

Effects of freshwater canal discharge on fish assemblages in a subtropical bay: field and laboratory observations

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ABSTRACT: A 14 mo trawl survey was conducted at 8 study sites in Biscayne Bay, Florida, USA, to compare the species composition and structure of juvenile fish assemblages found near the mouths of freshwater flood control canals with those in similar areas with relatively stable salinity regimes. Water temperature, salinity, dissolved oxygen and depth measurements were recorded during fish sampling and bottom vegetation was also quantified. The survey yielded a total of 38134 individuals from 95 taxa. Fish species composition was similar among sites, but more species were collected from stable- versus variable-salinity areas. Mean fish abundance and the mean abundances of *Eucinostomus gula*, *Lagodon rhomboides*, *Opsanus beta* and *Lutjanus griseus* shared a general pattern of increase from north to south, with highest values occurring at one or more of the canal-influenced sites. In contrast, mean species richness and the mean abundances of *Lucania parva*, *Haemulon sciurus*, *H. plumieri*, and *H. parra* were significantly greater at stable-salinity sites than at variable-salinity sites. Freshwater challenge experiments were then conducted on each of the fishes above, as well as on 2 relatively uncommon species, *Cynoscion nebulosus* and *Cyprinodon variegatus*. The mortality of groups exposed to a single, rapid, freshwater pulse (i.e. salinity was changed from approximately 32 ppt to 0 to 32 ppt over 2 h) was compared with that of controls. Of the 8 fishes that dominated the nearshore habitats of Biscayne Bay, 5 exhibited no mortality and *L. rhomboides*, *L. parva*, and *H. plumieri* exhibited 12.5, 50 and 100% mortality rates, respectively. Mortality was 100% for the relatively uncommon *C. nebulosus* and *C. variegatus*. Results suggest that the differential osmoregulatory abilities of the species tested may underlie some, but not all, of the structural differences observed between fish assemblages from stable-salinity habitats versus those adjacent to freshwater canals.

KEY WORDS: Salinity tolerance Fish assemblages Canal discharge Coastal bays

INTRODUCTION

Alteration of freshwater flows into coastal marine waters has changed temperature, salinity, and nutrient regimes, reduced the extent of wetlands, and degraded estuarine and nearshore marine habitats (Reddering 1988, Whitfield & Bruton 1989, Longley 1994). Profound changes to the South Florida (USA) ecosystem have occurred with the construction of an

extensive inland and coastal canal system by the U.S. Army Corps of Engineers which began as early as 1917 (Hoffmeister 1974, Teas 1976). Today, the system constitutes a 1400 mile (2253 km) network of canals, levees, locks and other flood control structures which modulates freshwater flow from Lake Okeechobee south to the Everglades and adjacent bays. These bays, which serve as nursery habitats for a wide diversity of organisms, have experienced drastic changes in both the amount of freshwater they receive and the fashion in which it is delivered. For example, in southern Biscayne Bay, Florida, canal locks are all that separate this occasionally hypersaline lagoon from the entirely

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freshwater canal systems. When the locks open, the salinity of marine waters downstream often drops 25 ppt within 60 min before recovering as rapidly (Fatt 1986, Wang & Coffey-Shabica 1988). While drastic drops in salinity can occur naturally in nearshore habitats, they usually result from infrequent events such as hurricanes or cyclones (Cyrus 1988). In Biscayne Bay, routine canal lock operation leads to large and abrupt salinity changes several times a day and over several months, particularly during the rainy season (i.e. May to October) (Fatt 1986).

Rapid salinity fluctuations can represent a significant stress for a marine organism, depending on its osmoregulatory ability and/or its behavioral response. In fishes, abrupt salinity changes can cause hydro-mineral imbalance in the blood, which tends to become diluted as salinity drops, and concentrated as it rises—either of which can be lethal (Mazeaud et al. 1977). Rectification of osmotic balance in response to salinity stress requires energy expenditure, often at the cost of growth, reproduction and/or resistance to other stressors, including high temperature (Moore 1972, Schreck 1990). Numerous studies have examined the effects of salinity fluctuation, and/or abrupt salinity changes, on invertebrates (e.g. Crisp & Costlow 1963, Davenport et al. 1975, Drouin et al. 1985, Kumlu & Jones 1995) and, to a lesser extent, temperate fishes (e.g. Davenport & Vahl 1979, McGreer et al. 1991, Provencher et al. 1993, De Vries et al. 1995). The impact of low salinity pulses on tropical and subtropical marine invertebrates has received only limited attention (Moore 1972, Albertson 1980, Brook 1982, Montague & Ley 1993, Irlandi et al. in press). No studies have examined the effects of freshwater pulses on subtropical marine fishes of the Western Atlantic.

In the present study, a trawl survey of nearshore fishes in subtropical Biscayne Bay was supplemented with a series of laboratory-based freshwater challenge experiments. To test the hypothesis of an osmoregulatory basis for fish distribution and abundance in Biscayne Bay, we examined the result of a single freshwater pulse on fishes that were common in field collections and also on species that were relatively uncommon. Our objective was to examine the extent to which a species' osmoregulatory ability, as measured by its post-challenge survival, correlated with its relative abundance at sites with narrow versus wide salinity variation regimes.

MATERIALS AND METHODS

Field survey. Fishes were sampled monthly from August 1993 to September 1994 from 8 sites identified,

from north to south as: Biscayne Canal (BC), Little River (LR), Sunset Harbor (SH), Miami River (MR), Rickenbacker Causeway (RC), Matheson Hammock (MH), Black Point (BP), and Turkey Point (TP) (Fig. 1). Abiotic habitat variables measured included surface water temperature, salinity, dissolved oxygen (DO) and depth; these were measured each month during fish sampling. Biotic habitat variables measured were the type and biomass of dominant macrophytes which were quantified from a single sampling effort conducted in June 1994. Vegetation was sampled by harvesting all above-ground vegetation from 3 randomly placed 1 m² quadrats. In the laboratory, samples were

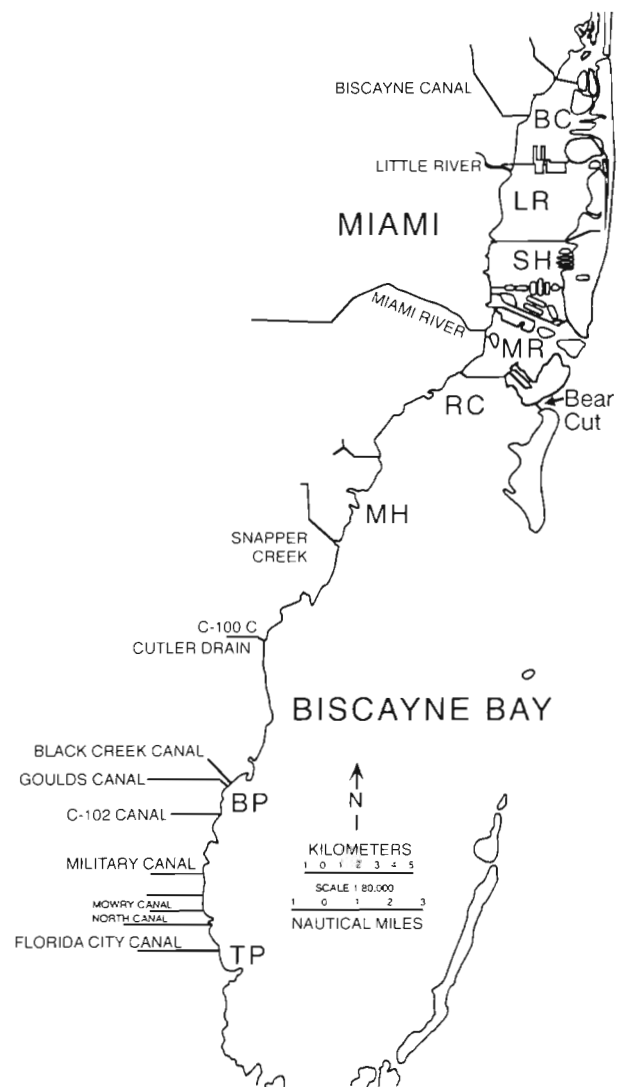


Fig. 1. Location of study sites within Biscayne Bay, Florida, USA. From north to south, sites were designated as Biscayne Canal (BC), Little River (LR), Sunset Harbor (SH), Miami River (MR), Rickenbacker Causeway (RC), Matheson Hammock (MH), Black Point (BP) and Turkey Point (TP)

separated by species when possible, placed in a drying oven for 72 h at 50°C, and then weighed to the nearest gram.

Fish sampling was conducted with 'rollerframe' trawls, the gear used almost exclusively by commercial fishermen to harvest live bait shrimp (*Penaeus* spp.) from the coastal bays of South Florida. Roller-frame trawls were towed in pairs on either side of a 10.1 m vessel with a shallow (0.3 m) draft. Each trawl measured 3 m wide and 1 m high; the attached netting was 7 m long with a mesh size of 10 mm. Trawling was conducted exclusively at night, typically 1 to 2 h after sunset and 3 to 6 h before sunrise. Monthly, at each site, two 10 min tows were conducted at a speed of approximately 2.8 km h⁻¹. Trawl catches obtained from each side of the vessel were averaged, thus $n = 2$ for each month at each site. All fishes were identified and measured for total length (TL). To allow an estimate of area sampled, latitude and longitude coordinates were recorded at the beginning and end of each tow using a hand-held global positioning system.

Freshwater challenge experiments. The same experimental set-up that Irlandi et al. (in press) employed in their investigation of freshwater pulses on Biscayne Bay invertebrates was used in this study. Based on the design of Davenport et al. (1975), the set-up consisted of 4 flow-through seawater systems, a 5000 l reservoir of aerated, dechlorinated freshwater, and 2 electric pumps with associated tubing. Each seawater system consisted of an array of five 19 l buckets with each array housed within an empty 1341 l fiberglass tank with a drain. Fish were placed in the 4 lower buckets of the array, while the fifth bucket served to mix water and regulate flow into those below. Plastic tubing extended from the central mixing bucket to the bottom of each fish-holding bucket, where an air stone was also placed. All 4 flow-through systems were plumbed to receive the mainly oceanic seawater of Bear Cut which varies in salinity from 30 to 35 ppt, depending on tide and season. All experiments were conducted during summer when ambient temperature ranged from 28 to 32°C. Pumps were used to draw freshwater from the reservoir into the mixing buckets of 2 of the systems, thus altering salinity in a subset of the fish-holding buckets. Together, therefore, 8 fish containers could be pulsed with freshwater, while 8 provided relatively stable, polyhaline (i.e. control) salinity conditions.

Each challenge experiment involved 16 individuals per species. With the exception of spotted seatrout *Cynoscion nebulosus*, which were reared from eggs at the University of Miami Experimental Hatchery (UMEH), experimental fish were obtained from sites SH, RC or MH or Bear Cut using either rollerframe

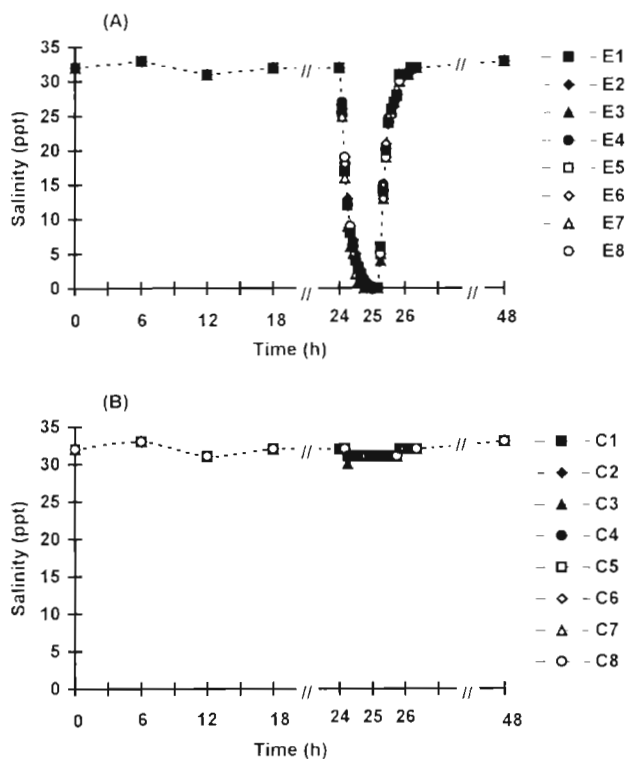


Fig. 2. Example of the standard freshwater challenge (A, challenge; B, control) to which fish were subjected in the laboratory. C1–8 and E1–8 indicate salinities in each of the 8 control and 8 freshwater-pulsed (experimental) containers, respectively

trawl, beach seine, or hook-and-line. Prior to experiments, all fish were maintained for 24 h at the ambient seawater salinities (i.e. 30 to 35 ppt) flowing into UMEH. Similarly sized individuals that were within the length ranges observed in field collections were used. The experiments began when fish were introduced individually into the lower buckets where they were further acclimated for a 24 h period. Salinity and temperature were measured 3 times during acclimation, every 5 min during a single, 2 h pulse event, and then once again, 24 h after the pulsing was initiated. Fig. 2 illustrates the pattern of salinity change in each of the 16 fish containers during experiments. Finally, the number of mortalities 24 h after salinity manipulation was recorded and compared with that of the unpulsed controls.

Data analyses. Statistical analyses were performed using SAS (1990) computer software. Variation in fish species richness, fish abundance (i.e. species combined) and the abundances of selected species were analyzed using analysis of variance (ANOVA) models with site as the independent variable. Numbers of individuals per 1000 m² were log_e-transformed prior to statistical analyses. Means were compared by using the

Bonferroni multiple comparison test in which 'experimentwise' error rate was held at the $p < 0.1$ level (Sokal & Rohlf 1987).

Cluster analyses were performed on our field data, with a focus on the abundances of those species for which we also had freshwater tolerance information. Ward's minimum-variance method (Milligan 1980) was used. Normal cluster analysis was performed to examine affinities among sites and seasons given their respective fish assemblages, and inverse cluster analysis was performed to examine affinities among species given their seasonal abundances across sites (Field et al. 1982, Sedberry & Carter 1993). Both analyses were conducted on a matrix composed of site-specific mean abundance values (\log_e -transformed) for each species during the wet season (May to October) and the dry season (November to April). Resulting intercluster distances are presented in dendrograms.

RESULTS

Field observations

Sites differed markedly in degree of salinity variation (Fig. 3A), but shared very similar temperature and dissolved oxygen regimes (Fig. 3B, C). Reflecting their respective proximities to freshwater canal mouths, relatively narrow salinity ranges of <9 ppt were observed at SH, MR, RC and MH, while relatively wide salinity ranges of 17 to 24 ppt were observed at the remaining sites. Water depths sampled at the study sites ranged from 1.6 to 3.9 m. Mean depth and depth variation were very similar from RC south to TP, but trends of increase in both were evident from MR north to BC (Fig. 3D).

Both rooted and unattached bottom vegetation was present at all study sites at biomass levels ranging from 83 to 539 g dry weight m^{-2} (Table 1). In terms of rooted macrophytes, *Thalassia testudinum* dominated at MR, MH and TP, *Syringodium filiforme* dominated at BC, LR and SH, and *Halodule wrightii* dominated at RC and BP. The biomass of unattached macroalgae, which consisted primarily of the red alga *Laurencia* spp., was especially high at LR and

MH at the time of vegetation sampling. Residence time of the unattached macroalgae at each site was unknown.

Trawling yielded a total 38134 fishes of 95 taxa from 224 samples (Table 2). Total number of taxa recorded at the relatively-stable-salinity sites (i.e. SH, MR, RC and MH) ranged from 43 to 57 taxa, whereas the remaining sites yielded from 40 to 43 taxa. Six species accounted for 88.5% of the total catch and from 74.1 to 92.0% of total catch at each site. In order of decreasing abundance, these were silver jenny

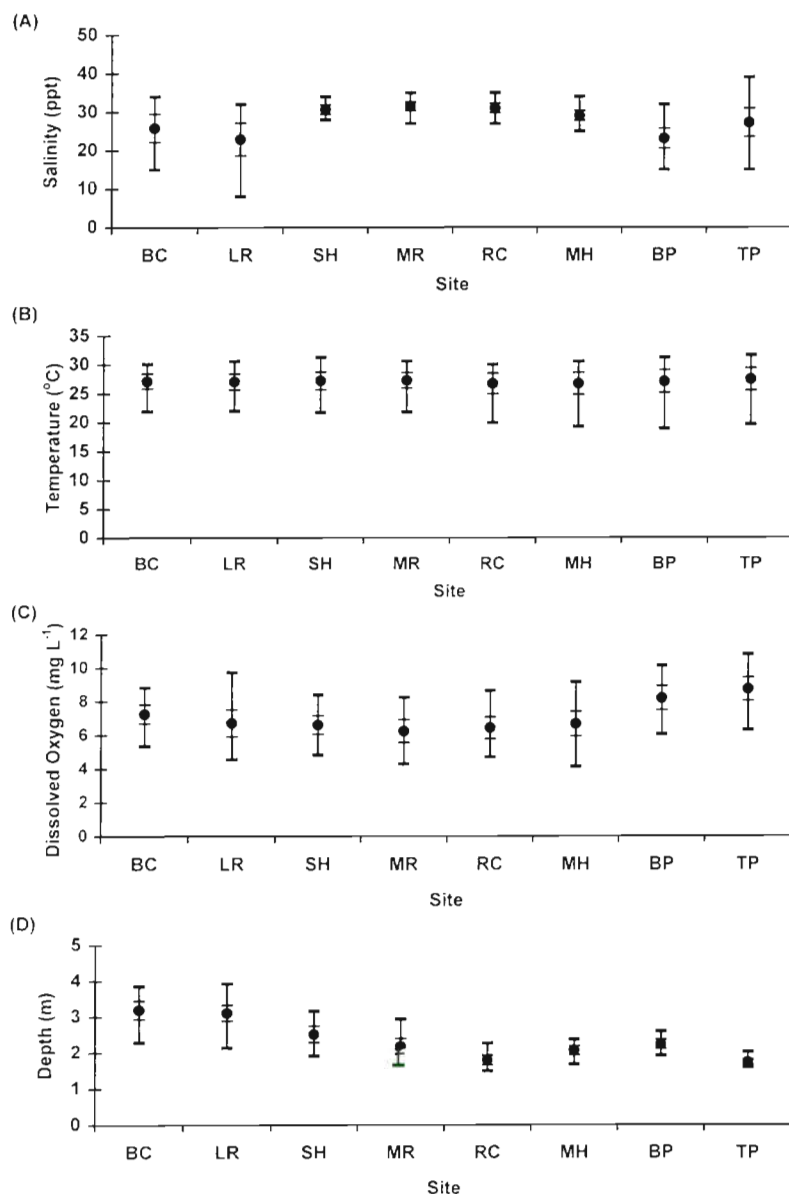


Fig. 3. Plots of (A) salinity, (B) temperature, (C) dissolved oxygen and (D) depth recorded at each site. Mean (solid circles), ± 1 SE (inner bars), and range (outer bars) are indicated. Sites are listed north to south along the x-axis (see Fig. 1)

Table 1. Types and quantities of bottom vegetation at each of the study sites during June 1994. Values are mean biomass (g dry weight) per m². See 'Materials and methods: field survey' and Fig. 1 for site names and locations

Site	Rooted macrophyte			Unattached macroalga	Total
	<i>Thalassia</i>	<i>Syringodium</i>	<i>Halodule</i>		
BC	0.0	10.1	0.0	80.6	90.7
LR	0.0	1.1	0.6	537.0	538.7
SH	0.0	142.2	2.1	142.2	286.5
MR	39.3	7.2	27.7	12.4	86.6
RC	0.2	0.2	63.3	19.4	83.1
MH	107.4	44.5	11.4	289.8	453.1
BP	0.0	18.2	35.7	40.4	94.3
TP	67.4	0.4	0.4	141.7	209.9

Eucinostomus gula, pinfish *Lagodon rhomboides*, bluestriped grunt *Haemulon sciurus*, gulf toadfish *Opsanus beta*, rainwater killifish *Lucania parva* and white grunt *H. plumieri*. Gray snapper *Lutjanus griseus* and sailors choice *H. parra* ranked eighth and eleventh in overall abundance, respectively. Present in the collections, but together constituting only 0.2% of the total catch, were spotted seatrout *Cynoscion nebulosus* and sheepshead minnow *Cyprinodon variegatus*.

Correlations between bottom vegetation biomass and fish species richness and abundance were statistically insignificant. Analysis of variance and subsequent multiple comparison tests revealed significant differences among sites in terms of both mean fish abundance (i.e. species combined) and mean species richness (Figs. 4 & 5). Upon examination of site-specific means, fish abundance followed the general pattern of increase from northern to southern sites (Fig. 4A). In contrast, site-specific species richness means followed a parabolic pattern from north to south (Fig. 5A): in general, the relatively-stable-salinity, central-bay sites (i.e. SH, MR, RC and MH) yielded significantly higher mean species richness values than the sites with wider salinity variation regimes.

Significant differences were also detected among sites in the respective abundances of 10 species. Silver jenny, pinfish, gulf toadfish and gray snapper each exhibited a mean abundance pattern similar to that observed for overall fish abundance, namely, a general increase from north to south (Fig. 4B to E). On the other hand, bluestriped grunt, rainwater killifish, white grunt, and sailors choice each exhibited parabolic abundance patterns from north to south (Fig. 5B to E) similar to the pattern observed for mean species richness. Spotted seatrout was the only species examined which was most abundant at the northernmost site (BC) and then declined southwards (Fig. 4F). Catches of sheepshead minnow were very low and entirely

restricted to SH, the site with the least salinity variation (Fig. 5F).

Laboratory observations

Laboratory-based salinity challenge experiments were conducted on selected size classes of each of the 10 species above (Table 3). While all fishes held under control conditions were found to survive, exposure to a single freshwater pulse elicited different mortality responses depending on the species. Silver jenny, bluestriped grunt, gulf toadfish, gray snapper and sailors choice

appeared to be highly tolerant of the challenge presented; these species exhibited 0% mortality 24 h after freshwater pulse exposure. Exposure of pinfish to a freshwater pulse resulted in 12.5% mortality, while rainwater killifish exhibited 50% mortality. White grunt, spotted seatrout and sheepshead minnow were completely intolerant of the challenge presented; mortality was 100% for all 3 species.

Cluster analyses

Normal and inverse cluster analyses were performed upon the seasonal field abundances of the 10 species for which we had freshwater tolerance information. Normal cluster analysis indicated that the 6 seasonal collections from the 3 southernmost sites (MH, BP and TP; wet and dry seasons) were structurally distinct from those to the north (Fig. 6). However, within the major southern and northern collection clusters, some separation by salinity regime was apparent. For example, within the northern site cluster, all 4 seasonal collections from the variable-salinity sites BC and LR grouped together, distinct from the stable-salinity site collections. The variable-salinity site collections did not separate as cleanly within the southern site cluster, although both TP collections and the BP wet-season collection did group separately from both MH collections. Inverse cluster analysis, in which species were grouped according to their seasonal distributions across sites, resulted in 2 major clusters (Fig. 7). One cluster contained the 4 most abundant species collected (i.e. silver jenny, pinfish, toadfish and bluestriped grunt) which also proved to be relatively tolerant of our freshwater challenge. The second cluster contained the 4 species that proved relatively intolerant of our freshwater challenge, although it also included the tolerant gray snapper and sailors choice.

Table 2. Numbers and sizes of fishes captured at each site over the entire 14 mo trawl study. Species are ranked in descending order of abundance

Rank	Common name	Species	BC	LR	SH	MR	RC	MH	BP	TP	Total	Min.	Mean	Max.
1	Silver jenny	<i>Eucinostomus gula</i>	2250	2428	2600	621	1699	1165	2206	5822	18791	13	61.3	150
2	Pinfish	<i>Lagodon rhomboides</i>	124	106	129	107	116	918	1204	1708	4412	7	92.4	235
3	Bluestriped grunt	<i>Haemulon sciurus</i>	89	83	690	1397	691	161	612	381	4104	18	73.7	275
4	Gulf toadfish	<i>Opsanus beta</i>	62	224	97	116	411	480	803	1400	3593	28	105.0	286
5	Rainwater killifish	<i>Lucania parva</i>	91	112	1797	1	56	5	10	30	2102	9	28.9	55
6	White grunt	<i>Haemulon plumieri</i>	73	3	76	337	214	16	47	2	768	33	74.6	203
7	Sea bream	<i>Archosargus rhomboidalis</i>	156	39	88	26	141	186	59	3	698	26	92.3	250
8	Gray snapper	<i>Lutjanus griseus</i>	57	32	38	67	28	91	69	131	613	28	94.0	265
9	Bronze cardinalfish	<i>Astrapogon alatus</i>	14	0	118	228	3	0	0	0	363	24	48.3	67
10	Fringed filefish	<i>Monocanthus ciliatus</i>	39	12	79	104	39	6	2	2	283	22	64.8	198
11	Sailors choice	<i>Haemulon parra</i>	3	2	33	80	31	68	32	16	265	23	47.7	149
12	Pipefish	<i>Syngnathus sp.</i>	4	7	138	10	46	6	14	13	238	39	130.3	205
13	Gulf pipefish	<i>Syngnathus scovelli</i>	11	17	125	6	44	11	1	1	216	39	92.4	191
14	Bandtail puffer	<i>Spheeroides spengleri</i>	5	3	8	81	8	10	26	3	144	22	103.5	155
15	Dusky pipefish	<i>Syngnathus floridae</i>	7	4	32	10	45	3	1	0	102	44	139.8	343
16	Trunkfish	<i>Lactophrys trigonus</i>	7	0	3	2	15	48	22	2	99	17	51.6	142
17	Scrawled cowfish	<i>Lactophrys quadricornis</i>	8	19	10	14	16	7	22	1	97	16	85.2	192
18	Spotfin mojarra	<i>Eucinostomus argenteus</i>	0	0	0	19	1	0	52	15	87	13	76.9	135
19	Redtail parrotfish	<i>Sparisoma chrysopteron</i>	2	0	8	50	22	0	2	0	84	42	99.3	222
20	Spotted seatrout	<i>Cynoscion nebulosus</i>	63	10	6	1	2	1	0	0	83	39	98.3	342
21	Lined seahorse	<i>Hippocampus erectus</i>	2	24	14	7	26	2	180	2	78	14	83.8	180
22	Bucktooth parrotfish	<i>Sparisoma radians</i>	1	0	5	61	6	0	3	0	76	40	107.1	203
23	Spotted dragonet	<i>Diplogrammus pauciradiatus</i>	1	1	49	6	12	1	4	1	75	25	49.8	67
24	Slender mojarra	<i>Eucinostomus jonesi</i>	0	0	0	13	2	17	12	23	67	26	57.9	115
25	Code goby	<i>Gobiosoma robustum</i>	10	12	43	0	0	0	1	9	66	24	31.3	39
25	Tomlate	<i>Haemulon aurolineatum</i>	4	1	8	10	21	11	8	3	66	24	52.5	181
27	Striped burrfish	<i>Chilomycterus schoepfi</i>	1	2	0	0	7	34	7	8	59	12	53.2	141
28	Dwarf seahorse	<i>Hippocampus zosterae</i>	0	6	7	0	29	0	0	0	42	15	29.4	43
29	Emerald parrotfish	<i>Nicholsina usta</i>	1	0	2	26	8	0	2	1	40	20	111.0	173
30	Lined sole	<i>Archirus lineatus</i>	0	5	1	1	4	2	16	1	30	20	70.7	121
31	Plumed scorpionfish	<i>Scorpaena grandicornis</i>	3	0	5	5	4	8	3	0	28	40	86.4	141
32	Silver perch	<i>Bairdiella chrysoura</i>	5	18	0	1	0	0	0	0	24	75	121.7	173
32	Grass porgy	<i>Calamus arctifrons</i>	0	0	0	0	0	11	11	2	24	45	74.3	124
34	Hogfish	<i>Lachnolaimus maximus</i>	3	1	3	14	0	1	1	0	23	50	126.0	211
35	Rockcut goby	<i>Gobiosoma grosvenori</i>	2	3	17	0	0	0	0	0	22	22	33.6	51
35	Schoolmaster	<i>Lutjanus apodus</i>	0	0	0	1	0	17	1	3	22	47	72.5	109
35	Northern puffer	<i>Sphoeroides maculatus</i>	0	2	0	0	0	6	2	12	22	46	81.9	160
38	Inshore lizardfish	<i>Synodus foetens</i>	0	1	3	4	0	1	6	6	21	117	237.0	335
39	Lane snapper	<i>Lutjanus synagris</i>	1	10	1	9	0	4	0	4	20	53	76.9	106
40	Insular pipefish	<i>Anarcopterus tectus</i>	3	0	3	0	7	0	0	0	19	51	72.6	119
41	Clown goby	<i>Microgobius gulosus</i>	0	2	12	1	0	0	0	0	18	33	40.4	46
42	Florida blenny	<i>Chasmodes saburrae</i>	0	0	8	0	6	4	4	3	17	50	72.6	109
43	Freshwater goby	<i>Gobionellus shufeldti</i>	0	5	8	0	2	0	0	0	15	15	25.7	35
43	Banner goby	<i>Microgobius microlepis</i>	2	4	2	7	0	0	0	0	15	26	39.6	59
45	Hardhead silverside	<i>Atherinomorus stipes</i>	0	0	8	0	0	3	1	1	13	42	50.8	59
46	Goldspotted killifish	<i>Floridichthys carpio</i>	0	0	11	0	0	0	0	1	12	29	41.8	50
47	Honeycomb cowfish	<i>Lactophrys polygona</i>	2	2	2	0	2	3	0	0	11	18	74.8	185
47	Yellowtail snapper	<i>Lutjanus chrysurus</i>	0	0	1	6	3	1	0	0	11	66	96.8	117
47	Pigfish	<i>Orthopristis chrysoptera</i>	0	0	0	2	0	0	0	0	11	60	138.8	185

Table 2 (continued)

Rank	Common name	Species	BC	LR	SH	MR	RC	MH	BP	TP	Total	Min.	Mean	Max.
47	Checkered puffer	<i>Sphoeroides testudineus</i>	1	0	1	3	5	1	0	0	11	157	177.4	199
51	Orange filefish	<i>Aluterus schoepfi</i>	0	0	0	1	4	4	0	0	9	78	117.7	158
52	Crested goby	<i>Lophogobius cyprinoides</i>	9	2	1	0	4	0	0	1	8	59	74.6	92
52	Great barracuda	<i>Sphyraena barracuda</i>	0	0	1	0	0	0	1	6	8	187	230.9	322
52	Whitenoise pipefish	<i>Cosmocampus albirostris</i>	1	1	0	1	1	0	2	2	8	65	111.0	117
55	Balloontail	<i>Diodon holocanthus</i>	4	0	0	1	1	0	0	1	7	20	65.7	95
55	Redfin parrotfish	<i>Sparisoma rubripinne</i>	0	0	0	0	6	1	0	0	7	75	116.9	148
57	Sergeant major	<i>Abudefduf saxatilis</i>	0	0	0	0	0	6	0	0	6	52	68.3	87
57	Marbled blenny	<i>Parachanna marmoratus</i>	0	2	0	2	1	0	0	1	6	68	71.0	75
57	Scaled sardine	<i>Harengula jaguana</i>	0	0	1	1	4	0	0	0	6	68	134.0	179
60	Notchlonge goby	<i>Bathygobius curacao</i>	0	0	0	1	4	0	0	0	5	47	52.0	57
60	Sheepshead minnow	<i>Cyprinodon variegatus</i>	0	0	5	0	0	0	0	0	5	30	36.6	41
60	Southern puffer	<i>Sphoeroides nephelus</i>	0	0	0	4	1	0	0	0	5	138	162.0	190
63	Sargassumfish	<i>Histrio histrio</i>	0	0	1	0	1	2	0	0	4	32	44.5	64
63	Striped parrotfish	<i>Scarus croicensis</i>	1	2	0	0	0	0	0	0	4	108	135.2	163
65	Sea catfish	<i>Arius felis</i>	0	0	0	0	0	0	0	0	3	435	442.3	451
65	Crested blenny	<i>Hypleurochilus geminatus</i>	0	0	0	0	0	2	1	0	3	65	76.7	89
67	Gray triggerfish	<i>Balistes capricus</i>	0	0	0	1	0	1	0	0	2	40	64.0	88
67	Bridled burrfish	<i>Chilomycterus antennatus</i>	0	0	0	1	0	1	0	0	2	25	42.5	60
67	Marsh killifish	<i>Fundulus confluentus</i>	0	0	2	0	0	0	0	0	2	35	36.0	37
67	Gulf killifish	<i>Fundulus grandis</i>	0	1	1	0	0	0	0	0	2	25	27.0	29
67	Honeycomb moray	<i>Gymnothorax saxicola</i>	0	0	0	1	1	0	0	0	2	400	405.0	410
67	French grunt	<i>Haemulon flavolineatum</i>	0	0	0	0	0	0	2	0	2	72	88.5	105
67	Banded pipefish	<i>Micrognathus crinitus</i>	1	0	0	0	0	1	0	0	2	60	62.0	64
67	Gag	<i>Mycteroperca microlepis</i>	1	0	0	1	0	0	0	0	2	144	292.0	440
67	Rainbow parrotfish	<i>Scarus guacamaia</i>	0	0	0	0	0	0	2	0	2	130	130.0	130
67	Redband parrotfish	<i>Sparisoma aurofrenatum</i>	0	0	0	1	1	0	0	0	2	117	131.0	145
67	Pugnose pipefish	<i>Syngnathus dunckeri</i>	0	1	1	0	0	0	0	0	2	61	71.0	81
78	Blue croaker	<i>Bairdiella batabana</i>	1	0	0	0	0	0	0	0	1	114	114.0	114
78	Eyed flounder	<i>Bothus ocellatus</i>	0	0	1	0	0	0	0	0	1	80	80.0	80
78	Four-eye butterflyfish	<i>Chaetodon capistratus</i>	0	0	0	1	0	0	0	0	1	71	71.0	71
78	Burrfish	<i>Chilomycterus</i> sp.	0	0	0	0	0	0	0	1	1	35	35.0	35
78	Bluelip parrotfish	<i>Cryptotomus</i> sp.	0	1	0	0	0	0	0	0	1	55	55.0	55
78	Sand whiff	<i>Citharichthys arenaceus</i>	0	0	0	1	0	0	0	0	1	118	118.0	118
78	Atlantic stingray	<i>Dasyatis sabina</i>	0	1	0	0	0	0	0	0	1	402	402.0	402
78	Spotfin flounder	<i>Egyngophrys senta</i>	0	0	0	0	0	0	1	0	1	82	82.0	82
78	Yellowfin mojarra	<i>Gerrus cinereus</i>	0	0	0	1	0	0	0	0	1	227	227.0	227
78	Spotfin goby	<i>Gobinellus stigmalophius</i>	0	0	1	0	0	0	0	0	1	47	47.0	47
78	Spiny butterfly ray	<i>Gymnura altavela</i>	0	0	0	1	0	0	0	0	1	144	144.0	144
78	Blackedge moray	<i>Gymnothorax nigromarginatus</i>	0	0	0	1	0	0	0	0	1	385	385.0	385
78	Mutton snapper	<i>Lutjanus analis</i>	0	0	0	1	0	0	0	0	1	62	62.0	62
78	Gulf flounder	<i>Paralichthys albigutta</i>	0	0	0	0	0	0	0	1	1	71	71.0	71
78	Gray angelfish	<i>Pomacanthus arcuatus</i>	1	0	0	0	0	0	0	0	1	90	90.0	90
78	Princess parrotfish	<i>Scarus taenioplerus</i>	0	0	0	0	1	0	0	0	1	78	78.0	78
78	Redfin needlefish	<i>Strongylura notata</i>	0	0	0	0	0	0	0	1	1	290	290.0	290
78	Hogchoker	<i>Trinectes maculatus</i>	0	1	0	0	0	0	0	0	1	163	163.0	163
Total number:			3126	3212	6296	3480	3802	3327	5277	9623	38134			
Total number of taxa:			43	42	51	57	49	43	41	40	95			

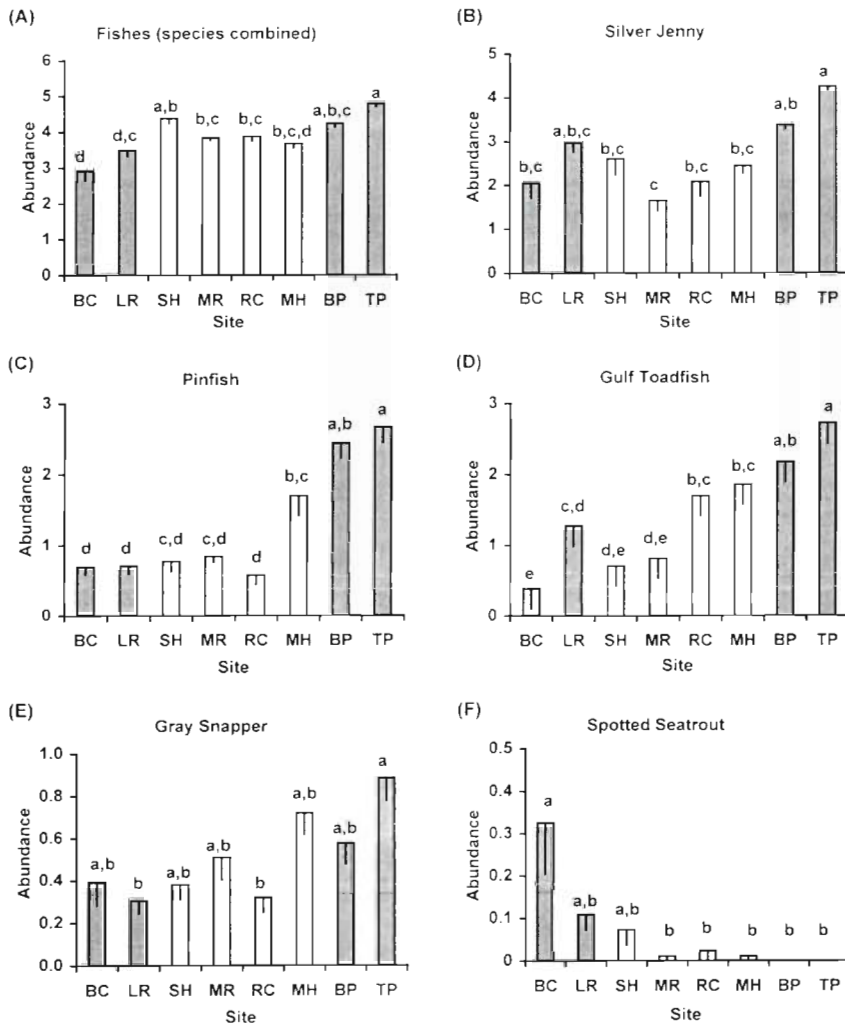


Fig. 4. (A) Mean fish abundance (species combined) at each site and (B–F) mean abundances of species that were highest at one or more of the variable-salinity sites. Sites are arranged from north to south along the x-axis. Shaded bars indicate sites with wide salinity regimes (>17 ppt) and open bars indicate those with narrow salinity regimes (<9 ppt). Abundance means are log_e-transformed numbers per 1000 m². Means (n = 28) sharing the same lower case letter are not statistically different. Vertical lines within bars indicate 1 SE.

DISCUSSION

The physiological suitability of habitats ultimately determines the demographic and ecological performance of animals (Huey 1991). Fishes that utilize areas subject to low salinity pulses may (1) remain, if physiologically capable, and expend energy osmoregulating (i.e. energy which might otherwise be used for growth or gamete production) or (2) leave and risk predation and/or food scarcity while searching for more benign habitats. In the present study, we began to investigate the hypothesis that physiological tolerance to dramatic salinity change underlies fish species composition and species-specific abundances at sites with wide- versus

narrow-salinity variation. Some of our results were consistent with this hypothesis while others were not.

Field collections revealed that areas subject to wide salinity fluctuations were dominated by many of the same species found in areas with relatively stable salinity regimes. Canal-influenced sites, however, tended to yield (1) fewer fish taxa overall, (2) significantly lower mean species richness values, and (3) significantly fewer rainwater killifish and white grunt. Subsequent laboratory experiments revealed that most (i.e. 6 of 8) fishes that were common to Biscayne Bay's nearshore habitats were tolerant of a single freshwater pulse (i.e. exhibited <13% mortality). However, rainwater killifish and white grunt, which overall ranked as the fifth and sixth most abundant fishes, proved to be relatively intolerant of freshwater exposure (i.e. exhibited 50 and 100% mortality, respectively). Similarly, the relatively uncommon sheepshead minnow, which occurred at only 1 of the 4 stable-salinity sites, also proved to be intolerant of the dramatic salinity change presented in the laboratory. The pattern of site-specific abundances of rainwater killifish, white grunt and possibly sheepshead minnow, therefore, may reflect their limited abilities to cope with dramatic salinity change relative to other species.

On the other hand, some of our results were only partially consistent or completely inconsistent with the hypothesis of an osmoregulatory basis for fish distribution and abundance in Biscayne Bay. One example was the general pattern of abundance decline from south to north in the 4 species that proved to be relatively tolerant of a freshwater pulse (i.e. silver jenny, pinfish, gulf toadfish and gray snapper). While the abundances of these fishes tended to be highest at the southern sites with wide salinity variation regimes, they were not abundant at the northern sites with wide salinity regimes. This was likely due to the confounding influence of other factors, perhaps bottom vegetation type, depth, or some

other habitat features not tested here.

Normal cluster analysis on field data also suggested a north-south gradient in assemblage structure existed. However, once geographic location was accounted for, structural differences between assemblages in variable-salinity areas versus stable-salinity areas were evident, especially in northern Biscayne Bay. The inverse cluster analysis was only partially consistent with laboratory results. Although the 4 most abundant, freshwater-tolerant species grouped together separate from all the freshwater-intolerant species, gray snapper and sailors choice grouped with intolerant fishes.

Our laboratory results on juvenile spotted seatrout were inconsistent with our field results. We expected this sciaenid, which uses both estuaries and lagoons as nursery areas, to be tolerant of the freshwater challenge we presented; it clearly was not. A complicating factor may have been that we tested juveniles that had been raised under the stable-salinity, hatchery conditions at UMEH (i.e. 30 to 35 ppt). We cannot rule out the possibility, therefore, that our test fish were physiologically unrepresentative of wild fish.

Finally, despite their ability to withstand our freshwater challenge, numbers of bluestriped grunt and sailors choice tended to be reduced at all 4 of the canal-influenced sites. Again, these species may have been responding to habitat characteristics unrelated to salinity variation, or possibly to consequences of variable salinity regimes that we did not measure, such as reduced invertebrate prey (Brook 1982, Cyrus 1988) or differences in shelter quality (Montague & Ley 1993). Because bluestriped grunt and white grunt share more morphological characteristics as early juveniles than any other pair of species within the genus *Haemulon* (Lindeman 1986), the apparent differences that we found in their respective abundances and osmoregulatory abilities deserve further attention. Martin (1988) suggested differential physical tolerance of salinity and temperature stress was the mechanism for spatial separation of 3 Asiatic glassfishes (genus *Ambassis*) in estuaries on Africa's

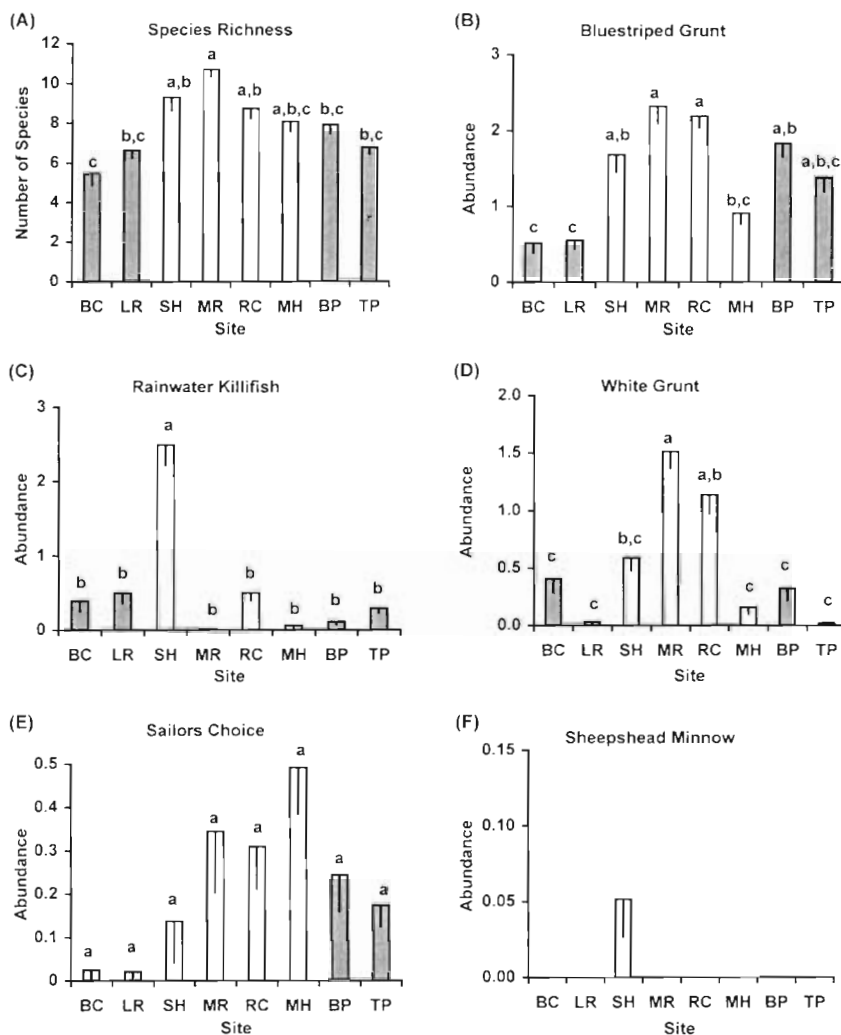


Fig. 5. (A) Mean fish species richness across sites and (B-F) mean abundance patterns of species that were generally highest at the central-bay, stable-salinity sites. Sites are arranged from north to south along the x-axis. Shaded bars indicate sites with wide salinity regimes (>17 ppt) and open bars indicate those with narrow salinity regimes (<9 ppt). Abundance means are \log_e -transformed numbers per 1000 m^2 . Means ($n = 28$) sharing the same lower case letter are not statistically different. Vertical lines within bars indicate 1 SE

southeast coast. Similarly, Sheaves (1996) suggested spatial differences in the abundances of 2 groupers, *Epinephelus coioides* and *E. malabaricus*, were reflective of their respective tolerances to hyper- and hyposaline conditions in estuaries of tropical Australia. If further laboratory and field results corroborate our findings, relative abundances of bluestriped and white grunt, or perhaps some measure of haemulid diversity, may serve as useful indicators of the stress associated with canal discharges in our region.

Obviously, the precise mechanism(s) causing reduced numbers of certain fishes near canals cannot be determined from this study. Our focus on lethal effects rather than behavior, physiology or growth perfor-

Table 3. Species and sizes tested, experimental conditions and results of freshwater challenge experiments. Percent mortality was determined 24 h after freshwater pulse exposure (n = 8 individuals per treatment)

Rank	Common name (Species)	Length range (mm TL)	Treatment	Temp. range (°C)	Salinity range (ppt)	Percent mortality
1	Silver jenny (<i>Eucinostomus gula</i>)	48–83	Control	29–31	34–35	0
			Challenge	30–31	0–35	0
2	Pinfish (<i>Lagodon rhomboides</i>)	49–81	Control	29–31	31–32	0
			Challenge	29–31	0–32	12.5
3	Bluestriped grunt (<i>Haemulon sciurus</i>)	44–82	Control	31–32	31–32	0
			Challenge	31–32	0–32	0
4	Gulf toadfish (<i>Opsanus beta</i>)	112–170	Control	30–32	31–32	0
			Challenge	29–32	0–32	0
5	Rainwater killifish (<i>Lucania parva</i>)	18–31	Control	28–30	30–31	0
			Challenge	28–30	0–31	50
6	White grunt (<i>Haemulon plumieri</i>)	50–75	Control	29–31	29–30	0
			Challenge	28–31	0–30	100
8	Gray snapper (<i>Lutjanus griseus</i>)	73–82	Control	29–31	30–31	0
			Challenge	30–31	0–31	0
11	Sailors choice (<i>Haemulon parra</i>)	54–65	Control	29–32	30–31	0
			Challenge	31–32	0–31	0
20	Spotted seatrout (<i>Cynoscion nebulosus</i>)	39–50	Control	29–31	32–33	0
			Challenge	29–31	0–33	100
60	Sheepshead minnow (<i>Cyprinodon variegatus</i>)	40–56	Control	28–31	31–32	0
			Challenge	28–30	0–32	100

mance, provides insight only into relative tolerance among nearshore fishes and has limited predictive value. Nevertheless, this study demonstrates that the potential exists for direct mortalities of certain fishes to result from a single, albeit dramatic, canal discharge event. Whether a fish actively avoids a freshwater pulse

or 'waits it out' will depend on size, species, and the perceived risk of predation associated with relocation. Without further research, we cannot assess whether the impact of freshwater pulses on Biscayne Bay's nearshore fishes is mainly direct or indirect, lethal or sublethal. Whatever the case, canal discharges apparently represent levels of disturbance sufficient to reduce the abundance of freshwater-sensitive species and, therefore, fish species diversity.

Comparisons of our field data with previous studies are complicated by differences in sampling gear, precise location of collection, and historical changes in habitat. In general, however, it appears that many of the same fishes have continued to dominate Biscayne Bay's nearshore habitats over the last 20 to 25 yr. For example, Low (1973) reported silver jenny, pinfish, gulf toadfish, white grunt, bluestriped grunt, gray snapper and sailors choice as 'very common' in his central Biscayne Bay seine collections, while he described spotted seatrout as 'common'. Rainwater killifish and sheepshead minnow were not captured by Low (1973).

About 10 yr later, Campos (1985) conducted a monthly survey of Biscayne Bay fishes using rollerframe trawls very similar to those used in the present study. Of the 22 stations that Campos (1985) sampled, 4

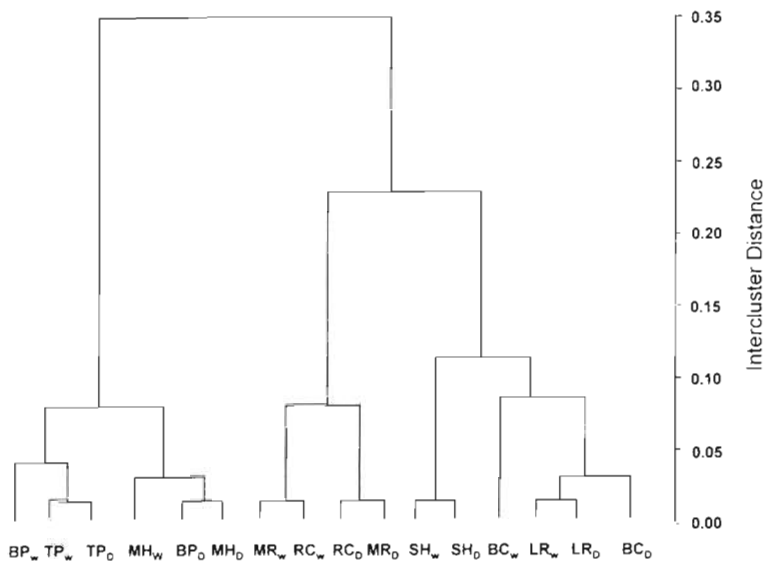


Fig. 6. Results of normal cluster analysis on field data. Dendrogram depicts affinities among sites and seasons (W: wet; D: dry) given the respective abundances of 10 species for which freshwater tolerance was determined (see text for details)

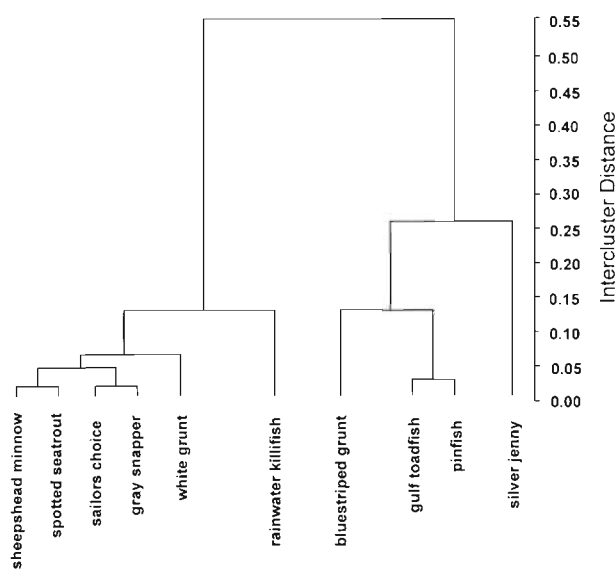


Fig. 7. Results of inverse cluster analysis on field data. Dendrogram depicts affinities among the 10 fishes (for which freshwater tolerance was determined) given their abundances across sites and seasons (see text for details)

were located along the Bay's southwestern shore (i.e. near BP and TP), where salinity was most variable, and 5 were located along the Bay's west-central shore (i.e. near RC and MH), where salinity was relatively stable. As in our study, pinfish, silver jenny, and gulf toadfish predominated at all of Campos' (1985) western shore stations, and differences in their respective abundances at southwestern versus west-central stations were minor. Spatial differences in the abundances of bluestriped grunt, sailors choice and gray snapper, which we found to be tolerant of a freshwater pulse, were negligible in the Campos (1985) study. Consistent with our results, Campos (1985) found that white grunt abundances were on average 5 times greater at the stable-salinity, west-central sites than at the variable-salinity, southwestern sites. Unlike our study, however, Campos (1985) found rainwater killifish was more abundant at southwestern sites, although this species was apparently much rarer in his collections than in ours. Campos (1985) did not capture sheepshead minnow.

Unfortunately, quantitative data on the ichthyofauna of Biscayne Bay prior to canal system construction are not available. The observations of Smith (1896) about 100 yr ago, however, do provide qualitative evidence of a more brackish bay supporting more estuarine species. He reported red drum *Sciaenops ocellatus*, black drum *Pogonias cromis*, and eastern oyster *Crassostrea virginicus* to be abundant in Biscayne Bay. Since at least the 1960s, these species have appeared to be very

rare or completely absent in the bay according to the scientific literature (Roessler 1964, Low 1973, Campos 1985) and personal accounts from local fishermen. We speculate that Biscayne Bay's coastal canal system, combined with the construction of permanent oceanic inlets, has contributed to (1) the virtual elimination of genuinely estuary-dependent species (e.g. red drum), (2) increases in generally stress-tolerant species (e.g. gulf toadfish), and (3) the reduction of juvenile habitat for reef-associated fishes that are vulnerable to rapid drops in salinity (e.g. white grunt).

The ecological consequences of the anthropogenically-driven shift of Biscayne Bay from an estuary to a freshwater-pulsed lagoon are poorly understood. The extent to which abrupt salinity changes result in osmoregulatory failure and death in fishes or compromise their reproduction, development, feeding, growth, and ability to avoid predators requires further study. It is also unclear how coastal organisms will respond to ongoing Everglades habitat restoration efforts which involve changing amounts of freshwater to adjacent bays and eliminating canals, road beds and other obstructions to natural sheet flow (Walters et al. 1992, Harwell et al. 1996). We found that coupling field observations with small-scale laboratory experiments was useful for gaining insight into complex relationships between altered coastal habitats and their fauna. While supplementing field work with laboratory studies has increased the understanding of the effects of extremes in turbidity (e.g. Cyrus & Blaber 1987a, b) and pH (Serafy & Harrell 1993) on temperate estuarine fishes, this combined approach has not been fully applied to the problem of salinity change in subtropical bays. We suggest that future research examine the relative importance of duration, intensity and frequency of freshwater pulses on marine fish assemblages using a combination of field and laboratory investigations.

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