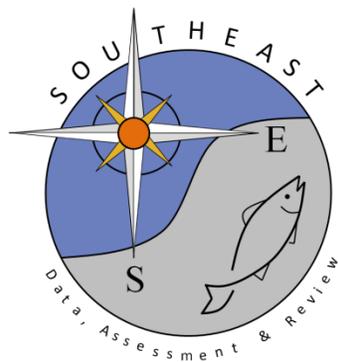# Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico

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Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico

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Abstract

Global temperatures are rising, and are expected to produce a poleward shift in the distribution of many organisms. We quantified changes in fish assemblages within seagrass meadows of the northern Gulf of Mexico (GOM) between the 1970s and 2006–2007, and observed changes consistent with this forecast. During 2006–2007 we sampled seagrass meadows using the same gears and methods previously employed by R. J. Livingston in coastal waters of northwest Florida throughout the 1970s. Comparisons between datasets revealed numerous additions to the fish fauna during 2006–2007 that were completely absent in the 1970s, including: *Lutjanus synagris* (lane snapper), *Epinephelus morio* (red grouper), *Chaetodon ocellatus* (spotfin butterflyfish), *Mycteroperca* sp (grouper, non gag), *Centropristis philadelphica* (rock sea bass), *Fistularia tabacaria* (bluespotted cornetfish), *Ocyurus chrysurus* (yellowtail snapper), *Thalassoma bifasciatum* (bluehead wrasse), *Abudefduf saxatilis* (sergeant major), Acanthuridae spp. (surgeonfishes) and *Sparisoma viride* (stoplight parrotfish). Several other species showed large increases in abundance during the interval between 1979 and 2006, including *Mycteroperca microlepis* (gag grouper, up $\sim 200 \times$), *Lutjanus griseus* (gray snapper, up $\sim 105 \times$), and *Nicholsina usta* (emerald parrotfish, up $\sim 22 \times$). All of these are tropical or subtropical species that now make up a greater percentage of seagrass-associated fish assemblages in the northern GOM than in the past. Additionally, we observed regional increases in air and sea surface temperatures ($>3 \, °C$) during the ~ 30 years that separate Livingston's samples and ours that correlate with northern shifts in the distribution of warm-water fishes. Documenting these range shifts is a critical first step in investigating the consequences of global warming for endemic marine communities and fishery production in the northern GOM.

Keywords: climate change, community composition, geographic range shifts, ichthyofauna, seagrass, species distributions, temperature records

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Introduction

Recent increases in global temperatures are expected to drive concurrent changes in the composition and ecology of terrestrial and marine communities worldwide (McCarty, 2001). The climate-related mechanisms behind these community transitions may include altered primary production resulting from increased CO_2 or photostress (Richardson & Schoeman, 2004); phenological changes in flowering, nesting or migration events (Ro-

ot *et al.*, 2003); and poleward shifts in the range/distribution of species (Perry *et al.*, 2005). Over the short-term, range expansions may increase local biodiversity as poleward-advancing species outpace poleward-retreating species (Hickling *et al.*, 2006). Over longer timescales, however, poleward range expansions may have consequences similar to those now being observed with nonnative species invasions, modifying local dynamics of competition, predation, herbivory and parasitism (C. Sorte, personal communication).

There is a growing literature documenting cases of range or distribution shifts involving taxa as diverse as fishes (Perry *et al.*, 2005), planktonic forams (Field *et al.*, 2006) and butterflies (Parmesan *et al.*, 1999). While these

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cases can be correlated with regional warming, both Sagarin *et al.* (1999) and Schiel *et al.* (2004) have noted difficulties in directly linking current warming to the dynamics and consequences of range shifts. For instance, many expectations regarding the rate and consequences of range shifts are drawn from ecosystem models, known biotic responses to temperature, biological responses to decadal or interglacial climate cycles, and point counts separated over several decades. Unfortunately, high-resolution historical data from closely monitored reference sites that could be used to more rigorously examine the relationship between temperature and species' distributions are largely absent. Thus, we ususally rely on opportunistic studies that correctly identify and explore range shifts to increase our predictive capacity for the effects of the potential continuation or acceleration of the $\sim 0.5\,^{\circ}$C global temperature increase observed over the last century (McCarty, 2001).

Despite reports on many taxa, documentation of range shifts within some groups or ecosystems remain relatively sparse. For instance, seagrass meadows provide numerous ecosystem services and may be biological sentinels of local and climatological perturbations (Orth *et al.*, 2006). Temperature, CO_2 concentration, sea-level rise, and precipitation all impact seagrasses (some positively, some negatively) making them valubale indicators of climate change. However, the lack of long-term records for seagrass distributions, combined with the confounding effects of other anthropogenic stressors, make any robust assessments of range shifts difficult (Orth *et al.*, 2006). Conversely, coastal seagrasses have long been identified as valuable nurseries for fishes and crustaceans (Heck *et al.*, 2003), and there is a comparatively rich literature on the distribution and characteristics of seagrass-associated fish communities (e.g., Pearson, 1929; Livingston, 1982). Temperature affects many vital rates in the life history of fishes (i.e., growth, reproduction; Pauly, 1994), and thus their geographic distribution. For instance, Kimball *et al.* (2004) concluded that the northern range limit of invading *Pterois volitans/miles* (lionfish) would be Cape Hatteras, NC, due to the temperature at which mass mortality occurs ($<10.0\,^{\circ}$C). Therefore, fishes can be valuable indicators of climate perturbations.

Here, we report on potential northern range shifts of fishes in to the northern Gulf of Mexico (GOM), many of which only use seagrass habitat as juveniles. Our analyses of climate-related changes in seagrass fish communities were based on comparisons between trawl surveys conducted during 1971–1979 (Livingston, 1985) and 2006–2007 within seagrass meadows of the northern GOM. We asked two climate-related questions regarding differences in these assemblages: (1) has there been an increase over the last three decades in the representation of tropical or subtropical species that would indicate a northern shift in the distribution of fishes during this time; and (2) for species that have exited (those collected only by Livingston) or entered (those collected only by us) the fish community over the last 30 years, are the average northern range limits of species in each of these groups equal? Additionally, we explored climate conditions that might have affected seagrass fauna in the northern GOM from 1971 to 2007 using daily minimum air and sea surface temperature (SST) data from the National Oceanographic and Atmospheric Administration National Climate Data Center (NCDC), and National Data Buoy Center (NDBC), respectively. Using these temperature data we asked if, and to what degree, seasonal temperature thresholds have been lifted for tropical or subtropical species due to increases in either duration (using air temperature) or intensity (using SST) of warm conditions? In the discussion that follows, we examine the potential effects newcomers may have on endemic estuarine food-webs, and subsequently, the offshore fishery production that originates from seagrass nurseries. We also consider a number of alternative hypotheses that may explain the changes we observed, including short-term population fluctuations/cycles, changes in regional physical oceanography that may have altered larval transport, indirect species interactions, and anthropogenic habitat alteration or degradation.

Materials and methods

The GOM is bisected (north–south) by the Tropic of Cancer, with temperate environments/habitats in the northern GOM and tropical environments/habitats in the southern GOM (becoming the Caribbean Sea). We expected the interface between two climate zones to provide an excellent location for examining climate-related range shifts of fishes. Additionally, the GOM is bounded by North America, and marine species/subpopulations that might otherwise retreat northward in response to global warming lack a latitudinal refuge. Therefore, the consequences of climate change in this region may be especially dramatic.

We analyzed changes over the last 30 years in ichthyofaunal communities within seagrass meadows of the northern GOM by comparing survey data obtained during 1971–1979 by Livingston (1985) to data from our own surveys in 2006–2007. Livingston provides the best reference point for comparisons between current fish communities and those from several decades ago within northern GOM seagrass meadows, but there are notable differences in the survey regimes. Livingston's collections were spatially restricted and temporally expansive, while our surveys covered a
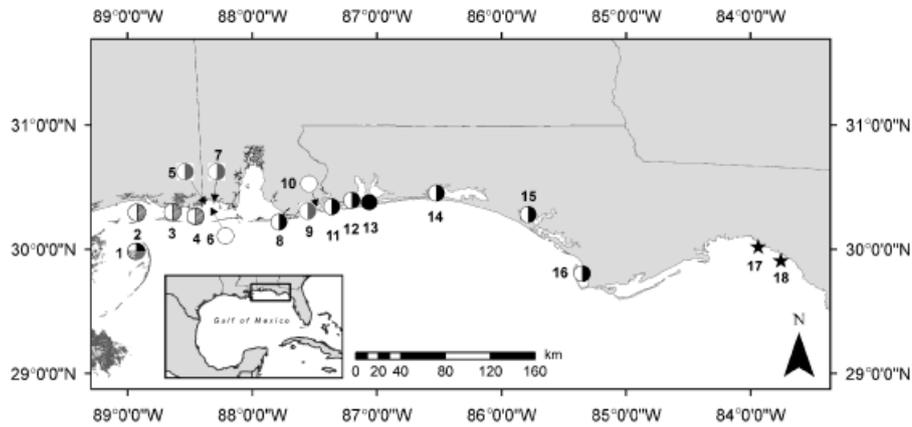
Fig. 1 Map of the 16 seagrass meadows sampled during 2006–2007 (circles), as well as the two seagrass sites sampled by Livingston (1985) throughout the 1970s (stars), to characterize fish communities within the northern Gulf of Mexico. (1) Chandeleur Islands, LA; (2) Ship Island, MS; (3) Horn Island, MS; (4) Petit Bois Island, MS; (5) Middle Bay, MS; (6) Grand Bature Shoal, AL; (7) Point Aux Pines, AL, (8) Little Lagoon, AL; (9) Bayou St John, AL/FL; (10) Perdido Bay, FL; (11) Big Lagoon, FL; (12) Pensacola Bay, FL; (13) Santa Rosa Sound, FL; (14) Choctawhatchee Bay, FL; (15) St Andrew Sound, FL; (16) St Joseph Bay, FL; (17) Econfina, FL; (18) Fenholloway, FL. At each site, *Thalassia testudinum* (black), *Halodule wrightii* (white), *Ruppia maritima* (grey) and/or *Syringodium filiforme* (hash-mark) meadows were sampled (indicated in pie charts).

wider range of sites but occurred over a relatively brief period. Although it would be preferable to make a temporal evaluation using survey data from the same location (e.g., Barry *et al.*, 1995), those data do not exist for our study sites. We propose that Livingston provided a valuable comparison study, especially because his sites were located at a lower latitude than all but two of our 16 sites. As a result, his sites were characterized by environmental conditions (higher water clarity, warmer temperature, closer proximity to the Loop Current) that are more similar to the southern GOM and Caribbean than most all of our sites. Therefore, any differences in fish communities should have tended toward a more tropical fauna at Livingston's sites rather than ours. Also, most species we collected occurred at nearly all our study sites, indicating that the trends we describe are general and not due, for example, to different assemblages at stations farthest removed from Livingston's, in which geographical separation could account for between-survey differences.

Livingston (1985) included detailed descriptions of his survey sites that are summarized here. Collections of fishes from seagrass meadows were conducted in two estuarine systems within Apalachee Bay, along the northern Gulf coast of Florida (30.02°N, 83.93°W). Livingston noted that the Apalachee system was one of the least polluted in the United States at the time of his surveys, although one of the rivers feeding the estuaries he surveyed (the Fenholloway River) was more polluted by kraft pulp-mill effluents than the other (the Econfina River). Sampling occurred annually from 1971 to 1979.

Our surveys occurred during the summer and fall of 2006 and 2007. We sampled 16 stations from the Chandeleur Islands, LA, to St Joseph Bay, FL, in the northern GOM (29.68–30.72°N, 85.30–89.10°W) (summarized in Fig. 1). Byron & Heck (2006) noted an east–west break in seagrass habitats along the northern GOM located near Mobile Bay, AL (30.72°N, 87.48°W). East of Mobile Bay, the seagrass habitats we sampled were more similar to the sites in Apalachee Bay [higher water clarity, *Thalassia testudinum* (turtle grass) dominated]. West of Mobile Bay, sites appeared more temperate: water clarity was much lower, sediments were muddier, and *Halodule wrightii* (shoal grass) was the most abundant seagrass species. Including sites west of Mobile Bay tended to produce a slight conservative bias that made our 2006–2007 assemblage appear more temperate.

In both Livingston's and our surveys, fishes were collected using a 5-m otter trawl (2.0-cm body mesh; 0.6-cm bag mesh; 0.3 m × 0.7 m doors). Both surveys employed trawls with the conventional four-seam balloon design including float and lead lines and without tickler chains. Trawls consisted of 2-min tows behind small (<7 m) research vessels traveling at approximately 2.5 knots. In both sets of surveys, trawls covered mosaics of seagrass meadows that included *T. testudinum*, *H. wrightii*, *Ruppia maritima* (widgeon grass), and *Syringodium filiforme* (manatee grass), along with scattered unvegetated patches. These trawls ranged from depths of 0.5–2.5-m, and were conducted during daylight hours. During our 2006–2007 surveys, species were enumerated in the field unless species-level identifications were not easily made. Unidentified specimens were

transported to the lab where meristics were used by at least two different technicians to identify each individual. In cases in which species could not be identified, specimens were classified to the lowest taxonomic level possible. Livingston's and our surveys each resulted in the collection of $\sim 125\,000$ individual specimens. As a result, differences in presence/absence of rare species between surveys should not have been influenced by sample size. Because Livingston reported his data as relative frequencies of each individual species, we did likewise to make the datasets directly comparable.

To place any faunal changes we observed in a climate-related context, we also explored changes in climatic conditions in the northern GOM from January 1971 to December 2007 using daily minimum air temperature data from the NCDC (1971–2007), and daily minimum SST data from the NDBC (1987–2004) and from an instrument array maintained by the Dauphin Island Sea Lab (2005–2007). Air temperature data from the Ft. Morgan (1971–1986) and the Dauphin Island #2 (1987–2007) stations, both at the mouth of Mobile Bay, were obtained from http://www.ncdc.noaa.gov/oa/mpp/freedata.html. Years with fewer than 300 days of data were excluded from our analyses in order to avoid errors in interpretation, yielding 35 years of data. For each of these years, the number of days with a nightly minimum air temperature $\geq 20\,°C$ was calculated. We selected this temperature because many fishes exit seagrass habitats in November–December when seawater temperatures dip below $20\,°C$ (J. Fodrie, unpublished results). We expected that an increasing window of 'warm-weather' conditions throughout the summer and fall could affect the composition of the fish community. As an additional comparison between climate and seagrass-associated fish communities in the northern GOM, we also determined the temporal trend in daily minimum SST during each fall from 1987 to 2007 (the years in which data were available). SST data were obtained from the NDBC DPIA1 station (http://www.ndbc.noaa.gov) at the mouth of Mobile Bay and from a nearshore instrument array (30.09°N, 88.21°W). Years with fewer than 60 days of data were excluded from our analyses, yielding 15 years of fall data that were used to determine the mean daily minimum SST during September–November (intensity of warming).

Statistical analyses

Typical multivariate approaches (ANOSIM, MANOVA, etc.) for comparisons between the seagrass ichthyofaunal assemblages during the 1970s and 2006–2007 could not be used because we did not have Livingston's trawl-by-trawl data (only his published summaries of community composition), and the formatting of the data as relative frequencies meant that variables (species abundances) were not independent. Rather, we decided that the simplest comparison between assemblages would also be the clearest, most appropriate, and most compelling for looking at climate-related shifts. Therefore, we compared the relative frequency of all fishes collected during Livingston's surveys to the relative frequency of all fishes collected during our 2006–2007 surveys. This comparison was done on a species-by-species basis, and changes in relative abundance were considered with respect to whether each species provided a relevant case for examining latitudinal distribution shifts [e.g., *Lagodon rhomboides* (pinfish) was not relevant in this context].

Seventeen species collected during these two surveys were notable for having historical distribution centers that were more than 5° latitude south of our study sites (http://www.fishbase.org). Because relative frequencies of each species were not independent, we could not employ multivariate or serial species-by-species statistical tests to explore how the abundance of these species have changed over time. However, we were able to conduct a single univariate test to look at the temporal changes in the aggregate of these 17 species. This involved pooling the relative frequencies of these 17 species into a single value and conducting a one-group *t*-test that compared our trawl-by-trawl data to the single datum provided by Livingston. Whereas one-group tests are usually compared with a hypothesized mean of 0, we made a comparison between the pooled relative frequency of these 17 species in each of our 2006–2007 trawls to the pooled relative frequency of these 17 species collected by Livingston (0.14%). Therefore, we transformed our trawl data by subtracting 0.14% to each data entry from our 2006–2007 tows before conducting this *t*-test.

To explore climate-related differences between fishes that entered or exited the assemblage over the last 30 + years, we also tested if there was a statistically meaningful difference in the reported latitudinal ranges of species (as a metric of temperature-related niches) collected only by Livingston vs. species collected only during 2006–2007. For this we used a unpaired *t*-test with northern range limit of each species, as reported by http://www.fishbase.org, as the response variable.

Temporal differences in air temperature (length of the 'warm season') near Mobile Bay, averaged among ~ 5 year periods, were evaluated using least squares regression on the number of days each year with a minimum temperature $\geq 20\,°C$. Least squares regression was also used to evaluate the temporal trend in daily minimums of fall SST among the years 1987–2007 (intensity of warming). Parametric tests were employed in all cases as data were normally distributed and variances were homogeneous at $\alpha = 0.05$.

Results

During our recent surveys in the northern GOM, 127 717 fishes belonging to at least 81 species and 48 families were collected (Table 1). Overall, the 10 most abundant species we collected were: *L. rhomboides*; *Orthopristis chrysoptera* (pigfish); *Bairdiella chrysoura* (silver perch); Gerridae spp. (mojarra); *Anchoa* spp. (anchovies); *Leiostomus xanthurus* (spot); *Lutjanus griseus* (gray snapper); *Lutjanus synagris* (lane snapper); *Cynosion nebulosus* (speckled trout)*;* and *Monacanthus hispidus* (planehead filefish). Livingston (1985) collected 120 003 fishes during 9 years of surveys in Econfina and Fenholloway. These collections included at least 91 species and 56 families (Table 1). During those 1970s surveys, the 10 most abundant species were: *L. rhomboides*; *L. xanthurus*; *B. chrysoura*; Anchoa spp.; *Monacanthus ciliatus* (fringed filefish); *Sygnathus* spp. (pipefishes); *O. chrysoptera*; *Diplodus holbrooki* (spottail pinfish); Gerridae spp.; and *Centropristis striata* (black seabass).

There were a number of clear differences in the frequency with which species were collected between Livingston's and our 2006–2007 surveys that are relevant for examining the impacts of climate change. Specifically, we collected *L. synagris* (the eighth most abundant species we collected), *Epinephelus morio* (red grouper), *Chaetodon ocellatus* (spotfin butterflyfish), *Mycteroperca* sp (grouper, non gag), *Centropristis philadelphica* (rock sea bass), *Fistularia tabacaria* (bluespotted cornetfish), *Ocyurus chrysurus* (yellowtail snapper), *Thalassoma bifasciatum* (bluehead wrasse), *Abudefduf saxatilis* (sergeant major), Acanthuridae spp. (surgeonfishes) and *Sparisoma viride* (stoplight parrotfish), in decreasing relative abundance; while Livingston's data indicate these species were completely absent during his surveys (Table 1). Additionally, *Mycteroperca microlepis* (gag grouper, nearly 200-fold greater in relative abundance, becoming the 18th most abundant species in 2006–2007), *L. gieseus* (nearly 105-fold greater in relative abundance, becoming the seventh most abundant species in 2006–2007), and *Nicholsina usta* (22-fold greater in relative abundance, becoming the 17th most abundant species in 2006–2007) all showed considerable increases (Table 1). Thirteen of these 14 species (17% of all species we caught in 2006–2007) are identified as tropical or subtropical species with distribution centers south of ours and Livingston's collection sites (http://www.fishbase.org). *M. microlepis* is an exception, but within the GOM it has historically been more abundant in south Florida.

Conversely, Livingston collected only three species absent in our recent surveys that had distribution centers south of our survey locations: *Apogon townsendi* (belted cardinalfish), *Lachnolaimus maximus* (hogfish), and *Astrapogon stellatus* (conchfish). *A. townsendi* and *L. maximus* are clearly tropical species and their absence

in our recent surveys is a notable exception to the overall trend we observed. *A. stellatus* has a commensal relationship with the conch *Strombus gigas* (http://www.fishbase.org), and its absence in our surveys may simply reflect that fact that we never collected a conch in our surveys.

In total, the representation of these 17 'southern' species increased by > 20-fold between Livingston's surveys and ours. These species comprised only 0.14% of all fishes collected during Livingston's 1970s surveys, whereas during our more recent surveys these 17 species accounted for 2.86% of all fishes. Based on a one-group *t*-test that compared our trawl-by-trawl dataset to Livingston's summary datum, this difference was highly significant (df = 592; *t* = 5.747; *P* < 0.001).

The remainder of fish collected by Livingston that were absent during our 2006–2007 surveys represented extrememly rare: *Lepisosteus osseus* (longnose gar), *Ogcocephalus pantostictus* (spotted batfish), *Raja texana* (roundel skate); cryptic: *Paraclinus fasciatus* (banded blenny), *Paraclinus marmoratus* (marbled blenny); or deeper-water taxa: *Mullus auratus* (red goatfish), *Ophidion beani* (cusk eel); rather than tropical species that have become less abundant over time (Table 1). *Scorpaena brasiliensis* (barbfish) were collected by Livingston and likely during 2006–2007 as well, as they are known to be common in the northern GOM, although we only identified specimens to the family level (Scorpaenidae). A few temperate species such as *Hemiramphus brasiliensis* (ballyhoo) and *Hyporhamphus unifasciatus* (halfbeak) are typically not caught using otter trawls but were collected by Livingston during the 1970s.

Overall, Livingston collected 31 species that were not collected during our surveys in 2006–2007, while we collected 21 species that went unrecorded during the 1971–1979 surveys within Apalachee Bay. The northern range limit (mean ± 1 SE) of species collected only during 1971–1979 was 41.4 ± 1.7° latitude, while the mean northern range limit of species collected only during 2006–2007 was 38.5 ± 1.4° latitude (Fig. 2). This difference was not statistically significant based on *t*-test results (df = 36; *t* = 1.237; *P* = 0.224).

Both the duration and intensity of 'warm' days during fall indicated the presence of a long-term shift in climate conditions in the northern GOM over the past 30 + years. The annual number of warm days with a daily minimum temperature ≥ 20 °C (mean ± 1 SE) steadily rose by over 30 days (a 21% increase) from 140 ± 13.3 in 1971–1975 to 170 ± 4.2 in 2001–2007 (Fig. 3a). This trend was significant over time ($r^2 = 0.89$, *P* < 0.001). SST during fall also increased markedly over the past 20 years (Fig. 3b). Nightly minimum SST rose from 20.5 ± 0.5 °C in 1987 to 25.1 ± 0.4 °C in 2007. Again, this trend was significant over time ($r^2 = 0.82$, *P* < 0.001).

Table 1 Relative abundance of fish species in northern Gulf of Mexico seagrass beds during 1971–1979 and 2006–2007

| Scientific name | Family | Percent abundance | | Absolute change in percent abundance between 1970s surveys and 2000s surveys | Relative change in percent abundance between 1970s surveys and 2000s surveys |
		1971–1979 Econfina & Fenholloway	2006–2007 St Joseph Bay – Chandeleur Is		
Lutjanus synagris	Lutjanidae		1.10%	1.10%	Not collected in 1970s
Citharichthys sp.	Bothidae		0.04	0.04	Not collected in 1970s
Epinephelus morio	Serranidae		0.01	0.01	Not collected in 1970s
Chaetodon ocellatus	Chaetodontidae		0.01	0.01	Not collected in 1970s
Scorpaenidae	Scorpaenidae		0.01	0.01	Not collected in 1970s
Mycteroperca sp.	Serranidae		0.01	0.01	Not collected in 1970s
Centropristis philadelphica	Serranidae		0.01	0.01	Not collected in 1970s
Caranx crysos	Carangidae		0.01	0.01	Not collected in 1970s
Fistularia tabacaria	Fistulariidae		<0.01	<0.01	Not collected in 1970s
Acanthuridae	Acanthuridae		<0.01	<0.01	Not collected in 1970s
Holocentrus ascensionis	Holocentridae		<0.01	<0.01	Not collected in 1970s
Halichoeres bivittatus	Labridae		<0.01	<0.01	Not collected in 1970s
Thalassoma bifasciatum	Labridae		<0.01	<0.01	Not collected in 1970s
Xyrichthys novacula	Labridae		<0.01	<0.01	Not collected in 1970s
Pomatomus saltatrix	Pomatomidae		<0.01	<0.01	Not collected in 1970s
Ocyurus chrysurus	Lutjanidae		<0.01	<0.01	Not collected in 1970s
Abudefduf saxatilis	Pomacentridae		<0.01	<0.01	Not collected in 1970s
Rachycentron canadum	Rachycentridae		<0.01	<0.01	Not collected in 1970s
Sparisoma viride	Scaridae		<0.01	<0.01	Not collected in 1970s
Scomberomorus sp.	Scombridae		<0.01	<0.01	Not collected in 1970s
Serraniculus pumilio	Serranidae		<0.01	<0.01	Not collected in 1970s
Haemulon sp.	Haemulidae	<0.01%	0.27	0.27	393.69
Mycteroperca microlepis	Serranidae	<0.01	0.13	0.13	194.56
Lutjanus griseus	Lutjanidae	0.01	1.37	1.36	104.55
Paralichthys sp.	Paralicthyidae	<0.01	0.07	0.07	98.17
Scaridea	Scaridae	<0.01	0.03	0.02	79.90
Harengula jaguana (was pensacolae)	Clupeidae	0.01	0.52	0.51	39.54
Archosargus probatocephalus	Sparidae	0.01	0.28	0.27	39.11
Nicholsina usta	Scaridae	0.01	0.15	0.14	21.58
Gambusia affinis	Poeciliidae	<0.01	0.01	0.01	16.42
Dasyatis say	Dasyatidae	<0.01	0.01	0.01	13.33
Trachinotus carolinus	Carangidae	<0.01	<0.01	<0.01	11.10
Sphyraena sp.	Sphyraenidae	0.01	0.06	0.04	4.22
Orthopritis chrysoptera	Haemulidae	3.35	13.34	10.00	3.99
Arius felis	Ariidae	0.08	0.25	0.17	3.09
Dasyatis sabina	Dasyatidae	0.04	0.11	0.07	3.07
Diplectrum formosum	Serranidae	0.11	0.31	0.21	2.93
Gerridae	Gerridae	3.03	7.86	4.82	2.59
Sciaenops ocellatus	Sciaenidae	0.01	0.02	0.01	2.45
Belonidae	Belonidae	<0.01	<0.01	<0.01	2.22
Cynoscion nebulosus	Sciaenidae	0.50	0.97	0.47	1.94
Echeneis naucrates	Echeneidae	<0.01	0.01	<0.01	1.63
Mugil cephalus	Mugilidae	0.01	0.01	<0.01	1.55
Bairdiella chrysoura	Sciaenidae	7.32	9.52	2.20	1.30
Chloroscombrus chrysurus	Carangidae	0.09	0.12	0.02	1.26
Menidia sp.	Atherinidae	0.04	0.05	0.01	1.25
Lagodon rhomboides	Sparidae	44.35	54.83	10.48	1.24

Continued

Table 1 Continued

		Percent abundance			
		1971–1979 Econfina & Fenholloway	2006–2007 St Joseph Bay – Chandeleur Is	Absolute change in percent abundance between 1970s surveys and 2000s surveys	Relative change in percent abundance between 1970s surveys and 2000s surveys
Scientific name	Family				
Hippocampus sp.	Sygnathidae	0.13	0.15	0.02	More in 2000s 1.18
Chilomycterus schoepfi	Diodontidae	0.82	0.73	−0.09	More in 1970s 0.89
Micropogonias undulatus	Sciaenidae	0.20	0.17	−0.03	0.84
Uranoscopidae	Uranoscopidae	0.02	0.02	>−0.01	0.78
Lactophrys quadricornis (was *Acanthostracion*)	Ostraciidae	0.21	0.16	−0.05	0.77
Paralichthys lethostigma	Paralicthyidae	0.02	0.02	−0.01	0.67
Fundulus sp.	Fundulidae	0.01	0.01	>−0.01	0.65
Sphoeroides sp.	Tetraodontidae	0.38	0.22	−0.16	0.59
Paralichthys albigutta	Paralicthyidae	0.23	0.13	−0.11	0.54
Stephanolepis hispidus	Balistidae	1.79	0.97	−0.82	0.54
Pogonias cromis	Sciaenidae	<0.01	<0.01	>−0.01	0.52
Anchoa sp.	Engraulidae	5.28	2.73	−2.55	0.52
Trinectes maculatus	Achiridae	0.02	0.01	−0.01	0.48
Menticirrhus sp.	Sciaenidae	0.06	0.03	−0.03	0.48
Synodus foetens	Synodontidae	0.22	0.10	−0.12	0.44
Blenniidae	Blenniidae	0.46	0.16	−0.30	0.34
Chaetodipterus faber	Ephippidae	0.07	0.02	−0.05	0.31
Gobiesox strumosus	Gobiesocidae	<0.01	<0.01	>−0.01	0.30
Brevoortia patronus	Clupeidae	0.06	0.02	−0.04	0.29
Triglidae	Triglidae	0.11	0.03	−0.08	0.26
Sygnathus sp.	Sygnathidae	3.86	0.95	−2.91	0.25
Gymnura micrura	Gymnuridae	<0.01	<0.01	>−0.01	0.22
Opsanus beta	Batrachoididae	1.02	0.17	−0.85	0.17
Cynoscion arenarius	Sciaenidae	0.15	0.02	−0.13	0.15
Peprilus burti	Stromateidae	0.05	0.01	−0.04	0.13
Leiostomus xanthurus	Sciaenidae	11.47	1.46	−10.01	0.13
Caranx hippos	Carangidae	0.02	<0.01	−0.02	0.12
Ancylopsetta quadrocellata	Bothidae	0.01	<0.01	−0.01	0.07
Symphurus sp.	Cynoglossidae	0.09	0.01	−0.09	0.07
Haemulon aurolineatum	Haemulidae	0.06	<0.01	−0.05	0.05
Lucania parva	Fundulidae	0.25	0.01	−0.24	0.04
Aluterus schoepfi	Balistidae	0.10	<0.01	−0.10	0.03
Gobiidae	Gobiidae	1.77	0.06	−1.71	0.03
Centropristis striata (was *melana*)	Serranidae	1.88	<0.01	−1.88	<0.01
Diplodus holbrooki	Sparidae	3.19	<0.01	−3.18	<0.01
Scorpaena brasiliensis	Scorpaenidae	<0.01		>−0.01	Not collected in 2000s
Lepisosteus osseus	Lepisosteidae	0.01		>−0.01	Not collected in 2000s
Myrophis punctatus	Ophichthidae	0.01		>−0.01	Not collected in 2000s
Selene vomer	Carangidae	0.01		>−0.01	Not collected in 2000s
Astrapogon stellatus	Apogonidae	<0.01		>−0.01	Not collected in 2000s
Hemiramphus brasiliensis	Exocetidae	<0.01		>−0.01	Not collected in 2000s
Hyporhamphus unifasciatus	Exocetidae	<0.01		>−0.01	Not collected in 2000s
Stenotomus caprinus	Sparidae	<0.01		>−0.01	Not collected in 2000s
Gymnothorax nigromarginatus	Muraenidae	0.01		>−0.01	Not collected in 2000s
Clupeidae sp.	Clupeidae	0.01		>−0.01	Not collected in 2000s
Cyprinodon variegatus	Cyprinodontidae	0.01		>−0.01	Not collected in 2000s
Ophidion beani (or *holbrooki*)	Ophidiidae	0.01		>−0.01	Not collected in 2000s

Continued

Table 1 Continued

		Percent abundance			
		1971–1979 Econfina & Fenholloway	2006–2007 St Joseph Bay – Chandeleur Is	Absolute change in percent abundance between 1970s surveys and 2000s surveys	Relative change in percent abundance between 1970s surveys and 2000s surveys
Scientific name	Family				
Mullus auratus	Mullidae	0.01		> −0.01	Not collected in 2000s
Lobotes surinamensis	Lobotidae	<0.01		> −0.01	Not collected in 2000s
Serranus subligarius	Serranidae	<0.01		> −0.01	Not collected in 2000s
Anguilla rostrata	Anguillidae	<0.01		> −0.01	Not collected in 2000s
Apogon townsendi	Apogonidae	<0.01		> −0.01	Not collected in 2000s
Porichtys plectodon (was *porosissimus*)	Batrachoididae	<0.01		> −0.01	Not collected in 2000s
Elops saurus	Elopidae	<0.01		> −0.01	Not collected in 2000s
Raja texana	Rajidae	<0.01		> −0.01	Not collected in 2000s
Paraclinus marmoratus	Labrisomidae	0.02		−0.02	Not collected in 2000s
Ogcocephalus pantostictus (was *radiatus*)	Ogcocephalidae	0.02		−0.02	Not collected in 2000s
Lachnolaimus maximus	Labridae	0.07		−0.07	Not collected in 2000s
Etropus crossotus	Bothidae	0.09		−0.09	Not collected in 2000s
Polydactylus octonemus	Polynemidae	0.23		−0.23	Not collected in 2000s
Urophycis floridana	Phycidae	0.54		−0.54	Not collected in 2000s
Calamus arctifrons	Sparidae	0.58		−0.58	Not collected in 2000s
Haemulon plumieri	Haemulidae	0.62		−0.62	Not collected in 2000s
Paraclinus fasciatus	Labrisomidae	0.82		−0.82	Not collected in 2000s
Monocanthus ciliatus	Balistidae	3.91		−3.91	Not collected in 2000s

Also shown are the absolute and relative changes in percent abundance of each species, with species listed in decreasing order from largest relative increase to largest relative decrease (far right-hand column).
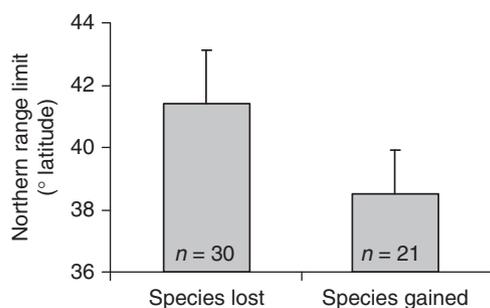

Fig. 2 Northern range limits (mean + 1 SE), as reported by http://www.fishbase.org, of fishes within northern Gulf of Mexico seagrass meadows collected only by Livingston (1985) or only during our 2006–2007 surveys, denoted as species lost and species gained, respectively.

Discussion

Nearly 20% of the fish species collected in northern GOM seagrass meadows during 2006–2007 were tropical or subtropical, and were either absent ($n = 11$), or much less abundant ($n = 3$) 30 + years ago (Table 1). Among these were multiple species of snappers (Lutja-

nidae; we collected three species while Livingston collected one), groupers (Serranidae; we collected seven species while Livingston collected four), and parrotfishes (Scaridae; we collected three species while Livingston collected one) – families that are typically dominant at lower latitudes (Sedberry & Carter, 1993; Thayer *et al.*, 1999; Acosta *et al.*, 2007). The presence of these fishes may be an early indicator for the extension of tropical conditions poleward in the northern GOM.

Recently, Seidel *et al.* (2007) reviewed five different climate models (based on factors such as ozone concentration and tropopause height) and, over the last three decades, reported tropical belt widening in the northern hemisphere that ranged between 2° and 8° latitude, depending on the model. These models are supported by data collected near the entrance to Mobile Bay, AL, that indicated a warming of air and SST of $\geq 3\,°C$ since 1979 (Fig. 3a and b). This temperature change corresponds to a southward relocation of 3–4° latitude based upon current minimum daily fall temperatures in the cities of New Orleans, LA, Mobile, AL, Tampa, FL and Miami, FL (http://www.weather.com). Unfortunately, thermal tolerance data are lacking
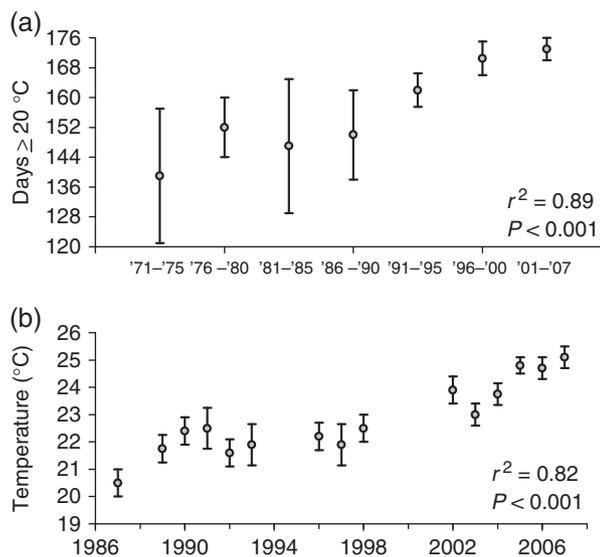
Fig. 3 (a) Number of days each year in ∼ 5-year intervals from 1971–2007 with a minimum air temperature ≥ 20 °C (mean ± 1 SE) near Mobile Bay, AL. (b) Daily minimum sea surface temperatures near Mobile Bay, AL, during fall (September–November) for the years 1987–2007 (mean ± 1 SE).

for nearly all of our key species for further exploring the causal link between recent temperature increases in the northern GOM and observed faunal shifts.

Our analysis of northern range limits of fishes also suggested a 3° latitude decrease between species that were captured only during the 1970s and those collected only during 2006–2007 (Fig. 2). Although this trend was not statistically significant, this 3° change in mean northern range limit is suggestive of a faunal shift that corresponds closely with the observed temperature patterns, whereby more northern species were replaced by a more southern fauna. This shift is particularly impressive given the influence the Gulf Stream has on the reported range limits of many species we collected. For instance, fishes that historically have been absent or rare in the northern GOM, such as *L. synagris* and *C. philadelphica*, are found far up the eastern seaboard due to the transport and temperatures associated with the Gulf Stream (e.g., Kimball *et al.*, 2004). This northern extension outside the GOM would tend to blur differences in range limits for species that are distributed both in the western Atlantic and in the GOM.

Sagarin *et al.* (1999) also investigated climate-related changes in communities over decadal time scales by examining intertidal invertebrate community data collected at Hopkins Marine Station, CA, in the 1930s and 1990s. Working at only one site (in the present study, we included multiple sites all within 1° latitude), these researchers had to prescribe methods for identifying

changes that were indicative of northern shifts by species, rather than local changes that were unrelated to climate. First, they suggested that southern species should increase in abundance while northern species should decrease. The geography of the GOM would preclude northern species shifting southward in to our survey areas, but we did observe a number of southern species that became notably more abundant in 2006–2007 than during the 1970s, such as *L. griseus*, *L. synagris*, *M. microlepis*, and *N. usta*. Second, Sagarin *et al.* (1999) indicated that some species should appear north of their ecological range, while other species should become ecologically (or completely) extinct near their southern range limit. We identified 11 rare species that were added to the community during the interval between 1979 and 2006 that had 'southern' distributions relative to our collection sites. Conversely, only three 'southern' species were lost during this same interval.

There are several additional reports of biological responses to increasing temperatures in the northern GOM that appear to constitute the beginning of a coherent 'climate fingerprint' (e.g., Parmesan & Yohe, 2003). Recently, two corals of the genus *Acropora* have expanded their ranges poleward along the east coast of Florida and in to the northern GOM. The discovery of *A. palmata* within the northern GOM occurred during 2003 inside the Flower Garden Banks National Marine Sanctuary, coincident with rising temperature (Precht & Aronson, 2004). Inshore, the occurrence of *Trichechus manatus* (west indian manatee) sightings have dramatically increased during the last decade in Alabama, Mississipi, and Louisiana, northwest of the core population in Florida and the Caribbean (Fertl *et al.*, 2005). In Louisiana, *Avicenna germinans* (black mangrove) has historically been confined to creekbanks by the temperate *Spartina alterniflora* (smooth cordgrass), but recently *A. germinans* has begun to expand at mangrove-salt marsh interfaces (McKee, 2004). The first reported citings of *Albula vulpes* (bonefish), *Epinephelus itajara* (goliath grouper), and *E. morio* in Mississippi waters have occurred within the last 5 years (Cuevas *et al.*, 2004; Franks, 2005). Additional northward range extensions have recently been documented for fishes within the GOM that occur outside of seagrass meadows, including *Mobula tarapacana* (Chilean devil ray; Childs, 1997).

Alternative mechanisms for community shifts

There are a number of alternative hypotheses that might explain the changes we observed among seagrass fishes between Livingston's and our collection programs. These include changes in regional oceanography that may have altered larval transport, indirect species interactions coupled with anthropogenic habitat alteration/

degradation, or short-term population fluctuations. Coupled physical–biological models have suggested that larval transport can establish the range of marine species regardless of local environmental conditions such as temperature (Gaylord & Gaines, 2000). Within the northern GOM, there have been no reported changes in basin-scale current patterns or local passage of cold fronts (K. Robinson, unpublished results) that might have redirected larval transport during the interval between Livingston's and our surveys. Conversely, there has been a recent (1995-present) upswing in hurricane activity within the GOM (Saunders & Lea, 2008). These weather systems typically start at low latitudes and travel through the GOM transporting water and, potentially, larvae northward (Checkley et al., 1988). However, no hurricanes made landfall in the northern GOM during 2006–2007 that could have transported the fish we collected from southern sources. Therefore, it seems unlikely that changes in physical transport were behind the community differences we observed.

Changes in the abundance of fishes could also result from modifications to either the habitat they utilize, or the biological interactions (competition, predation) they have with other species (e.g., Paine, 1974). Globally, and within the GOM, seagrasses have declined or become fragmented (Orth et al., 2006). If these changes impacted the individual fitness of certain species over others, they could have facilitated the addition of 'southern' species during our 2006–2007 surveys. Recent experiments within northern GOM seagrasses by Johnson & Heck (2006) indicated there are negligible differences among fish communities across gradients of seagrass patch size, patch perimeter-to-area ratio, or within-patch shoot density. Therefore, changes in seagrass habitats likely did not play a role in the changes we observed. Because we collected most all of the common fishes that Livingston collected (Table 1), it also seems unlikely that decreased competition or predation within seagrass meadows opened niches for 'southern' species to invade. We do note that adult *Lujanus campechanus* (red snapper) stocks have fluctuated in response to harvest pressure (Coleman et al., 2004), and artificial reef programs have increased habitat availability within offshore environments. These changes could have decreased competition among adults for many species that co-occur on offshore reefs with *L. campechanus*, such as *L. synagris*, *M. microlepis*, and *L. griseus*, thereby allowing them to establish spawning stocks that are now able to seed nearby seagrass meadows with larvae.

Since our sampling occurred over only 2 years, it is important to consider whether these data represent a brief anomaly rather than a long-term trend. The strongest evidence that our data do not represent a short-term perturbation are provided by Livingston, who collected data over 9 years. Throughout an entire decade, he collected no *L. synagris* (the eighth most abundant species we collected), *E. morio*, *C. ocellatus*, *Mycteroperca* sp other than gag, *C. philadelphica*, *F. tabacaria*, *O. chrysurus*, *T. bifasciatum*, *A. saxatilis*, Acanthuridae spp., and *S. viride*. The complete absence of these fishes throughout the 1970s suggest a temporally stable system that has experienced a significant perturbation. Based on 4 years of consecutive intertidal community data (1993–1996), Sagarin et al. (1999) concluded similarly that short-term fluctuations could not account for the differences observed between communities at Hopkins Marine Station during the 1930s and 1990s.

Conversely, we think it is likely that decadal-scale climate cycles, such as the North Atlantic Oscillation, are an important component of the changes we recorded (Appenzellar et al., 1998). Extending back to the 1940s, weather data from the Ft. Morgan and Dauphin Island #2 stations suggest that the 1970s were a cooler decade that interrupted warmer conditions in the preceding and subsequent decades (K. Robinson, unpublished results). We lack data to establish the characteristics of local seagrass communities during the earlier, warmer 1930s–1940s, but speculate that 'southern' species occupied northern GOM seagrass meadows during that period, and were then expatriated during the 1970s. Therefore, our data are valuable as a forecast of community composition as regional temperatures become elevated, regardless of whether the forcing is natural decadal cycles or anthropogenic global warming. Similarly, El Niño conditions are thought to forecast the potential impacts of climate change in the eastern Pacific (Peterson et al., 1993), and both phenomena can be explored to consider how future warming might alter endemic communities and ecosystem productivity.

Potential impacts for seagrass communities

The 17 species identified as 'southern' comprised only 0.14% of all fishes collected in northern GOM seagrass meadows during Livingston's 1970s surveys. During our more recent surveys, these 17 species accounted for 2.86% of all fishes. This is a statistically unequivocal change in the composition of the seagrass fish community (based on one-group *t*-test results). *L. griseus* (seventh most abundant) and *L. synagris* (eighth most abundant) were particularly abundant members of the current assemblage. Without detailed experiments, we can only speculate how this increase in 'southern' species will impact food-web dynamics and fish productivity in the northern GOM. Typically, range shifts over the short-term are expected to elevate diversity of

local communities similar to species invasions (Hickling *et al.*, 2006). However, we actually sampled a community that was slightly less species rich than the community sampled by Livingston 30 years ago. This change could impact the foraging rates of larger predators that feed upon relatively small fishes due to sampling effects or the development of search images (Duffy, 2006). If warming persists and 'southern' species remain in seagrass habitats over many years, competition (for refuge or foraging space) may also change dramatically in response to the co-occurrence of temperate, subtropical, and tropical species (but see Sax *et al.*, 2007). The ultimate consequences of these dynamics are beyond the reach of our dataset.

Because our survey and temperature data focus on summer and fall patterns, it cannot be determined if any of these 'southern' species overwinter successfully, although we did observe a significant lengthening of annual 'warm' conditions near Mobile Bay during the last 30 + years. Also, mild winters are associated with the current, positive NAO phase (Appenzellar *et al.*, 1998), which could allow species such as *L. griseus*, *L. synagris*, and *M. mycteroperca* to survive throughout the year at a sufficient rate to contribute significantly to the offshore adult stock. There is evidence of this: *L. griseus* landings in the Louisiana recreational fishery have increased from 6561 kg in 1996 to 476 456 kg in 2006 (Thomas, 2008). Furthermore, the Alabama Deep-Sea Fishing Rodeo has been held annually since 1929, and includes nearly all nearshore and offshore hook-and-line fishes as target species. Although *L. synagris* and *M. mycteroperca* are caught regularly by fishermen today, there is no record of either species ever being included in the Rodeo's target species list (J. Fodrie, unpublished results). *L. griseus* were not included until 2004, but the recent addition of this species may reflect the growing awareness of Rodeo fishermen to the changes in local communities, similar to what we have documented in seagrass habitats.

Our data contribute to a growing literature that has documented range shifts among diverse taxa that are correlated with global climate change (e.g., Barry *et al.*, 1995; Sagarin *et al.*, 1999; Perry *et al.*, 2005; Field *et al.*, 2006). For fish assemblages in the northern GOM, the 30-year changes we documented involved many species that when considered together indicate a shifting 'climate fingerprint' in northern GOM seagrass habitats (Parmesan & Yohe, 2003). These data should be used as a reference point, and reevaluated by future studies to better quantify the composition of this community as climate continues to change. Determining the trajectory of change is crucial for understanding the consequences of global warming for endemic marine communities and fishery production in the northern GOM.

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