Biological response to changes in climate patterns: population increases of gray snapper (Lutjanus griseus) in Texas bays and estuaries

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Abstract—The increase in the abundance of gray snapper (*Lutjanus griseus*) in Texas bays and estuaries over the past 30 years is correlated to increased wintertime surface water temperatures. Trends in the relative abundance of gray snapper are evaluated by using monthly fishery-independent monitoring data from each of the seven major estuaries along the Texas coast from 1978 through 2006. Environmental conditions during this period demonstrated increasing annual sea surface temperatures, although this increase was not seasonally uniform. The largest proportion of temperature increases was attributed to higher winter temperature minimums since 1993. Positive phases of the North Atlantic Oscillation, resulting in wetter, warmer winters in the eastern United States have occurred nearly uninterrupted since the late 1970s, and unprecedented positive index values occurred between 1989 and 1995. Increases in water temperature in Texas estuaries, beginning in the early 1990s, are postulated to provide both favorable over-wintering conditions for the newly settled juveniles and increased recruitment success. In the absence of cold winters, this species has established semipermanent estuarine populations across the entire Texas coast. A shift to negative phases of the North Atlantic Oscillation will likely result in returns to colder winter temperature minimums that could reverse any recent population gains.

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Biological response to changes in climate patterns: population increases of gray snapper (*Lutjanus griseus*) in Texas bays and estuaries

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Decadal and multidecadal climate variability in the eastern United States and North Atlantic Ocean are sensitive to natural climate variability associated with the North Atlantic Oscillation-Arctic Oscillation (NAO-AO; Okumura et al., 2001). Ocean-atmosphere interactions between sea-level atmospheric pressure and sea surface temperature have resulted in periods of intensified climate variability at 50–80 year cycles (Enfield et al., 2001; Cronin et al., 2003). Interannual fluctuations in fishery catches that are linked to climate variability occur in many marine systems; the best examples are found in the North Pacific Ocean and Bering Sea (reviewed in Roessig et al., 2004, but also see Perry et al., 2005; Zeeburg et al., 2008). Huge increases in fish populations in the North Atlantic Ocean ("fish outbursts" in Hare and Able [2007]) have been linked to decadal-scale fluctuations in both atmospheric pressure gradients and water temperatures. Examples include dramatic fluctuations in gadoids (Sirabella et al., 2001), sciaenids (Hare and Able, 2007), pleuronectids (Sullivan et al., 2005), and in the size of fish assemblages—the latter caused by changes to the estuarine ecosystem (Attrill and Power, 2002). Changes in fish populations along the west coast of the Americas have also been related to shorter time-scale climate variation associated with El Niño patterns (Arcos et al., 2001; Smith and Moser, 2003). Few studies have examined the link between ecosystem structure, fisheries production, and climatic forcing along the southeastern coasts of the United States (including "the Gulf" of Mexico, hereafter referred to as "the gulf"), but those that have (Parker and Dixon, 1998; Sullivan et al., 2005) generally identify warmer winter temperatures as the cause of distributional changes in fish populations (Oviatt, 2004; Preston, 2004).

The gray snapper (*Lutjanus griseus*) is a temperate and tropical reef fish, commonly found in marine and estuarine waters in the western Atlantic Ocean from Florida through Brazil, including Bermuda, the Caribbean, and the northern Gulf (Randall, 1968; Rutherford et al., 1989a). Although the young of this species have been collected as far north as Cape Cod, Massachusetts (Denit and Sponaugle, 2004), they are most prevalent in continental and island shelf waters in the vicinity of south Florida, Cuba, and Venezuela (Allman and Grimes, 2002). Larvae and juvenile fish are common inshore in seagrass and mangrove nursery areas and have been even found in freshwater estuaries. Adults are usually associated with complex structures (such as rocky areas, coral reefs, pilings, and docks) and mangrove sloughs (gaining them the often-used local name of mangrove snapper). Because of their affinity for hard bottom substrates, gray snapper are especially common on the numerous artificial reefs, such as oil and gas platforms, and on other man-made structures located on the northern gulf continental shelf from Alabama to Texas (Fischer et al., 2005).

Studies of the life history characteristics of gray snapper (Rutherford et al., 1989b; Burton, 2001) have revealed this species to be both euryhaline (they have been observed in salinities ranging from 0 to 67) and thermally tolerant (in temperatures ranging from 12.8° to 31.7°C). The lower lethal temperature limit is reported to be 11–14°C (Starck and Schroeder, 1971) and increased mortalities accompany sudden temperature drops. Cold kills of gray snapper (along with other estuarine and coastal fishes) have been reported at numerous times along the Texas Gulf coast (Gunter, 1941, 1951; McEachron et al., 1994). These cold kills of tropical species in Texas waters have previously been associated with warmer than usual summer and fall temperatures that stimulate tropical species either to move inshore or to remain inshore much later into the winter than would otherwise occur, thereby leaving them more vulnerable to sudden cold spells (Moore, 1976, Holt and Holt, 1983).

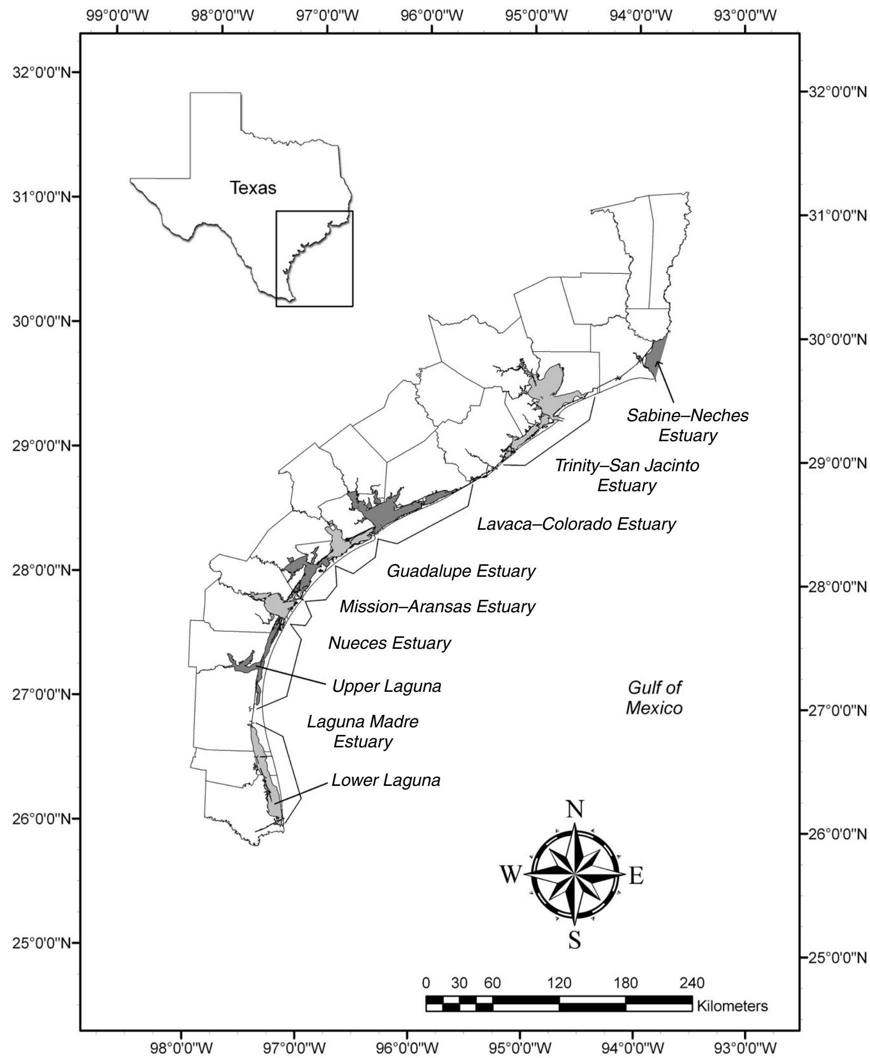

Figure 1

Map of the Texas coastline showing the location along the coast of each of the major estuarine systems sampled as part of the Resource Monitoring Program conducted by the Texas Parks and Wildlife Department from 1978 through December 2006. The fine line trailing the coastline represents the outline of the barrier island that runs from the pass at Sabine to Brazos-Santiago Pass, just north of Rio Grande.

Texas Parks and Wildlife Department (TPWD) has used various gears systematically in Texas estuaries since 1975 to assess changes in the abundance and size of organisms, their spatial and temporal distributions, species compositions of the community, and selected environmental parameters known to influence their distribution and abundance. The purpose of this study was to examine the relationship between water temperature and population trends in juvenile and adult gray snapper within the seven major estuaries along the Texas gulf coast.

Methods and materials

Gray snappers were collected from November 1978 through December 2006 with bag seines, otter trawls, and gill nets as part of a survey conducted by the Resource Monitoring Program of the Texas Parks and Wildlife Department within each of the seven major estuaries on the Texas Gulf coast: Sabine-Neches, Trinity-San Jacinto, Lavaca-Colorado, Guadalupe, Mission-Aransas, Nueces, and Laguna Madre (further subdivided into an Upper and Lower section, see Fig. 1). Bag seines (18.3 m wide, 1.8 m deep, and equipped with 1.3-cm stretched nylon multifilament mesh in the 1.8-m wide central bag and with 1.9-cm stretched mesh in the remaining webbing) were pulled parallel to the shoreline for 15.2 m for a total area swept of 0.03 ha. Sampling frequencies of the bag seines have not been uniform since the inception of the Routine Monitoring Program. Before 1981, only six bag seine samples were collected in each month in each bay (except for June 1978 when none was collected). From January 1982 through August 1984, 10 samples were

Table 1

Numbers of gray snapper (Lutjanus griseus) collected by each of the fishery-independent gears used in the eight major estuaries along the Texas coast. The increase in numbers of gray snapper from before to after the 1993 time period is presented as an ×-fold increase.

	Bag seine			Otter trawl			Gill net		
Estuary	Before 1993	After 1993	×-fold increase	Before 1993	After 1993	×-fold increase	Before 1993	After 1993	×-fold increase
Sabine-Neches	0	6	—	0	8	—	0	4	—
Trinity-San Jacinto	4	20	5.0	0	5	—	3	52	7.3
Lavaca-Colorado	17	72	4.2	1	6	6.0	14	232	16.6
Guadalupe	26	71	2.7	1	10	10.0	8	163	20.4
Mission-Aransas	7	73	10.4	3	22	7.3	8	103	12.9
Nueces	13	35	2.7	0	1	—	233	926	3.9
Upper Laguna Madre	2	6	3.0	0	2	—	6	46	7.7
Lower Laguna Madre	4	34	8.5	22	159	7.2	64	461	7.2
Total	73	317	4.3	27	213	7.9	336	1987	5.9

collected each month in each bay, except Sabine Lake (Sabine Lake sampling began in 1986). From August 1984 through January 1992, sampling frequency within each estuary increased to 12 samples per month, then to 16 per month, and finally to 20 samples each month. Since 1992, a total of 20 bag-seine samples have been collected from randomly selected locations within each bay in each month, resulting in 1920 samples per year. Otter trawls (6.1 m wide and with 3.8-cm stretched nylon multifilament mesh) were pulled for 10 minutes in water ≥1.0 m depth. Twenty trawl samples were taken from randomly selected sites in each bay each month (except for 10 per month in Nueces and the upper Laguna Madre). A total of 1920 trawl samples were collected each year. Gill nets (monofilament, 183 m long, 1.2 m deep, and equipped with separate 45.7-m sections of 7.6-, 10.2-, 12.7-, and 15.2-cm stretched mesh tied together in a sequence of ascending mesh size) were set overnight during each spring and fall season. The spring season begins with the second full week in April and extends for 10 weeks; the fall season begins with the second full week in September and also extends for 10 weeks. Gill nets were set perpendicular to the shore with the smallest mesh facing shoreward. Nets were set within 1 hour before sunset and retrieved within 4 hours after the following sunrise. In each bay, a total of 90 gill nets were set at randomly selected sites (720 samples per year).

Total lengths (TL) of gray snapper were measured for each gear type. Catch rates (relative abundance expressed as catch per unit of effort) from each gear were calculated for each bay, month, season, or year. Environmental measurements of surface salinity, water temperature (°C), and dissolved oxygen (mg/L and percent saturation) were measured both before the set and retrieval of gear for each gillnet collection and before each bag-seine collection. Bottom salinity, water temperature, and dissolved oxygen were measured before each trawl sample.

Analytical techniques

In order to directly compare the time series of abundance patterns of gray snapper across the disparate gears, relative abundance estimates for each gear were first Z-transformed (Snedecor and Cochran, 1980). The temperature records from each estuary were aggregated by month and year and expressed as monthly arithmetic averages to produce a time series compatible with the monthly abundance series. The temperature records were then analyzed with an empirical orthogonal function (EOF), a statistical tool used to decompose a spatially multivariate data set into its principal components. With this tool, the bulk of the variance can be described by a few orthogonal modes, so that the major properties of the data set can be more easily understood (Keiner and Yan, 1997). Principal modes of the spatial EOFs were seasonally detrended (multiplicative seasonal adjustment; SYSTAT, vers. 12, SYSTAT Software Inc., San Jose, CA) to reveal either periodicity or trends in the data. Detrended EOF slopes were assessed with linear regressions to test any departure from zero.

Results

From 1978 through 2006, a total of 2953 gray snappers were sampled from Texas bays and estuaries. The seasonal patterns revealed with the fishery-independent gears agreed well with published reports of spawning and movement patterns. Most juvenile and subadults taken in the bag seines and otter trawls were collected in the late summer to early fall, from August to October. Adult gray snapper were collected with gill nets in every month when this gear was deployed and were most prevalent during the fall from September to November. The vast majority of individuals were collected with gill nets from the middle Texas coast (from Lavaca-Colorado Estuary

Table 2

Percent and cumulative percent of the total variation explained by the eight empirical orthogonal function (EOF) modes. The eight modes correspond to the eight major Texas estuaries, spatially interpolated by means of an objective analysis scheme by means of a series consisting of 288 monthly averaged mean salinity readings collected from the Resource Monitoring Program of the Texas Parks and Wildlife Department.

	EOF							
	1	2	3	4	5	6	7	8
Percent	96.40	0.81	0.65	0.55	0.47	0.41	0.39	0.33
Cumulative percent	96.40	97.21	97.86	98.26	98.73	99.14	99.53	100

to the Nueces Estuary; see Table 1). Given the affinity of this species for structured habitats, it is no surprise that the otter trawl was the least effective gear for capturing this species.

Environmental data during this same period demonstrated increasing annual water temperatures, although these increases were not seasonally uniform. Summer maximum water temperatures remained relatively stable, whereas winter minimums increased through time. The largest proportion of temperature increases were attributed to higher winter temperature minimums since 1993 (Fig. 2). Before 1993, winter minimum temperatures routinely fell below the lower lethal limit for gray snapper, and these events were especially common in the upper coast estuaries of Sabine-Neches, Trinity-San Jacinto, and Lavaca-Colorado. Since 1993, winter temperatures along the coast of Texas have generally been mild, although particularly powerful polar fronts caused dramatic declines in surface water temperatures in both 1997 and 2001.

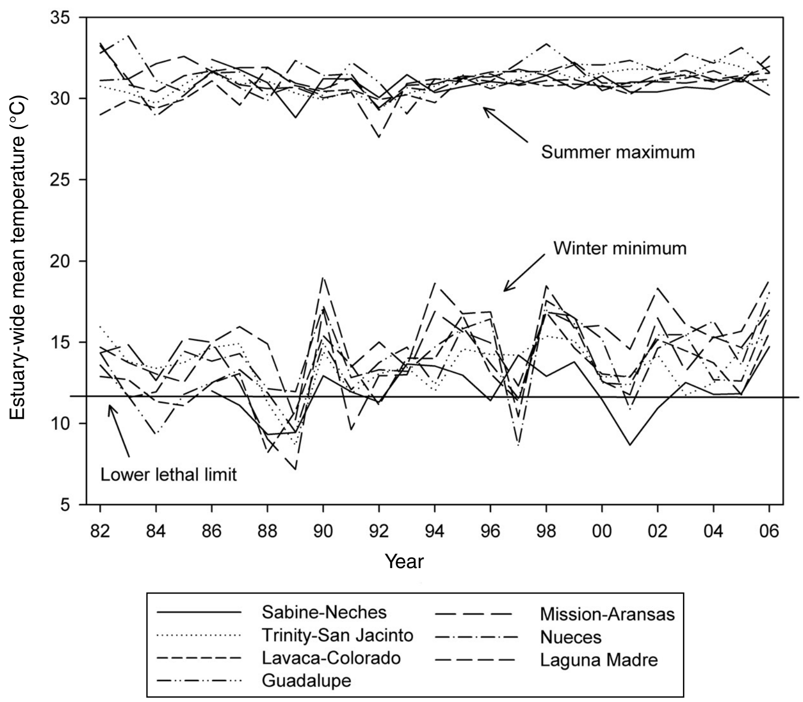

Figure 2

Time series of mean yearly temperatures (summer maximum and winter minimums, in °C) of Texas coastal estuaries. The solid horizontal line identifies the lower lethal limit (12°C) for gray snapper (Lutjanus griseus).

The 288 months of average surface temperatures from the seven major estuaries along the Texas coast were combined into a data matrix and interpreted with a spatial EOF. The variance pattern for the principal EOF mode is shown in Figure 3. The fundamental periodicity within the first mode (capturing 96% of the total variability, Table 2) represents the yearly signal inherent in the series (0.083 cycles per month, or 1 cycle per year). Temperature structure in each estuary was effectively described by the first mode of the EOF, and positive component loadings ranged from 0.976 to 0.985 for each estuary. Seasonally detrended EOF mode 1 revealed that increases in winter minimum temperatures, especially after 1993, corresponded to the largest positive amplitude values seen in the series. Before 1993, the slope of the detrended temperature record was not significantly different from zero ($F_{1,\ 143}$=1.194; P=0.276), whereas after 1993, the trend in water temperature was significantly upward and warmer ($F_{1,\ 153}$=5.055; P=0.026).

Before 1993, gray snapper were generally uncommon in all estuaries on the Texas gulf coast, but since then, increases in abundances have ranged from near 3- to over 20-fold (see Table 1). The temporal pattern of increasing abundances, especially within the mid-coast estuaries where gray snapper are most prevalent, is shown in Figure 4. A winter temperature minimum near or below the lower lethal limit appears to inhibit

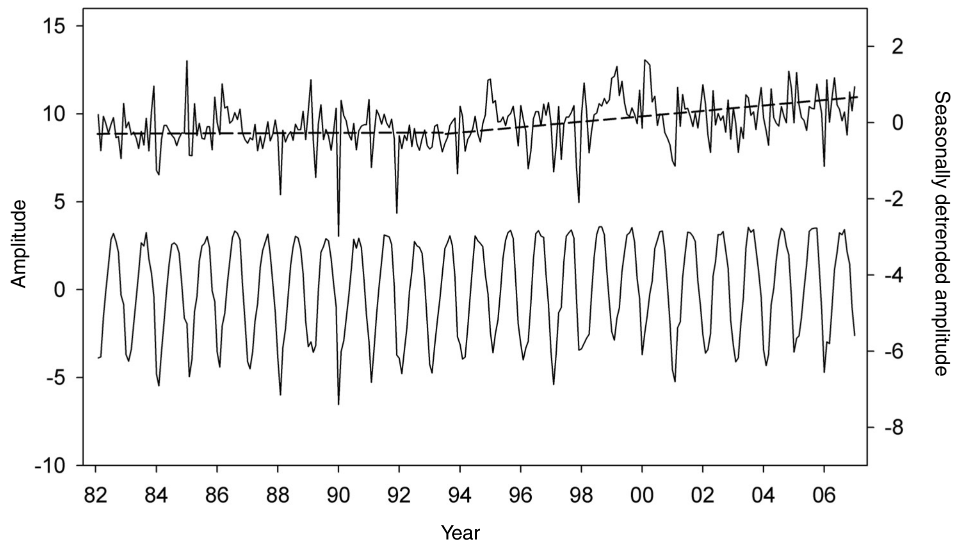

Figure 3

Amplitudes of the spatial empirical orthogonal function, mode 1. Lower panel is the seasonal signal, upper panel is the seasonally detrended signal. Dashed line within the upper panel is the slope derived independently for the period before 1993 and after 1993. Amplitudes are nondimensional.

Table 3

Separate variance t-test results from a comparison of the mean size and standard deviation (SD) of gray snapper (Lutjanus griseus) collected with bag seines, otter trawls, and gill nets (before and after 1993) from Texas estuaries, pooled by sampling gear and time period. Effective degrees of freedom (df) for each test were approximated with the Welch-Satterthwaite equation; therefore degrees of freedom (df) are not reported as whole numbers.

	Bag seine		Otter trawl		Gill net	
	Before	After	Before	After	Before	After
Mean size (mm)	50.1	61.4	110.7	138.9	268.8	308.0
SD	19.2	22.8	44.3	49.1	59.0	36.3
t-test value		2.77		2.24		9.62
df		38.5		16.7		230.6
P value		0.008		0.039		<0.001

recruitment (as evidenced by the young-of-the-year abundance estimates determined from the bag-seine collections), as well as limit the survival of over-wintering juveniles. An absence of cold winters has allowed for dramatic increases in the abundance of gray snapper in nearly every estuary along Texas gulf coast. Accompanying these increases there has been a concomitant increase in the mean size of gray snapper collected with all gear types. Separate variance *t*-tests revealed that coast-wide post-1993 collections of gray snapper were significantly greater in numbers (for all gear types) than the pre-1993 collections (Table 3).

The exponential increase in estuarine abundance of gray snapper in Texas, as recorded with the fisheries-independent gill nets, has been confirmed with fishery-dependent data of population trends from nearby locations. A time series of state-wide recreational landings from both Texas (primarily bay and estuary landings) and Louisiana (primarily nearshore continental shelf landings) virtually mirrors the exponential increase in abundance recorded with the gill nets (Fig. 5).

Discussion

Time series have become increasingly important in the studies of climate influences on biological patterns (Reid et al., 2001; Edwards et al., 2002), especially during recent years when unusual climate trends have been reported and major events have affected living resources and fisheries management (Rebstock, 2003; Woehrling et al., 2005). The uninterrupted, 30+ year record of systematic monitoring within every estuary on the Texas Gulf coast is almost unprecedented in terms of both spatial and temporal coverage. These collections encompass a scale sufficient to document ecosystem-level responses to climate variation and may provide insight into any biological responses that are revealed. Analyses of proxy-based reconstructions of temperatures, with particular emphasis on the Atlantic Coast region during the past millennium, have shown patterns of multidecadal variation in sea surface temperature with a distinct oscillatory mode of variation at an approximate time scale of 70 years (Delworth and Mann, 2000; Cronin et al., 2003). Embedded within this climate signal is an overall warming trend on the order of 0.16°C to 0.21°C per decade (Preston, 2004). Some researchers have reported that this warming trend accelerated during the latter half of the 20th century (Hoerling et al., 2004; Zeeburg et al., 2008). A general trend of increasing water temperature was also found along the Texas coast, but this increase was not seasonally consistent. Maximum water temperatures during summer months were relatively stable over the study period, whereas increases in winter minimum temperatures were seen to drive this mean increase. Seasonally nonlinear temperature patterns have also been reported in other estuarine systems (Nixon et al., 2004; Hare and Able, 2007), along with the common feature of warming winter surface waters.

A link between large-scale climate drivers and biotic variability in the Gulf of Mexico has been attempted in only a few studies. Tolan (2006), however, did find a connection between short-phase NAO-AO forcing and Texas estuarine salinity patterns, and the greatest influence was found in three mid- and northern coast estuaries (Guadalupe, Lavaca-Colorado, and Sabine-Neches). An abrupt transition to positive phases of the NAO-AO index (wetter, warmer winters along the eastern U.S. coasts; Rajagopalan et al., 1998) occurred during the late 1970s, and the atmosphere generally remained in this positive mode through the 2005 winter season. During this 25 year interval, substantial negative phases of this pattern appeared only four times (1985, 1987, 1996, and 2001). The height of the current positive phase of the NAO-AO index (values from 1989 through 1995 represent some of the largest positive values ever recorded) temporally corresponds to the onset of the increase in gray snapper populations along the Texas coast. Zeeburg et al. (2008) identified a similar NAO-AO linked biological response in mid-1990s in the east central Atlantic Ocean off Africa. Their study showed that the response of Spanish sardine (*Sardinella aurita*) to changes in surface water temperatures (namely a surge in population numbers) began in 1995, around the same time that the temperature-mediated biological effects on gray snapper were seen in western Gulf of Mexico estuaries.

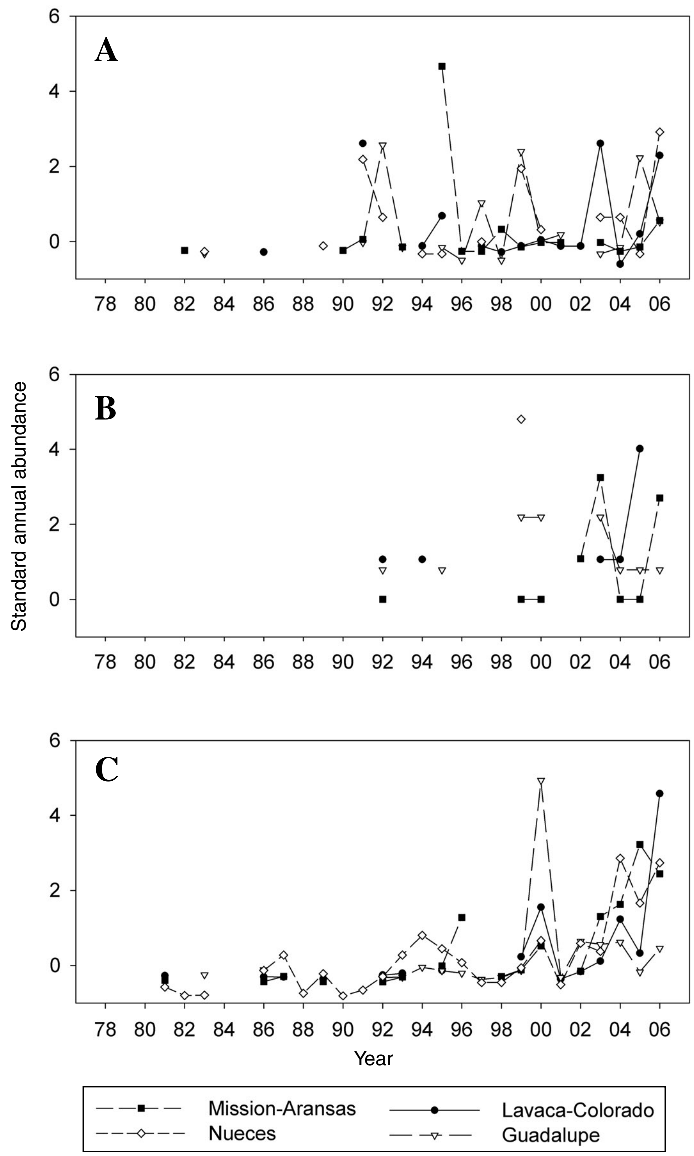

Figure 4

Time series of yearly catch rates for gray snapper (Lutjanus griseus) with (**A**) bag seines, (**B**) otter trawls, and (**C**) gill nets from four mid-coast Texas estuaries. To allow direct comparisons, each series has been standardized to a mean of zero and a unit variance of 1.

Recent increases in gray snapper appear to follow the "thermal opening of the estuary" theory that Hare and Able (2007) presented for what the authors term as "outbursts" of Atlantic croaker (*Micropogonias undulatus*) populations along the east coast of the United States. Warmer winters result in higher juvenile survival, which allows for the formation of larger year classes. Sequential warm winters lead to sequentially large year classes that extend the duration of an outburst. In the Atlantic croaker example, the outburst allowed population ranges to expand north and, as a result, spawning extended farther north, supplying larvae to estuaries not normally inhabited. The outburst was continued as a result of additional juvenile habitat that was then available to the population. This appeared to be the case for gray snapper populations in the western Gulf of Mexico. A decade of nearly uninterrupted warm winters has allowed this species to flourish in estuaries where they were not historically encountered in great numbers. Following the winter temperature shift of 1993, the only precipitous dips in the exponential rise in gray snapper population numbers (declines seen in 1998 and 2002) followed years with sharply colder winters (1997 and 2001, see Fig. 3).

In the Hare and Able (2007) model, the role of larval supply was minimal, because the spatial expansion of the spawning range was a direct consequence of the outburst, not the cause. Temperature-related overwintering mortality of juvenile fish establishes year-class strength, and these strong year classes carry the population for 3–5 years. Based on established von Bertalanffy growth parameters (derived separately from Louisiana recreational harvest [Fischer et al., 2005] and eastern Florida commercial harvest [Burton, 2001]), the mean size of Texas gray snapper collected with gill nets represents 3–4 year-old fully mature fish. Fischer et al. (2005) found a multimodal distribution in gray snapper age structure from Louisiana and attributed the variation in year-class strength to intraspecific competition among juveniles for resources within the estuaries before recruiting to the offshore fisheries. The successive peaks in age-class abundance (strong year classes every 2–3 years) could also be attributed to juvenile overwintering mortality associated with thermal limits within the estuaries. Interestingly, year of birth distributions from Louisiana recreational catches from 1998 through 2002 (Fig. 5B in Fischer et al., 2005) showed that the largest percentage of gray snapper came from 1994, around the same time that the slope of seasonally detrended EOF mode 1 turned positive.

An alternative explanation for the exponential rise in the landings of gray snapper recorded from the northern Gulf may be attributed to a directed recreational fishing effort. To reverse the condition of overfishing of red snapper (*Lutjanus campechanus*), increasingly restrictive fish-size limits and bag limits were placed on the recreational fishing sector for red snapper in 1991. Anglers began to target the more nearshore populations of gray snappers once their bag limits of red snapper were reached. Peak landings of gray snapper in Louisiana generally coincided with the red snapper recreational season (April–October), and as a result, landings of gray snapper increased exponentially from 3.25 metric tons in 1983 to 175 metric tons in 2002 (Fischer et al., 2005). Even though the landing data for both Texas and Louisiana presented in Figure 5 were not adjusted for effort, it should be noted that both the fishery-independent and fishery-dependent indices of population abundance for each state both showed similar increases after the winter temperature shift of the mid-1990s. From 2000 to 2006, increasingly restrictive limits on red snapper have dramatically increased the fishing effort for gray snapper; yet the trends of the fishery-independent index (determined from TPWD gillnet effort over the period of record (1978–2007) has displayed similar temperature-related fluctuations as those displayed by the fishery-dependent indices.

Gray snapper are particularly susceptible to cold weather; their lower thermal limits range from 11° to 14°C (Starck and Schroeder, 1971). The effects of cold weather on marine organisms in Texas bays vary substantially, depending on how rapidly the temperature drops, on the severity and duration of the cold temperatures, on the physiographic characteristics of the affected area, and on

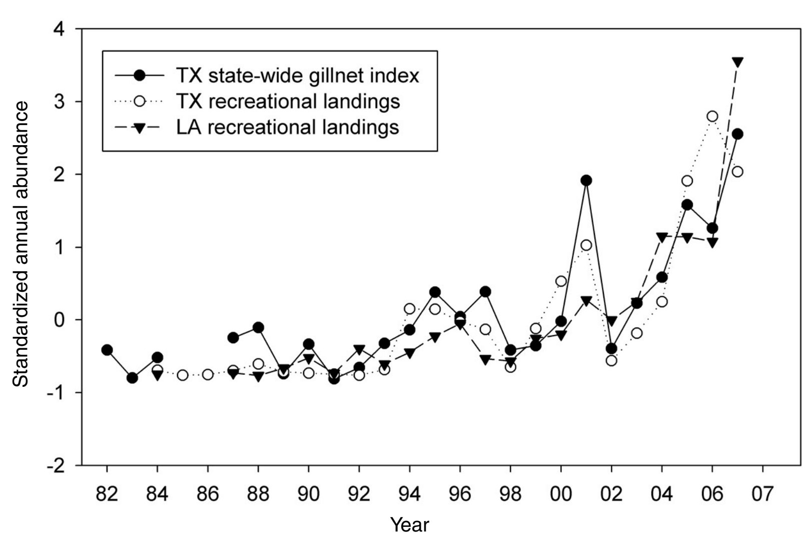

Figure 5

Time series of landing of adult gray snapper (Lutjanus griseus) from gill nets (Texas estuaries) and recreational landings (both Texas and Louisiana) from 1982 to 2006. To allow direct comparisons, each series has been standardized to a mean of zero and a unit variance of 1.

the life history, behavior, and population dynamics of the affected animals (McEachron et al., 1994). During our study period, three severe polar cold fronts caused coast-wide fish-kill events during December 1983, February 1989, and December 1989. In the absence of cold winters, this species has established semipermanent populations in nearly every estuary along the Texas coast, and these populations are likely to continue to flourish until the next polar front either diminishes these estuarine populations, or a series of successive cold winters creates a "thermal closure" of the nursery habitats (*sensu* Hare and Able, 2007). Gray snapper are far less abundant in the northernmost estuary (Sabine-Neches), presumably because the winter minimum temperatures regularly fall below 12°C. December 2004 was remarkable in that a strong cold front brought measurable snowfall to most of coastal south Texas for the first time in over 100 years and resulted in a localized cold kill of approximately 12,000 gray snapper on the gulf beach side of Boca Chica, near the lower end of the Laguna Madre estuary. Declines in gray snapper abundance after the snowfall event of 2004 can be seen in three of the four mid-coast estuaries shown in Figure 4C.

Although only a single species was examined in our study, there may well be many species along the Texas coast for which recruitment and population dynamics are linked to climatic forcing (e.g., sand drum, [*Umbrina coroides*]; common snook [*Centropomus undecimalis*]; tarpon [*Megalops atlanticus*], and African pompano [*Alectis ciliaris*], see Moore, 1975). In the past few years alone, both snook and tarpon have become exceedingly more common along the rock jetty passes at both Mansfield Pass (gulf connection at the far upper end of Lower Laguna Madre) and Aransas Pass (gulf pass connection for both the Nueces and Mission-Aransas estuaries). Connections between fish population dynamics and climate patterns need to be better quantified and incorporated into stock assessment models to ensure successful long-term management of fishery stocks.

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