the exception of Secchi depth for pelagic samples), most fish assemblage change occurred among sampling periods (i.e., along a temporal gradient unrelated to changing environmental variables). Assemblage instability was the most pronounced for fishes collected by trawls from demersal habitats. A marked lack of cyclicity in the trawl data CCA diagram indicated a shift away from a baseline demersal assemblage of 50 yr ago. Centroid positions for the five most collected species indicated that three benthic fishes, Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and hardhead catfish (*Arius felis*), were more dominant in past demersal assemblages (1954 and 1978). A different situation was shown for planktivorous species collected by trawls with bay anchovy (*Anchoa mitchilli*) becoming more dominant in recent assemblages and Gulf menhaden (*Brevoortia patronus*) remaining equally represented in assemblages over time. Changes in fish assemblages from nearshore (beach seine) and pelagic (gill net) habitats were more closely related to environmental fluctuations, though the CCA for beach seine data also indicated a decrease in the dominance of *M. undulatus* and an increase in the proportion of *A. mitchilli* over time. The reduced assemblage role of benthic fishes and the marked assemblage change indicated by trawl data suggest that over the last half century demersal habitats in Lake Pontchartrain have been impacted more by multiple anthropogenic stressors than nearshore or pelagic habitats.

Introduction

The environmental degradation of essential estuarine habitats in the United States threatens fishes of commercial, recreational, and ecological importance (Thayer et al. 1996; Waste 1996; Peterson et al. 2000; Baltz and Jones 2003). The highly variable physiochemical and biotic nature of estuaries precludes simple diagnoses of significant environmental problems (Peterson and Ross 1991; Nordstrom and Roman 1996; Matern et al. 2002). Determining the effects of natural and anthropogenic disturbances on fishes is particularly difficult because of their mobility relative to other estuarine organisms (Poff and Allan 1995; Able and Fahay 1998; Wagner 1999). In estuaries, interhabitat movement, especially by migrating estuarine-dependent fishes, creates temporally dynamic fish faunas (Thompson and Fitzhugh 1985; Peterson and Ross 1991). Accurate assessment of fish assemblage changes relative to possible habitat degradation effects requires the comparison of data along large temporal and spatial scales (Poff and Allan 1995).

Lake Pontchartrain, an oligohaline estuary in southeastern Louisiana, has been subject to numerous anthropogenic impacts over the last half century including urban and agricultural runoff, shell dredging, overfishing, artificial saltwater and freshwater inputs, shoreline alteration, and industrial discharges (Francis and Poirrier 1999; Penland et al. 2002). Although some of these environmental stressors (urban and agricultural runoff, artificial saltwater and freshwater inputs) exist presently within the estuary while others (shell dredging) have been discontinued, the environmental degradation of Lake Pontchartrain has increased over time (Penland et al. 2002). Between 1900 and 1980, fisheries production in Lake Pont-

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chartrain declined by 49% (Stone 1980). Without substantial conservation efforts, environmental degradation will continue as the local human population increases, further straining natural resources (Beall and Peters 2002). If important Lake Pontchartrain fish assemblages are to be protected from increasing environmental threats and restored to past functional levels, it is essential to understand their long-term stability. When assemblage stability can be assessed over long time periods (e.g., 50 yrs), the relative influence of natural versus anthropogenic effects on the assemblages can be better discriminated (Nordstrom and Roman 1996; Araujo et al. 1998; Marshall and Elliott 1998; Power et al. 2002).

To assess fish assemblage changes in Lake Pontchartrain, we used canonical correspondence analysis (CCA), a multivariate method that elucidates the relationships between biological assemblages of species and their environment. Synthetic environmental gradients are extracted from the ecological data and are used to develop an ordination diagram whereby relationships between species, environmental variables, and sampling sites can be compared over time (ter Braak and Verdonschot 1995). Our goal was to compare fish assemblage stability in demersal, nearshore, and pelagic habitat types. We define a stable fish assemblage as one that may vary over time in response to environmental fluctuations, but returns to a consistent species composition (exhibits cyclicity). An unstable assemblage will show directional, linear change in species composition over time. By using large temporal and spatial scales we hoped to discriminate whether long-term trends reflected responses to natural fluctuations in environmental conditions or suggested noncyclic assemblage changes (a sign of habitat degradation). We addressed two questions: over fifty years, did fish assemblages in Lake Pontchartrain change, and did the dominant fish species in these assemblages respond differently over time based on ecological differences (benthic feeders versus planktivores, resident species versus transient species)?

Materials and Methods

Study Location

Lake Pontchartrain has a surface area of 1,630 km^2 and a mean depth of 3.7 m (Sikora and Kjerfve 1985). To assess possible fish assemblage changes within Lake Pontchartrain, we divided the estuary into five regions of approximately equal area (Fig. 1). Each region exhibits a discernable combination of natural and anthropogenic influences. The northwest region has the highest natural freshwater input (mostly from Lake Maurepas to the west and the Tangipahoa River to the north) and the least modified hydrology. Increases of urbanization and agricultural runoff from dairy farms have recently begun to affect this region (Penland et al. 2002). In the southwest region, the largest environmental influence is the Bonnet Carre Spillway (BCS). This structure was built in 1931 as a means of flood control and forms an artificial connection between the Mississippi River and Lake Pontchartrain (Sikora and Kjerfve 1985). During periods of exceptionally high discharge in the Mississippi River (1937, 1945, 1950, 1973, 1975, 1979, 1983, and 1997) fresh water is diverted from the river, through the BCS, and into southwestern Lake Pontchartrain. Other factors that impact this region are industrial discharge from oil refineries and urban runoff from canals draining New Orleans. The northeast region has the majority of submersed aquatic vegetation in Lake Pontchartrain. Like the northwest region, this area receives natural freshwater input from rivers, but exhibits more degradation from agricultural and urban runoff. Southeastern Lake Pontchartrain is the area of the estuary that is most impacted by anthropogenic influences. An extensive artificial shoreline (concrete sea wall, riprap) and high urban runoff are the characteristics that best describe this region. The influence of greatest magnitude on this region is the artificial connection between Lake Pontchartrain and the Gulf of Mexico created by the construction of the Mississippi River-Gulf Outlet (MR-GO), a deep-water canal completed in 1963 (Sikora and Kjerfve 1985). Through its connections with the Inner Harbor Navigation Canal and the Intracoastal Waterway, the MR-GO has allowed unnaturally high salinity water to enter this region of the estuary (Poirrier

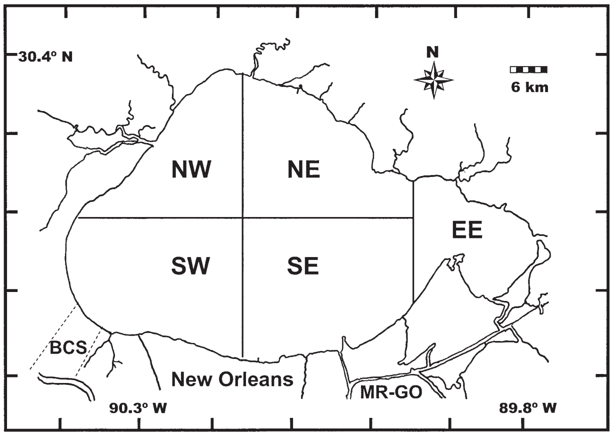

Fig. 1. Location map of the Lake Pontchartrain estuary, Louisiana, U.S. Sources of artificial disturbances shown are the Bonnet Carre Spillway (BCS), the City of New Orleans, and the Mississippi River Gulf Outlet (MR-GO).

1978). Lake Pontchartrain's natural connection to marine waters occurs in the eastern-most region. This region receives saltwater input from Lake Borgne to the east and is consistently the region of highest salinity in Lake Pontchartrain. Based on locality information, each fish collection was assigned to one of these five regions for analyses.

DATA COLLECTION

Using original field notes and museum records, we compiled fish survey data from four time periods: 1954, 1978, October 1996–September 1998, and October 1998–October 2000. To address possible meteorological differences among sampling periods, we examined rainfall and discharge records to determine if fishes were collected during a typically dry or wet period. The 1954 and 1978 surveys were conducted monthly throughout the year, with collections being made at both established and arbitrary sampling sites throughout the lake (Suttkus et al. 1954; Thompson and Fitzhugh 1985). Based on meteorological data, 1954 was a moderately dry year for southeastern Louisiana whereas the area experienced high amounts of rainfall in 1978 (Sikora and Kjerfve 1985). October 1996 through September 1998 was a wet period for Lake Pontchartrain. The fish survey conducted during this 2-yr period consisted of quarterly samples taken at established sites throughout the Lake. A March 1997 opening of the BCS filled Lake Pontchartrain with Mississippi River water and the Lake was entirely fresh for 2–3 wk (Haralampides and McCorquodale 2002; Dufrechou and Poirrier personal observations). The fourth sampling period (October 1998–October 2000) was immediately subsequent to the third sampling period and began after Hurricane Georges passed through southeastern Louisiana on September 29, 1998. During the next 2 yr of sampling the Lake Pontchartrain region experienced its driest period on record, with annual rainfall for both 1999 (115.24 cm) and 2000 (96.90 cm) measuring more than 70 cm below the long-term average of 188.98 cm (National Weather Service 2001). Sampling during this period was quarterly at established sites throughout the lake, until June 2000 when monthly sampling was initiated.

Catch abundance data from three gear types (trawls, beach seines, and gill nets) were compared among the sampling periods (Table 1). Collection data from original field notes were used to exclude samples that proved to be inconsistent with the majority of collections (e.g., extremes of sampling time and effort) or that did not include data for water temperature (°C), salinity (‰), and Secchi depth (m). Among the sampling periods, three possible trawl sizes (4.88, 6.71, or 10.68 m with 19.1 mm mesh) were fished for three possible durations (10, 15, or 30 min). Beach seining for all sampling periods involved the use of both small (3.05–4.58 m) and large (15.25–106.75 m) seines (either separately or in combination) with mesh sizes of 4.3–12.7 mm. All gill nets were 91.50 m in length, 3.05–3.66 m deep, and fished for 1 to 6 h. The mesh sizes (bar measurement) for each of four equal-sized gill net panels were 25.4, 50.8, 76.2, and 101.6 mm. No gill net data from the 1954 survey were used in analyses due to a lack of sampling consistency with other survey periods.

TABLE 1. Number of samples collected by each gear type (trawl, beach seine, and gill net) for the four sampling periods (1954, 1978, 1996–1998, and 1998–2000). Within sampling periods, the number of samples collected from each of the five regions of Lake Pontchartrain is reported (e.g., NW refers to the northwestern region, etc.). No data denotes incidents when a lack of sampling consistency with other survey periods precluded analyses.

Sampling Period	Region	Trawl Samples	Beach Seine Samples	Gill Net Samples
1954	EE	46	27	No data
	NE	6	9	No data
	SE	31	15	No data
	NW	16	15	No data
	SW	29	14	No data
1978	EE	22	5	9
	NE	24	19	15
	SE	25	12	12
	NW	42	14	14
	SW	24	11	12
1996–1998	EE	16	15	2
	NE	10	11	3
	SE	19	20	No data
	NW	12	6	No data
	SW	15	6	1
1998–2000	EE	9	15	4
	NE	11	16	5
	SE	14	12	3
	NW	7	10	4
	SW	18	8	4

DATA ANALYSES AND INTERPRETATION OF CCA DIAGRAMS

Fish assemblage data and the corresponding environmental data were analyzed using CCA, a multivariate method used for comparing the relationships among biological assemblages of species and their environment (ter Braak and Verdonschot 1995; Penczak et al. 2002). For all analyses, the CANOCO software package (Version 4) was used (ter Braak and Verdonschot 1995). Although CCA has been widely used in analyses of fish assemblages (Copp 1992; Winemiller and Leslie 1992; Taylor et al. 1993; Rodriguez and Lewis 1997; Fairchild et al. 1998) a simplified explanation of how CCA diagrams are interpreted is necessary. A CCA ordination diagram optimally displays how assemblage composition varies with environmental conditions by combining data for sample collections, species, and environmental variables into a single two-dimensional illustration (ter Braak and Smilauer 1998). The two ordination axes (CCA Axis I and II) in each diagram represent linear combinations of the environmental variables. These two orthogonal axes are constructed such that they explain the highest variation in the environmental data, with Axis I explaining more than Axis II. In the resulting diagram, three elements are used to describe relationships among the data: sample points, species points, and environmental vectors. The position of a sample point in the diagram is determined by both the composition of the species collection (i.e., the number of each species collected in the sample) and the environmental conditions at the time of sampling. If two samples differ in either species composition or environmental conditions they will appear separate in the ordination diagram; similar sampling sites will appear closer together. A species point will occur at a central position, or centroid, among those sample points in which it was collected. Sample points around a species point will contain more of that species than sample points located elsewhere in the diagram. Environmental vectors (represented by arrows in the diagrams) show the direction of change along a gradient for each environmental variable. The direction also shows how closely each variable is correlated to either CCA Axes I or II. Environmental conditions of a given sample or species can be interpreted from where its point occurs relative to a specific vector (i.e., arrow); points located toward the ends of a vector are associated with extreme values of the environmental variable. The relative strength of each environmental vector is represented by the length of the arrow. By combining all three elements into one diagram, CCA allows direct interpretation of how environmental variables affect the species composition of multiple samples and can be used to compare assemblage compositions among samples.

To assess possible differences in Lake Pontchartrain fish assemblages among the four sampling periods, centroids representing the assemblages of each of the five regions were used to construct five-sided polygons, each representing a sampling period. That is, each corner of a five-sided polygon represents the average environmental and species composition for that region and sampling period. Polygons were created by connecting a centroid to its two closest neighbor centroids (from the same sampling period) with a line. Because centroids that are close in ordinal space represent fish assemblages that are similar to each other, polygons that overlap represent periods in Lake Pontchartrain when the fish assemblages and environmental conditions were similar. We developed and compared CCA ordination diagrams for each of the gear types to assess changes in assemblages over time for demersal (represented by trawl data), nearshore (beach seine data), and pelagic habitats (gill net data). Included in these three diagrams are centroids (i.e., species points) that represent the five numerically dominant species for each gear type. The purpose of analyzing the position of these centroids in ordinate space was to determine if the role of these fish species in assemblages changed over time. This method can also establish how fishes with different ecological characteristics responded to increasing habitat degradation over time.

For each data set the following analytical options in CANOCO were used: direct gradient analysis (extracted patterns from the explained variation only), diagrams optimized intersample distances, all catch abundance data were square-root transformed, and rare species were down-weighted to adjust for possible sampling biases (ter Braak and Verdonschot 1995). Square-root transformation of abundance data was used to standardize data among samples and account for possible differences in sampling durations. Down-weighting of rare species was based on their frequency relative to the most common species. If a species' frequency was less than $\frac{1}{5}$ that of the most common species, then it was down-weighted in proportion to its frequency. For each gear type, permutation tests were run to determine the statistical significance of the relationship between species composition and environmental data along the first ordination axis. If the relationship was nonrandom, then further permutations tested the significance of each environmental variable in describing variation in the overall data.

Results

During the four sampling periods, 366,358 fishes were collected representing 97 species (Table 2). Total numbers of individuals collected by gear type were 246,863 for trawls, 117,307 for beach seines, and 2,188 for gill nets. Significant eigenvalues for CCA Axis I (Table 3) and a lack of polygon overlap in the ordination diagrams (Figs. 2–4) showed that fish assemblages in all three habitat types changed over time. Assemblage separation in ordinate space was the greatest in trawl samples (highest eigenvalues, Table 3) with none of the polygons representing fish assemblages overlapping in the CCA diagram (Fig. 2). Although salinity ($p = 0.005$), water temperature ($p = 0.005$), and Secchi depth ($p = 0.020$) were significantly related to the overall fish compositions, most separation of assemblages

TABLE 2. Most common fishes collected by trawls (T), beach seines (S), and gill nets (G) from Lake Pontchartrain during four sampling periods (1954, 1978, 1996–1998, and 1998–2000). Fishes representing less than 1% of the total catch are not shown (84 species). Letters in sampling period columns represent the gear used to collect a species during that sampling period. A list of all species collected can be requested from the first author at moconnel@uno.edu.

			Occurrence in Gear Types by Sampling Period			
Species	Number	%	1954	1978	96–98	98–'00
Bay anchovy (*Anchoa mitchilli*)	221,004	60	T, S	T, S	T, S	T, S
Gulf menhaden (*Brevoortia patronus*)	37,900	10	T, S, G	T, S, G	T, S, G	T, S, G
Atlantic croaker (*Micropogonias undulatus*)	37,421	10	T, S	T, S, G	T, S, G	T, S, G
Inland silverside (*Menidia beryllina*)	22,506	6	S	T, S	T, S	S
Sheepshead minnow (*Cyprinodon variegatus*)	8,302	2	S	S	S	S
Hardhead catfish (*Arius felis*)	5,120	1	T, S	T, S, G	T, G	S, G
Rainwater killifish (*Lucania parva*)	5,108	1	S	S	S	S
Spot (*Leiostomus xanthurus*)	4,437	1	T, S	T, S, G	T, S, G	S, G
Gulf pipefish (*Syngnathus scovelli*)	3,017	1	T, S	T, S	T, S	T, S
Striped mullet (*Mugil cephalus*)	2,618	1	T, S	T, S, G	T, S	T, S, G
Silver perch (*Bairdiella chrysoura*)	2,121	1	T, S	S	S	T, S, G
Sand seatrout (*Cynoscion arenarius*)	2,032	1	T, S	T, S, G	T, S, G	T, S, G
Hogchoker (*Trinectes maculatus*)	1,972	1	T, S	T, S, G	T, S	S, G

for demersal fishes appeared along a temporal gradient associated with CCA Axis I (i.e., 1954 to 2000). A similar pattern was seen in the CCA ordination diagram representing beach seine samples with salinity (p = 0.005), water temperature (p = 0.005), and Secchi depth (p = 0.010) being significantly related to overall fish compositions, though most separation among polygons appeared along CCA Axis I (Fig. 3). Unlike the trawl samples, the polygons representing the 1978 and 1996–1998 periods (both wet periods) overlapped, indicating a lack of assemblage change between these sampling periods. None of the polygons representing sampling periods for gill net samples overlapped, with salinity (p = 0.015) and water temperature (p = 0.005) being significantly related to overall fish compositions; Secchi depth (p = 0.750) was not significantly related to overall fish assemblage compositions (Fig. 4). In contrast to trawl and seine samples, changes in assemblages among sampling periods for gill net samples were more associated with changes in salinity than a temporal gradient, although gill net data for 1954 were not available for these analyses.

The five numerically dominant species for each gear type were denoted by centroids in each of the CCA diagrams with a total of nine species being represented (Figs. 2–4). In trawl samples, the bay anchovy (*Anchoa mitchilli*) was the most common species (81% of total trawl catch over all sampling periods) with a centroid that was the most closely associated with the 1996–1998 and 1998–2000 sampling periods (Fig. 2). The centroid for trawl-collected Atlantic croaker (*Micropogonias undulates*; 12%) was within the polygon representing the 1978 sampling period. The Gulf menhaden (*Brevoortia patronus*; 1.6%) centroid was the most centrally located in the trawl CCA diagram, while the centroids for hardhead catfish (*Arius felis*; 1.3%) and spot (*Leiostomus xanthurus*; 0.9%) were associated with both increased salinity and the 1954 and 1978 sampling periods. The CCA diagram for

TABLE 3. Results from canonical correspondence analyses (CCA) of fish assemblages collected by three gear types over four sampling periods (1954, 1978, 1996–1998, and 1998–2000) from five regions of the Lake Pontchartrain estuary in southeastern Louisiana. Eigenvalues measure the separation of assemblages and species along ordination axes with eigenvalues > 0.3 indicating strong gradients. Probabilities for the first ordination axes are based on 1,000 permutations. The species-environment correlation represents the correlation between sample scores that are derived from the species scores and sample scores that are linear combinations of the environmental variables. These values are measures of how well the predicted sample scores (based on species scores) correlate with actual sample scores (based on actual environmental scores). For each environmental variable, numbers are correlations with the respective ordination axis.

	Trawl		Beach Seine		Gill Net	
	Axis I	Axis II	Axis I	Axis II	Axis I	Axis II
Eigenvalue (probability)	0.311 (0.005)	0.099	0.305 (0.005)	0.153	0.301 (0.02)	0.180
Species-environment correlation	0.817	0.701	0.796	0.652	0.804	0.761
Salinity	−0.100	−0.348	0.002	−0.392	0.377	0.659
Water temperature	0.022	−0.470	0.050	−0.117	0.785	−0.163
Secchi depth	0.186	−0.430	0.137	−0.282	0.439	0.330

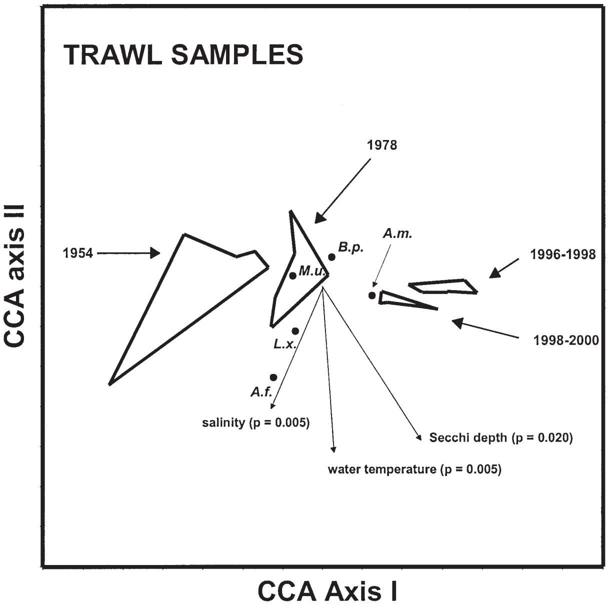

Fig. 2. Site-conditional biplot based on a canonical correspondence analysis (CCA) of data representing fish species collected by trawl sampling from Lake Pontchartrain, Louisiana, during four sampling periods (1954, 1978, 1996–1998, and 1998–2000). Centroids representing the five numerically dominant species of total trawl catch are shown as black circles with labels as follows: *A.m.* = *Anchoa mitchilli, M.u.* = *Micropogonias undulatus, B.p.* = *Brevoortia patronus, L.x.* = *Leiostomus xanthurus,* and *A.f.* = *Arius felis.*

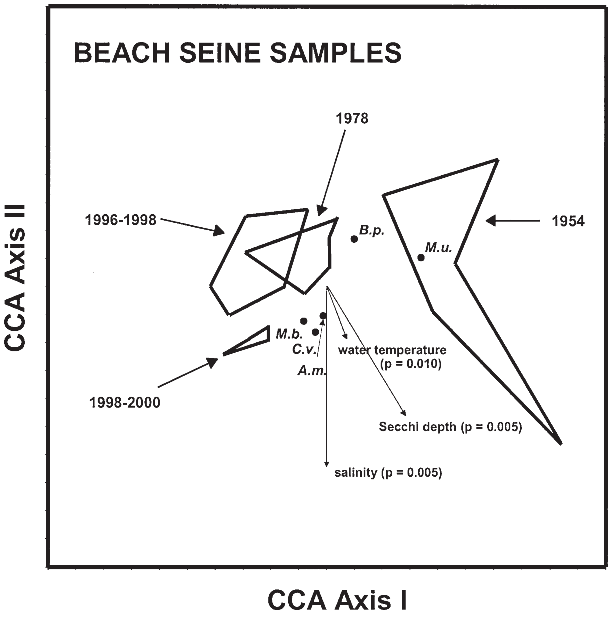

Fig. 3. Site-conditional biplot based on a canonical correspondence analysis (CCA) of data representing fish species collected by beach seine sampling from Lake Pontchartrain, Louisiana, during four sampling periods (1954, 1978, 1996–1998, and 1998–2000). Centroids representing the five numerically dominant species of total beach seine catch are shown as black circles with labels as follows: *A.m.* = *Anchoa mitchilli, M.u.* = *Micropogonias undulatus, B.p.* = *Brevoortia patronus, C.v.* = *Cyprinodon variegatus,* and *M.b.* = *Menidia beryllina.*

beach seine samples includes a *B. patronus* (28.3% of total beach seine catch over all sampling periods) centroid that is between the 1954 sampling period and the remaining three sampling periods (Fig. 3). Centroids representing *A. mitchilli* (17.5%) and two resident species, inland silverside (*Menidia beryllina*; 19.1%) and sheepshead minnow (*Cyprinodon variegatus*; 7.1%), are clumped and centrally located in the beach seine CCA diagram. The fifth most common species collected by beach seines, *M. undulatus* (5.7%), was represented by a centroid within the polygon representing the 1954 sampling period. In gill net samples, *B. patronus* (38.2% of total gill net catch over all sampling periods) was the most common species with a centrally located centroid (Fig. 4). The centroid for skipjack herring (*Alosa chrysochloris*; 7.9%) was also centrally located, while centroids for *A. felis* (11.3%) and *L. xanthurus* (6.9%) were associated with increased water temperature and the 1978 sampling period. Gizzard shad (*Dorosoma cepedianum*; 5.6%), a freshwater species, had the centroid most associated with the 1978 sampling period.

Discussion

Over the last half century, fish assemblages in Lake Pontchartrain have not remained stable. The

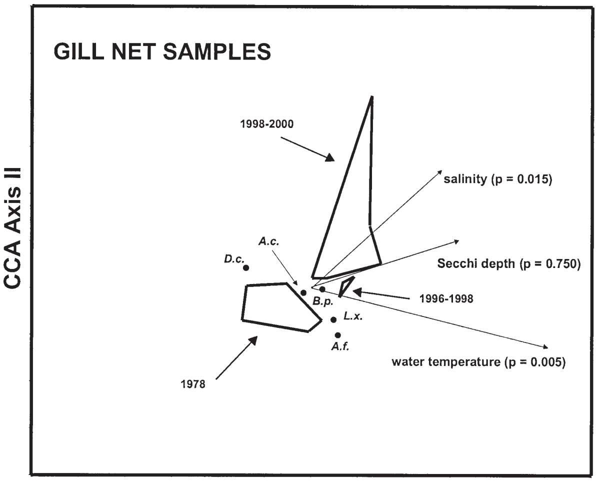

Fig. 4. Site-conditional biplot based on a canonical correspondence analysis (CCA) of data representing fish species collected by gill net sampling from Lake Pontchartrain, Louisiana, during four sampling periods (1954, 1978, 1996–1998, and 1998–2000). Centroids representing the five numerically dominant species of total gill net catch are shown as black circles with labels as follows: *B.p.* = *Brevoortia patronus, L.x.* = *Leiostomus xanthurus, A.f.* = *Arius felis, A.c.* = *Alosa chrysochloris,* and *D.c.* = *Dorosoma cepedianum.*

lack of overlap among sampling period polygons in the CCA diagrams denotes definitive fish assemblage change over time in all three habitat types sampled. This type of fish assemblage instability in estuaries is normally associated with severe habitat degradation (Araujo et al. 2000; Peterson et al. 2000; Clarke and Warwick 2001; Matern et al. 2002). For undisturbed or minimally disturbed habitat types, fish assemblages are relatively stable and any slight variations in species composition tend to reflect changes in local environmental conditions (Wagner 1999; Gido and Matthews 2000; Able et al. 2001). Although our analyses included no attempts to quantify or directly link 50 yr of multiple anthropogenic impacts to assemblage instability, the CCA results allowed for the logical interpretation of available ecological and environmental data to identify those fishes and habitat types that have changed the most over time. This approach allowed us to address our questions about fish assemblage change without incorporating intractable and likely subjective data regarding multiple causes of habitat degradation in Lake Pontchartrain.

Fish assemblages changed the most in demersal habitat types. Although some variation among sampling periods was associated with gradients of salinity, temperature, and Secchi depth (as would be expected in less disturbed estuaries), it is clear that fish assemblages collected by trawls have changed since 1954 and that the change is not in response to natural environmental fluctuations (e.g., differences between wet or dry periods). The lack of cyclicity in the trawl CCA diagram (Fig. 2, especially from the 1954 through the 1996–1998 sampling periods) further emphasizes the greater degree of change over time in these assemblages in comparison to those fishes collected by beach seines and gill nets (Matthews 1998). The unidirectional shift in demersal assemblages over time (left to right in the trawl CCA diagram) is typical of aquatic assemblages that have experienced persistent habitat degradation (Clarke and Warwick 2001). Because demersal fishes are more directly reliant on habitat condition than fishes that remain mostly in the water column (Jones et al. 1999), the stronger response shown by trawl data versus beach seine and gill net data is further evidence that demersal fish assemblage change in Lake Pontchartrain is related to anthropogenic impacts.

The CCA diagram for beach seine collections also showed assemblage change along CCA Axis I with little association with the environmental variables, but the pattern of change was less severely unidirectional. The fish assemblages collected in 1954 were separated from the remaining sampling periods along CCA Axis I, but the assemblages collected during the two wet periods (1978 and 1996–1998) overlapped in ordinate space. This shows that these assemblages were similar although the collections were made 18–20 yr apart. The relative stability of nearshore fish assemblages in comparison to demersal assemblages may be due to the high proportion (36% of total catch) of tolerant resident fishes that were collected by beach seines. In comparison with estuarine dependent fishes, these resident fish species (e.g., members of the families Cyprinodontidae and Fundulidae) can withstand environmental extremes and are less likely to be affected by habitat degradation (Peterson and Ross 1991; Crego and Peterson 1997; Araujo et al. 2000). A similar pattern of assemblage stability in resident fishes was noted during wet periods in the highly degraded San Francisco estuary (Matern et al. 2002). The separation of the 1954 sampling period from the other periods represents a change in nearshore fish assemblages that was not associated with fluctuations in the three measured environmental variables. In Fig. 3, the vectors representing change in water temperature, salinity, and Secchi depth are oriented vertically in the diagram while the change from the 1954 sampling period to the other periods is along a horizontal gradient (CCA Axis I).

Unlike demersal and nearshore assemblages, changes in pelagic fish assemblages were highly associated with the salinity gradient. This is more typical of healthy estuaries where fish assemblages respond closely to environmental change with cyclical seasonal fluctuations (Wagner 1999; Able et al. 2001; Matern et al. 2002). The separation between the 1978 period (wet) and the 1998–2000 period (dry) is clearly along the axis representing salinity (Fig. 4). This pattern likely represents the common occurrence of freshwater transients in estuaries during periods of low salinity and the movement of marine transients into these areas during high salinity (Darnell 1962; Peterson and Ross 1991; Wagner 1999; Able et al. 2001; Matern et al. 2002). Secchi depth, a measure of water clarity, was not significantly related to overall pelagic fish assemblage compositions, whereas it was important for demersal and nearshore assemblages. This result may reflect a difference in gear avoidance between active (trawls and beach seines) and passive (gill nets) gear types. While a nearly invisible monofilament gill net may remain undetected by fishes across a wide range of water clarity and light conditions, detecting and avoiding an oncoming trawl or beach seine would be more highly dependent on underwater visibility (Schieble et al. 2002).

Instability in the demersal and nearshore fish assemblages was further supported by significant changes over time in the two dominant member species, *M. undulatus* and *A. mitchilli*. Centroids for *M. undulatus* in the trawl and beach seine CCA diagrams showed that this species was a principal assemblage member in 1954 and 1978, but played a reduced role in assemblage composition in 1996–1998 and 1998–2000. The position of the *A. mitchilli* centroid in the trawl CCA diagram exhibited an opposite trend, with this species dominating the assemblages in the later two sampling periods. These results are supported by the fact that between 1954 and 1998–2000 the percent composition of *A. mitchilli* in trawl collections increased significantly (Wilcoxon Rank Sums, $p < 0.0001$) while the percent composition of *M. undulatus* decreased significantly (Wilcoxon Rank Sums, $p < 0.0001$; O'Connell unpublished data). Further evidence of a significant decrease in *M. undulatus* in the estuary was seen in nearby Lake Maurepas, which is connected to Lake Pontchartrain to the west via a natural pass. Hastings (2002) found that although *A. mitchilli* and *M. undulatus* were the two dominant species in Lake Maurepas, there was a significant decrease in *M. undulatus* between 1983–1984 and 2000. While this type of large interannual change in population size is a natural phenomenon for many estuarine species (Able and Fahay 1998; Matern et al. 2002), the degree and trend of the *A. mitchilli-M. undulatus* shift in both lakes suggest something beyond natural variation. One possibility is that these species responded differently to the long-term alteration of mid lake demersal habitat by widespread shell-dredging between 1933 and 1990 (Francis and Poirrier 1998). Such large-scale destruction of demersal habitat types would likely affect populations of benthic fishes like *M. undulatus* more than pelagic planktivorous fishes such as *A. mitchilli*. It should be recognized that Lake Pontchartrain is an open system and that many other anthropogenic influences that have occurred outside of the estuary (e.g., increased mortality of *M. undulatus* due to shrimp trawl bycatch) may have played a role in these assemblage changes (Diamond et al. 2000). It should also be noted that the dominance of *A. mitchilli* in trawl collections of more recent sampling periods does not necessarily mean this species has increased in abundance in Lake Pontchartrain since 1954. In other estuaries, numbers of *A. mitchilli* have declined in recent years (Cowan personal communication) and their present relative dominance of the assemblage may just reflect a more drastic decrease of other local estuarine fish species.

Other species represented by centroids in the CCA diagrams exhibited either consistent membership in assemblages over time (i.e., centrally located centroids), a slight association with particular sampling periods, or some degree of change that was correlated to the measured environmental variables. The estuarine dependent *B. patronus* was the only species to occur in the top five species in all three gear types. Unlike the centroids for *A. mitchilli* and *M. undulatus,* the *B. patronus* centroids are generally equidistant from the polygons representing the different sampling periods that suggests that this species' representation in these assemblages has changed little over time. An analysis of the percent composition of *B. patronus* in trawl catches over time supports this assumption (O'Connell unpublished data). State-wide fisheries data suggest that numbers of this abundant estuarine-dependent species had not decreased between 1972 and 1992 (Chesney et al. 2000). The centroid position for the pelagic *A. chrysochloris* in the gill net CCA diagram reflects a similar lack of change over time. The only two resident species with centroids in the seine CCA diagram, *M. beryllina* and *C. variegatus,* showed a slight association with the environmental variables: the position of their centroids is in the same general direction away from the center of the CCA diagram as the three environmental variables (ter Braak and Verdonschot 1995). A similar relationship with the environmental variables is seen for two demersal species, *A. felis* and *L. xanthurus.* These species have centroids associated with each other in both the trawl and gill net CCA diagrams. It is also interesting that these two demersal species, like *M. undulatus,* are more associated with the earlier sampling periods for each of these gear types. This is further evidence that demersal habitat types have been degraded the most over the last half century. The centroid for the freshwater species *D. cepedianum* is most associated with the polygon representing gill net collections for the 1978 sampling period. This reflects a logical conclusion that a freshwater species would be more likely to occur in Lake Pontchartrain during wetter periods of reduced salinity.

For most of these species (i.e., *B. patronus, A. chrysochloris, M. beryllina, C. variegatus,* and *D. cepedianum*) it appears that environmental conditions more likely determined their representation in assemblages rather than factors associated with a temporal gradient (i.e., differences among sampling periods). For *A. felis* and *L. xanthurus,* their association with the earlier sampling periods may be similar to the pattern of declining importance seen with *M. undulatus* over time in Lake Pontchartrain. Unlike these benthic species, freshwater species (*A. chrysochloris* and *D. cepedianum*) and nearshore resident species (*M. beryllina* and *C. variegatus*) rarely occur in mid lake demersal habitat types. Mid lake habitat degradation by shell-dredging would have had less of an effect on these species compared to the impact on those species that use open water habitat types. Resident fishes of estuaries are generally more tolerant to environmental variability than estuarine dependent fishes such as *A. felis, L. xanthurus,* and *M. undulatus* (Hackney and de la Cruz 1981; Peterson and Ross 1991; Crego and Peterson 1997; Araujo et al. 2000).

The trawl and beach seine CCA showed that gradients for salinity, Secchi depth, and temperature were not strongly related to the major patterns of fish assemblage change over time. Although these environmental variables significantly affected the composition of assemblages in Lake Pontchartrain (see results of CCAs) and other estuaries (Marshall and Elliott 1998; Wagner 1999; Araujo et al. 2000; Matern et al. 2002; Power et al. 2002), their role in determining fish assemblages is minor relative to the temporal gradient associated with CCA Axis I. The explicit evidence of this is that for these two gear types none of the environmental gradients are highly correlated with CCA Axis I (arrows in diagram more vertically oriented than horizontal). This is the axis that explains most of the variation in the data and the sampling periods are clearly separated along it. If we make the assumption that this temporal gradient represents increasing environmental degradation of Lake Pontchartrain over time (Penland et al. 2002), then the scenario matches that of other estuaries. For example, in two relatively healthy estuaries of the east coast of the United States, fish assemblages that appeared stable over 16-yr (Wagner 1999) and 25-yr (Able et al. 2001) periods were clearly discriminated along a salinity gradient. More simply, the differences among assemblages were easily explained by the salinity tolerances of the fish species each contained. Studies in more disturbed estuaries show the reduced influence of environmental variables on fish assemblages (as is seen in the present study). Salinity was not correlated with the occurrence of major species in an oligohaline marsh characterized as being part of a system that was composed of abandoned rice fields crisscrossed by numerous canals and ditches (Rozas and Hackney 1984). In a large estuarine system severely impacted by introduced species and hydrologic alterations, the relationship between environmental variables and the composition of the fish assemblage was considered correlative, but not causative (Matern et al. 2002). Two separate estuarine studies also showed that degraded habitat types played a larger role in determining local species richness than changes in environmental variables (Able et al. 1998; Peterson et al. 2000). These results do not signify a total lack of influence by these three factors. The CCA revealed that the three environmental variables were significantly ($p < 0.05$) associated with the distribution and abundance patterns of fish assemblage (with the exception of Secchi depth for gill net samples, $p = 0.750$). This response by fishes to natural fluctuations occurs in other estuaries (Hastings et al. 1987; Wagner 1999; Matern et al. 2002) and is likely to become more prevalent in degraded systems when anthropogenic factors are reduced (Araujo et al. 2000; Matern et al. 2002).

Lake Pontchartrain fish assemblages have changed over the last half century. Fish assemblages occurring in demersal habitat types showed the most change over time. Changes in fish assemblages from nearshore and pelagic habitat types were more closely related to changes in environmental conditions, though change along an inferred temporal gradient was also evident. Examination of the dominant fish species in these habitat types revealed that these assemblage changes were associated with a decrease in the occurrence of *M. undulatus* (a demersal species) over time and an increase in *A. mitchilli* (a planktivorous species). This pattern was observed in both trawl and beach seine data and could not have been detected without the use of data that spanned large spatial and temporal scales (Poff and Allan 1995). Analysis of long-term data can allow the discrimination of natural effects from other, possibly anthropogenic, effects in complex and highly variable estuarine systems (Nordstrom and Roman 1996; Araujo et al. 1998; Marshall and Elliott 1998; Power et al. 2002). As with other degraded estuaries (Matern et al. 2002), it is unlikely that fish assemblages in Lake Pontchartrain will stabilize until more natural processes return and the effects of human disturbance seriously reduced.

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