Range expansion and population shifts of estuarine fishes in a changing subtropical estuary

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ABSTRACT: Catastrophic losses (ca. 95%) of seagrass and increased environmental degradation have occurred during the past decade in the Indian River Lagoon (IRL) estuary on the US Atlantic coast of Florida. Changes were observed in the abundance of 2 closely related sparid fishes in these estuarine waters based on fishery-independent monitoring efforts over 22 yr: sea bream *Archosargus rhomboidalis* significantly increased, while sheepshead *A. probatocephalus* simultaneously declined. These abundance trends and a northward expansion of sea bream into areas where they had never been documented were associated with an annual minimum water temperature increase of approximately 1.5°C, an annual mean water temperature increase of 0.9°C, and an annual mean salinity increase of 7.6 ppt. Lost seagrass habitat was often replaced by species belonging to the attached macroalgae genus *Caulerpa* or remained bare. Our findings suggest that sea bream, a tropical herbivore, are expanding poleward into the northern IRL, which may further negatively impact the potential recovery of sheepshead populations via competition. Furthermore, observed declines in seagrasses and populations of dependent species, including sheepshead, will likely continue if anthropogenic perturbations persist or expand. Long-term monitoring is essential for the timely detection of population changes and range shifts to better refine direct fisheries management of existing species and determine the potential need for management of recently expanding fish species should new fisheries emerge. Effective monitoring also allows for more proactive restoration of critical habitats and water conditions to minimize further adverse effects on fishes and other estuarine biota.

KEY WORDS: Range expansion · Fisheries · Sparidae · Seagrass habitat loss · Hot spot analysis · Population dynamics · Climate change

1. INTRODUCTION

Human-related activities linked to climate change and habitat destruction are resulting in alterations of natural systems at rapid, observable rates (Poloczanska et al. 2013, Pardini et al. 2017, IPCC 2022). In marine systems specifically, anthropogenic climate change is elevating sea surface temperatures and thus shifting isotherms poleward in all regions of the world ocean (Sen Gupta et al. 2015, Laufkötter et al. 2020, IPCC 2022). These shifts in sea surface temperature regimes are altering ecological communities across the globe. Ocean warming can cause declines in local cold-water species' niche space with reduced suitable habitat at a given latitude, directly altering trophic linkages as organisms adapt to changing thermal regimes and novel species interactions (Rosenzweig et al. 2007, Gilbert et al. 2014, Paukert et al. 2021). The thermal range for optimal function for many marine species is relatively narrow (Sen Gupta

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et al. 2015), and tropical organisms are commensurately expanding their geographic ranges poleward into novel ecosystems (Rosenzweig et al. 2007, Vergés et al. 2016, Free et al. 2019, Osland et al. 2021). This phenomenon, known as tropicalization, has been documented in several systems worldwide for a plethora of taxonomic groups and is considered a major contemporary driver of changes in species composition (Rosenzweig et al. 2007, Ling 2008, Yamano et al. 2011, Vergés et al. 2014b, 2016, Fowler et al. 2018, Purtlebaugh et al. 2020).

Geographic range expansions in response to shifting isotherms have been well documented for marine fishes and other marine taxa (Rosenzweig et al. 2007, Brander 2010, Paukert et al. 2021, Osland et al. 2022). Such shifts have been recorded for an array of fishes in nearly every region of the marine biome (Rosenzweig et al. 2007, Brander 2010, Vergés et al. 2014a, 2016, Heck et al. 2015, Checkley et al. 2017, Fowler et al. 2018, Purtlebaugh et al. 2020). Poleward shifts of fisheries can occur relatively rapidly (up to 50 km yr^{-1}) and are frequently associated with long-term warming trends (Rosenzweig et al. 2007, Brander 2010, Vergés et al. 2014a, Fowler et al. 2018). Some poleward expansions are also observed following equivalent shifts in planktonic prey bases, suggesting that climate-related changes in biotic factors, such as trophic resources, may compound the effects of warming sea surface temperatures on marine communities (Beaugrand et al. 2003, Brander 2010, Auth et al. 2018, Smith et al. 2021).

Direct community-altering effects of warming waters are indeed pervasive, but indirect effects of tropicalization are believed to be even more disruptive to ecological communities (Zarnetske et al. 2012, Ockendon et al. 2014, Vergés et al. 2014a, 2016). Upon arrival in a novel system, tropical species may modify interaction webs by creating new interactions or changing the magnitude or direction of existing ones. New interactions can manifest in changes in predator–prey dynamics and modifications to local food webs, including altered rates of herbivory (Ockendon et al. 2014, Vergés et al. 2014a, 2016). Consequences are particularly severe when herbivores begin to overgraze locally reduced foundational macrophytes undergoing acute disturbances. By degrading essential habitat provided by foundation species, such as seagrasses or macroalgae, tropical herbivores can cause ecological cascades, leading to extensive decreases in faunal abundance, lower biodiversity, and declines in fisheries productivity (Ockendon et al. 2014, Vergés et al. 2014a, 2016, Fowler et al. 2018, Free et al. 2019).

Catastrophic seagrass habitat losses have occurred in the Indian River Lagoon (IRL) estuary on the US Atlantic coast of Florida from 2011–2021. Approximately 95% of seagrasses have been lost in some parts of the ecosystem due to eutrophication, subsequent harmful algal blooms, and reduced availability of light (Lapointe et al. 2018, 2020). Long-term harmful algal blooms continue in the system (Phlips et al. 2020, Lopez et al. 2021, Florida Fish and Wildlife Conservation Commission [FWC]-Fish and Wildlife Research Institute [FWRI] unpubl. data), contributing to habitat degradation via seagrass die-offs and fish kills (Adams et al. 2019, FWC-FWRI unpubl. data). These perturbations, combined with additional factors related to climate change (e.g. ocean warming), may be linked to shifts in fish community structure and to fish population declines for some species and range expansions for others within the IRL. Large-scale population declines or lack of recovery of some resident estuarine fish species have recently been documented in the ecosystem, directly related to habitat losses, habitat alteration, and extreme climatic events (Adams et al. 2022, Boucek et al. 2023).

The western Atlantic sea bream *Archosargus rhomboidalis* (Linnaeus, 1758) was functionally absent from the northern Indian River Lagoon (NIRL) before approximately 2016 (Snelson 1983, Tremain & Adams 1995, FWC-FWRI unpubl. data). Preliminary data suggest that the abundance of this tropical herbivore has increased markedly since then (FWC-FWRI unpubl. data). Sea bream are characteristic of warm tropical–subtropical coastal systems centered around the Caribbean Sea (Randall 1967, Hammerschlag et al. 2010, Kendall et al. 2021). The life history and distribution of this species based on long-term FWC-FWRI Fisheries-Independent Monitoring (FIM) efforts suggests that they may have expanded poleward into northern regions of the IRL, potentially as a result of ocean warming and local shifts in the relative abundance of marine macrophytes. Conversely, the abundance of sheepshead *A. probatocephalus* (Walbaum, 1792), a widespread marine sparid occurring from Nova Scotia to Brazil, may have declined in the lagoon system (FWC-FWRI unpubl. data). Sheepshead have historically constituted a major component of the region's estuarine ichthyofauna and represented the only species belonging to *Archosargus* in the NIRL (Snelson 1983, Tremain & Adams 1995). The timing of the population expansion of sea bream has coincided with local declines in sheepshead catch, warranting an investigation into the population dynamics of these sister species.

Current understanding of the life history of both sparids suggests the potential for dietary overlap between these congeners. Although invertebrate prey comprises a major proportion of sheepshead diets, they also consume algae and seagrasses in coastal waters across their range (Overstreet & Heard 1982, Fernandez & Motta 1997, Castillo-Rivera et al. 2007). Sheepshead exhibit morphologic plasticity according to their diet. Specifically, the jaw muscles and bones of sheepshead in the IRL are smaller in mass than conspecifics from other systems where they have been examined. This is related to the specialized diet of this ecotype, which is dominated by plant matter (Cutwa & Turingan 2000). Vascular plants and macroalgae are a range-wide staple of the adult sea bream diet as well (Randall 1967, Vaughan 1978, Vega-Cendejas et al. 1994, Hammerschlag et al. 2010). These 2 species risk direct competition that may be less likely in other regions. Additionally, Seyoum et al. (2020) recently documented hybridization between sheepshead and sea bream in the IRL. Intensifying competitive and demographic pressures imposed by the ingress of sea bream may further stress any potential future recovery of sheepshead in the region. Furthermore, a rise in the primarily herbivorous sea bream could exacerbate the already dire status of seagrasses, which are major foundation species in the IRL.

In this study, we explored the population dynamics of sea bream and sheepshead in the waters of the IRL. Our objectives were to (1) quantify changes in the abundance of sea bream and sheepshead in the IRL over time, (2) characterize changes in the geographic range of these species within the lagoon system, and (3) identify environmental correlates of these changes. Understanding these emerging trends is of the utmost importance, as sheepshead support significant recreational and commercial fisheries in the region, which may be threatened by continual declines in local abundance. Sea bream are also recreationally harvested in Florida waters in limited numbers, including the Florida Atlantic coast, but are not a regulated or directly managed species (National Marine Fisheries Service, Fisheries Statistics Division pers. comm). This study provides an in-depth investigation into the spatiotemporal dynamics of a recreationally and commercially important fish species and a tropical congener. A thorough understanding of these processes is essential to developing pertinent management and adaptation strategies as tropicalization becomes more common globally, especially in temperate–subtropical regions, which are at the forefront of tropicalization.

2. MATERIALS AND METHODS

2.1. Study area

The IRL is a 260 km long estuary comprising 3 interconnected, relatively shallow basins along the US Atlantic coast of Florida (Fig. 1). This bar-built estuary is directly connected to the Atlantic Ocean via 5 permanent inlets, of which Ponce de Leon Inlet and Jupiter Inlet mark the northern and southern extents, respectively. One intermittently open conduit via the Canaveral Locks also links the Banana River Lagoon basin of the IRL to the Atlantic Ocean just south of Cape Canaveral.

The IRL is highly biodiverse, spanning a latitudinal biogeographic transition zone between temperate and subtropical regions, with a recognized geographical boundary of Cape Canaveral (Briggs 1974) and subtropical/tropical conditions as far north as latitude 28.00° (Gilmore 1995). For design and analysis purposes, the study area was subdivided into northern and southern regions. The NIRL; (28.606307°, −80.598719° to 27.650000°, −80.373000°) included all
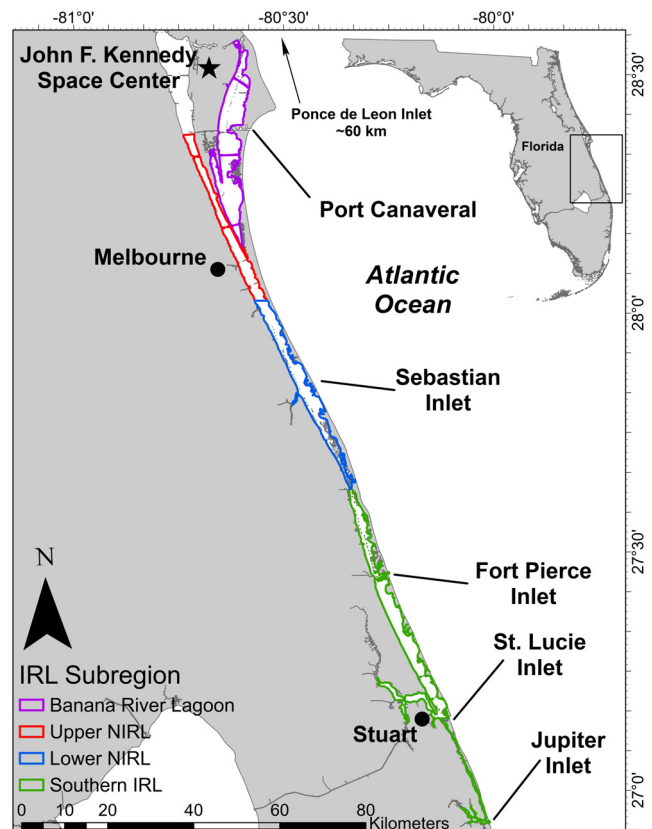

Fig. 1. Study area map of the Indian River Lagoon (IRL), Florida, USA, shown in the top right with extent indicator highlighting the study area. NIRL: northern IRL

of the Banana River Lagoon and a northern portion of the IRL proper. Sebastian Inlet is the only permanent connection of the NIRL to the adjacent Atlantic Ocean in the study region. To isolate meaningful differences in faunal assemblages and associated habitat characteristics, we divided the NIRL into 3 subregions: upper NIRL, lower NIRL, and Banana River Lagoon. These subregions emphasized geographic coverage, natural boundaries, environmental differences, and habitat availability. The southern IRL (SIRL) extended from the lower bounds of the NIRL to Jupiter Inlet (27.650000°, −80.373000° to 26.944210°, −80.072321°).

2.2. Design and sampling methodology

The FIM program of the FWC's FWRI uses a multiple-gear-type stratified-random sampling design in monthly collections of fishes and macroinvertebrates within the study area. A 21.3 m center-bag seine (1.8 m deep with 3.2 mm mesh) targeted young-of-the-year (YOY) and subadult fishes in all waters (≤1.5 m depth) directly on shorelines and nearshore shallow areas, and a 183 m center-bag haul seine (3 m deep, 38 mm mesh) targeted subadult and adult fishes in shoreline habitats in water ≤2.5 m deep. The study area was partitioned into a grid of 1 minute latitude × 1 minute longitude cells; each of those cells was further subdivided into 100 microcells of equal area. Within each subregion, cells and then microcells were randomly selected for monthly sampling.

All fishes and selected macroinvertebrates captured were identified to the lowest practical taxonomic level, counted, and a random sample of at least 10 individuals was measured for standard length (SL, mm). Additionally, at least 40 individuals of recreationally and commercially important fishes were measured for both gear types. Water temperature (°C), salinity (ppt), pH, and dissolved oxygen (mg l^{-1}) were recorded at each sampling site using a Hydrolab Surveyor 4 series, YSI 6 series, or YSI pro DSS series instrument. Coverage area and relative dominance of any species of submersed aquatic vegetation (SAV), defined as any species of seagrass or macroalga of the genus *Caulerpa* spp. (hereafter referred to as *Caulerpa*) growing in the substratum, were recorded at each site deploying the 21.3 m center-bag seine. SAV cover at each site deploying the 183 m center-bag haul seine was recorded as presence–absence by species owing to the difficulty of visually assessing the large sample area, especially when water clarity was low. Low water clarity has frequently been observed during long-duration

and widespread harmful algal blooms since approximately 2011. Substratum type (e.g. sand, mud), shoreline type (e.g. mangroves, terrestrial vegetation, emergent aquatic vegetation), and water depth were also recorded at each sampling site.

2.3. Data analyses

We focused analyses on data collected between 1998 and 2019. Generalized linear models (GLMs) were used to identify significant environmental and temporal variables associated with abundance of species and life-history classes (i.e. adult sea bream, adult sheepshead, and YOY sheepshead). Indices of abundance were calculated for adult sparids and YOY sheepshead using GLMs computed with the 'GLIMMIX' procedure (SAS Institute 2013). Sea bream were not frequently collected in the NIRL during the early years of the study, so GLM analysis focused on a shorter time series, from 2014–2019, for this species. Length–frequency analysis was completed for captured sea bream to determine a minimum size for inclusion in GLM analyses, which was further supported by the estimated size at first maturity for this species (80 mm SL; Chavance et al. 1982). Although the shorter time series from 2014–2019 did not allow for direct comparisons of the study's early years, results over this shorter time series were important in determining significant environmental predictors of sea bream abundance.

Count data for the species and classes were bounded by zero and often had a highly non-normal distribution. A negative binomial distribution was used because the variance was greater than the mean in all models. Class variables used in the initial models included temporal classes (year, month), subregion, substratum, SAV presence, shoreline type, and seine configuration (directly on shoreline or shallow nearshore set). Covariates included in the initial model runs were water temperature, salinity, and depth. The GLM for YOY sheepshead was further reduced to include only months in which YOY were present in the system. The final models included all significant class variables and covariates as determined by *F*-value and ordered for best model fit based on Akaike's information criterion (Akaike 1974).

Abundance was then calculated as the median annual number of fish per haul. These medians were calculated from the least-square means by multiplying the standard error by a random normal deviate (μ = 0, σ = 1) and adding it to the least-squares mean.

Back-transformations (e^x) were calculated, and the process was repeated 500 times for each year in the data set. This created a sample distribution of back-transformed values, summary statistics, and resultant 25th–75th percentiles that were then plotted to illustrate annual trends. Tukey-Kramer post hoc tests were conducted on all significant class variables to compare least-square means between categorical variables in each class. This procedure reliably identified meaningful predictors of the relative abundance of adult sparids and YOY sheepshead.

We used principal component analysis (PCA) to further explore relationships among water condition variables and annual abundance estimates (R Core Team 2018). This analysis allowed for a more comprehensive understanding of water conditions associated with sparid abundance. Annual minimum, maximum, and mean temperatures as well as a 3 mo winter average (January–March) that represented historic yearly low-temperature regimes were calculated for use in the PCA. In addition, 2 non-temperature-related variables were considered: mean salinity and dissolved oxygen. To determine patterns of abundance with respect to these water conditions, annual catch-per-unit-effort (CPUE; number of individuals per net haul) from 183 m haul seine hauls for adults of each species were overlaid onto the PCA plot. This method allowed abundance to be associated with year and specific aspects of water conditions.

Changes in SAV composition over time were investigated using data from 21.3 m seine sites that contained area coverage estimates as well as each SAV species' relative contribution. For these comparisons, all seagrass species were combined into one metric. Mean annual ratios of seagrass to *Caulerpa* sampled each year were calculated for the NIRL. In addition, the percentage of area covered by each SAV type was multiplied by the total area (m^2) sampled to determine area coverage (m^2). Sampling effort was consistent across all years (mode = 336 total seine hauls yr^{-1}) with little variation in annual effort (±3 hauls) during the study period. These data were used to reveal trends in SAV coverage at our sampling sites rather than being considered as an absolute measure of coverage in the entire IRL study area.

We identified a need for more in-depth exploration of the broad components of SAV and any influence they had on adult sparid abundance (GLM application was limited in scope for this specific environmental metric). To accomplish this goal, relationships between the annual abundance of adult sea bream and sheepshead and the mean annual ratios of sea-

grass species to *Caulerpa* were examined using a 1-factor regression. A Shapiro-Wilk test in the R package 'dplyr' (Wickham et al. 2023) and a Durbin-Watson test in the R package 'car' (Fox & Weisberg 2019) were conducted, respectively, to test normality and autocorrelation of residuals. To correct for issues with autocorrelation of residuals, a response variable lagged one unit of time was fitted as a predictor variable where appropriate. Before fitting the final regression, model data were square-root or arcsine transformed as appropriate to reduce the influence of a few large catches.

Classical time series decomposition was conducted to identify spatiotemporal trends in species abundance in NIRL subregions (R Core Team 2018). This analysis was more effective than the GLMs in examining sea bream abundance during the early years (1998–2013) and so allowed for comparisons between species for the full study period. Monthly CPUEs of adult sea bream (≥80 mm SL) and adult sheepshead (≥242 mm SL) were calculated using catch data from 183 m haul seines, while YOY sheepshead (≤40 mm SL) CPUEs were calculated from 21.3 m seines, as that gear effectively samples juvenile and small adult fish communities. Time series models were then created using month as the time interval. Classical decomposition assumes that time series models can be one of 2 types: additive or multiplicative (Casals et al. 2002, Hsieh et al. 2009). Each time series was decomposed by removing the overall trend and seasonality, according to Eqs. (1) & (2), where the model (Y_t) at time t is a function of the overall trend (T_t), seasonality (S_t), and random variation (e_t):

$$Y_t = T_t + S_t + e_t \qquad (1)$$
$$Y_t = T_t \times S_t \times e_t \qquad (2)$$

Models with the least variation attributed to random chance were used for each time series. Trends were calculated using a 12 mo moving average and then removed from models according to the appropriate equation (either additive or multiplicative equations). Seasonality was calculated by averaging the detrended values for each time unit (i.e. month). Random variation was then examined graphically to determine which model best fit the data (R Core Team 2018). Based on those results, multiplicative models were used to decompose the adult sheepshead time series, and additive models were used to decompose that of YOY sheepshead. An additive time series model attributed the least variation in sea bream catch to random effects for the majority of the study period. However, in 2017, the variance attrib-

utable to random effects began to increase markedly. Due to the stark difference in abundance and variance, sea bream seasonality was assessed separately for 1998–2016 and 2017–2019. Time series analysis was determined to be ineffective for YOY sea bream (≤40 mm SL), as only 37 YOY individuals were captured in 22 yr.

Spatial statistics tools in ArcGIS Pro (ESRI) were used to visualize and investigate trends in the fine-scale spatial distributions of sparids in the IRL. Sea bream and adult sheepshead hot spot intensity was determined using data from 183 m haul seines deployed throughout the NIRL and the SIRL. YOY sheepshead hot spot intensity was determined using data from 21.3 m seines. This seine was not used in the SIRL, so hot spot analysis for YOY sheepshead focused on the NIRL. Abundance data were split into 4 periods: 1998–2003, 2004–2009, 2010–2014, and 2015–2019. The following analyses were conducted for each species group and time period. Incremental spatial autocorrelation, which uses Global Moran's I, was used to simultaneously calculate z-scores of distance bands in increments of 50 m from 50–1500 m to determine the distances over which spatial clustering and autocorrelation in abundance occur (Moran 1950, Jalali et al. 2015). The smallest distance band associated with a peak in z-score was used in subsequent analyses. Based on selected distance bands, the Getis-Ord Gi* statistic was used to identify areas of high and low abundance and classify them as statistically significant hot spots or cold spots (Ord & Getis 1995). The resulting vector layer was then interpolated using inverse distance weighting to create a statistically based heatmap of abundance. This method identifies spatial autocorrelation by assuming that correlation is proportional to the distance between 2 points (Setianto & Triandini 2013, Burrough et al. 2015, Jalali et al. 2015). The method's accuracy relies heavily on the number of neighboring samples and the spatial extent of the study area. The large sample size in each 5–6 yr period and the thorough Global Moran's I analysis sufficiently addressed these dependencies and thus ensured accurate interpolation of hot spots. The IRL study area was set as the spatial extent and mask for the output raster (Flanders Marine Institute 2021). Resultant hot spot rasters were compared over time to evaluate any significant changes in the distribution of sheepshead and sea bream in the IRL. Spatial analyses were paired with time series analysis to detect shifts in abundance as a driver of range shifts in the IRL.

3. RESULTS

A total of 5019 seine hauls (183 m seines) were completed in the NIRL during standardized FIM sampling during 1998–2019, capturing 5195 sea bream and 20 876 sheepshead. During peak recruitment months for sheepshead (April–June), 2454 seine hauls (21.3 m seines) were completed in the NIRL, capturing 2161 YOY sheepshead. In the SIRL, 3688 seine hauls (183 m seines) were completed during 1998–2019, capturing 6907 sea bream and 16 597 sheepshead. No 21.3 m seine hauls were conducted in the SIRL region. Only 37 YOY sea bream were captured over all types of gear used throughout the study area over the 22 yr study period. Both gear types were used to sample an array of habitats, including seagrass meadows, mixed SAV areas, open sand or mud flats, mangrove shorelines, and urbanized areas with seawalls, hardened structures (i.e. rocks, rubble), or docks.

3.1. Time series analysis

Seasonal and long-term trends in the abundance of sea bream and sheepshead were evident over the course of the study. The adult sea bream time series revealed novel seasonal patterns of abundance in the NIRL. During 1998–2016, no seasonality in sea bream catch was detected, likely due to the overall low catch of sea bream during that time. During 2017–2019, large seasonal fluctuations were seen in sea bream abundance in the NIRL (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m14314_supp.pdf). Sea bream abundance peaked twice annually, during June and December, with minima during February–May.

Catches of adult sheepshead varied seasonally, with minima during winter (i.e. December–February) and peaked during August and September. Unlike adults, abundance of YOY sheepshead varied seasonally, with maxima during April–June, corresponding with peak YOY recruitment months for sheepshead. Lowest abundances were observed during late fall and winter (October–March).

Sea bream and sheepshead followed disparate patterns of abundance across years; in general, sea bream increased in abundance and sheepshead decreased. Adult sea bream abundance began trending upward in 2017 after having been relatively low and stable for most of the study period (Fig. S2). An approximately 49-fold increase in mean yearly CPUE was observed from 2016–2019. The largest increase

in the abundance of sea bream was observed in the lower NIRL subregion (i.e. near Sebastian Inlet; Fig. 2).

Adult sheepshead abundance remained relatively stable during 1998–2010, but overall abundance increased during 2011–2016, resulting in a 5.4-fold increase at its peak in 2013. Adult sheepshead abundance then declined 8.9-fold through 2019. Changes in sheepshead abundance in the Banana River Lagoon accounted for most of the recorded change during 2013–2019 as abundance in other subregions remained relatively stable but low. Slight downward trends in adult sheepshead abundance, however, were observed during 2015–2019 in all subregions. YOY sheepshead abundance was dynamic over the course of the study (1998–2019). Early in the study (1998–2008), YOY sheepshead were most abundant in the lower NIRL and generally followed a boom–bust cycle. However, abundance decreased drastically in the lower NIRL in 2009 and did not recover during the remainder of the study period (2009–2019). Abundance of YOY sheepshead in the Banana River Lagoon and upper NIRL remained relatively stable.

3.2. Hot spot analysis

Geographic expansion of sea bream distribution was observed over the course of the study (1998–2019). The most notable difference in the spatial distribution of sea bream was evident from 2015–2019 (Fig. 3). The lower NIRL subregion near Sebastian Inlet accounted for most of the noticeable change between these 2 periods. The shift in sea bream hot spot intensity in this region accounted for a spatial expansion of approximately 25 km north of initial habitats utilized in the NIRL. Little to no change in hot spot intensity was observed in the upper NIRL and Banana River Lagoon subregions. Cold spots in sea bream abundance were characteristic of these subregions for the entirety of the study (1998–2019). The SIRL yielded high hot spot intensity of sea bream over all time periods, with little change during the 22 yr study.

Contrary to that of sea bream, the hot spot intensity of adult sheepshead CPUE in the NIRL decreased over time. At the beginning of the study (1998–2003), hot spots of adult sheepshead were identified throughout much of the NIRL and SIRL,
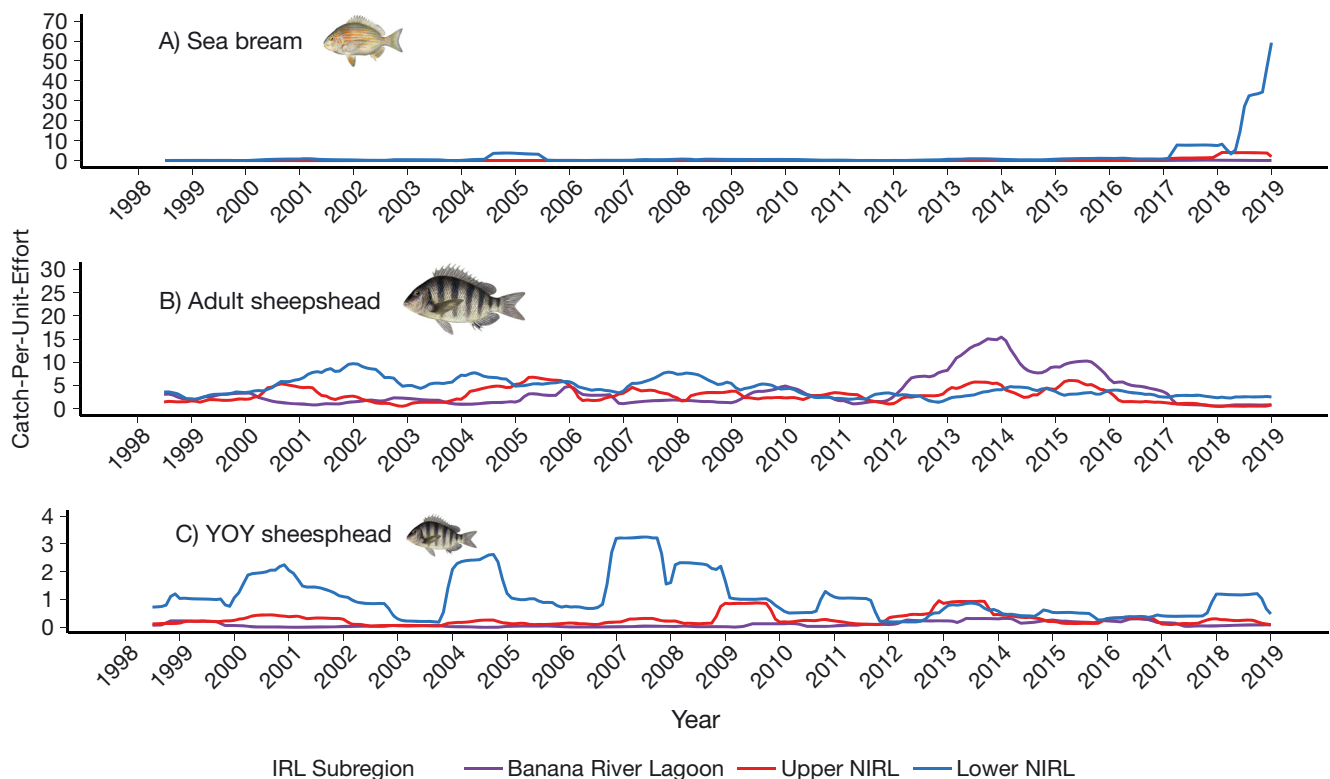

Fig. 2. Time series of (A) sea bream, (B) sheepshead, and (C) young-of-the-year (YOY) sheepshead catch-per-unit-effort by Indian River Lagoon (IRL) subregion. The 12 mo moving average used to calculate trend values at each time period results in null values for the first and last 6 mo of the series. NIRL: northern IRL
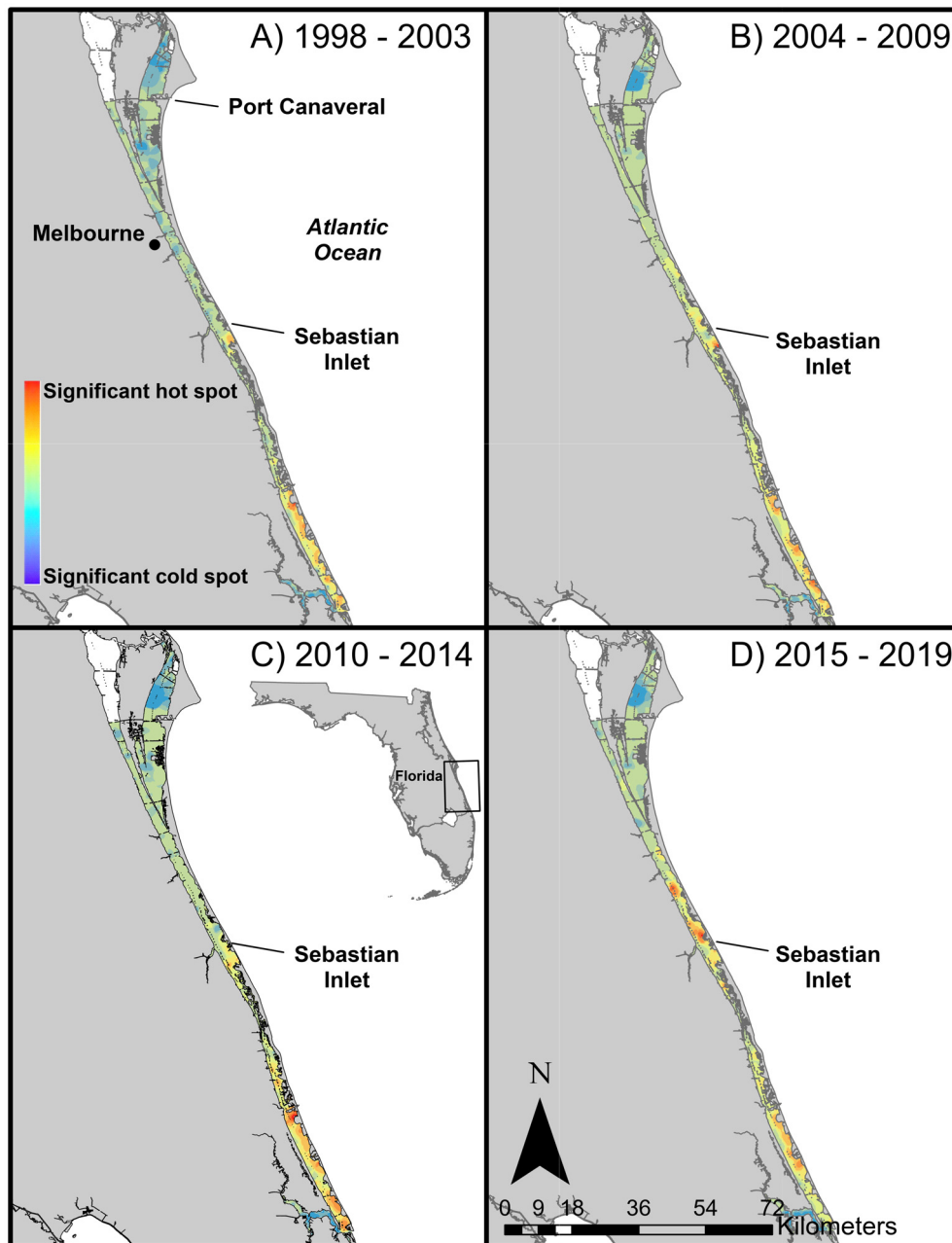
Fig. 3. Hot spot analysis interpolation of sea bream catch-per-unit-effort during (A) 1998–2003, (B) 2004–2009, (C) 2010–2014, and (D) 2015–2019. Red cells: significantly large sea bream catches; blue cells: significantly small sea bream catches. Hot and cold spots are based on spatial interpolation of samples of significantly high and low catch, as determined by z-score. In panel C, Florida, USA, shown (top right) with extent indicator highlighting the study area

with the exception of the Banana River Lagoon. By 2019, most of the upper NIRL had transitioned to significant cold spots for adult sheepshead, while the Banana River Lagoon had become a significant hot spot. The lower NIRL likewise experienced large reductions in hot spot intensity. Similar reductions were observed in the SIRL near Fort Pierce Inlet, though little change in hot spot intensity was observed to its north. The largest decreases in hot spot intensity throughout the study area were observed between the periods 2004–2009 and 2010–2014 (Fig. 4). The hot spot intensity of YOY sheepshead CPUE was likewise dynamic over the 22 yr study period in most regions of the NIRL (Fig. S3). High catches of YOY sheepshead were common throughout the lower NIRL during 1998–2003, but
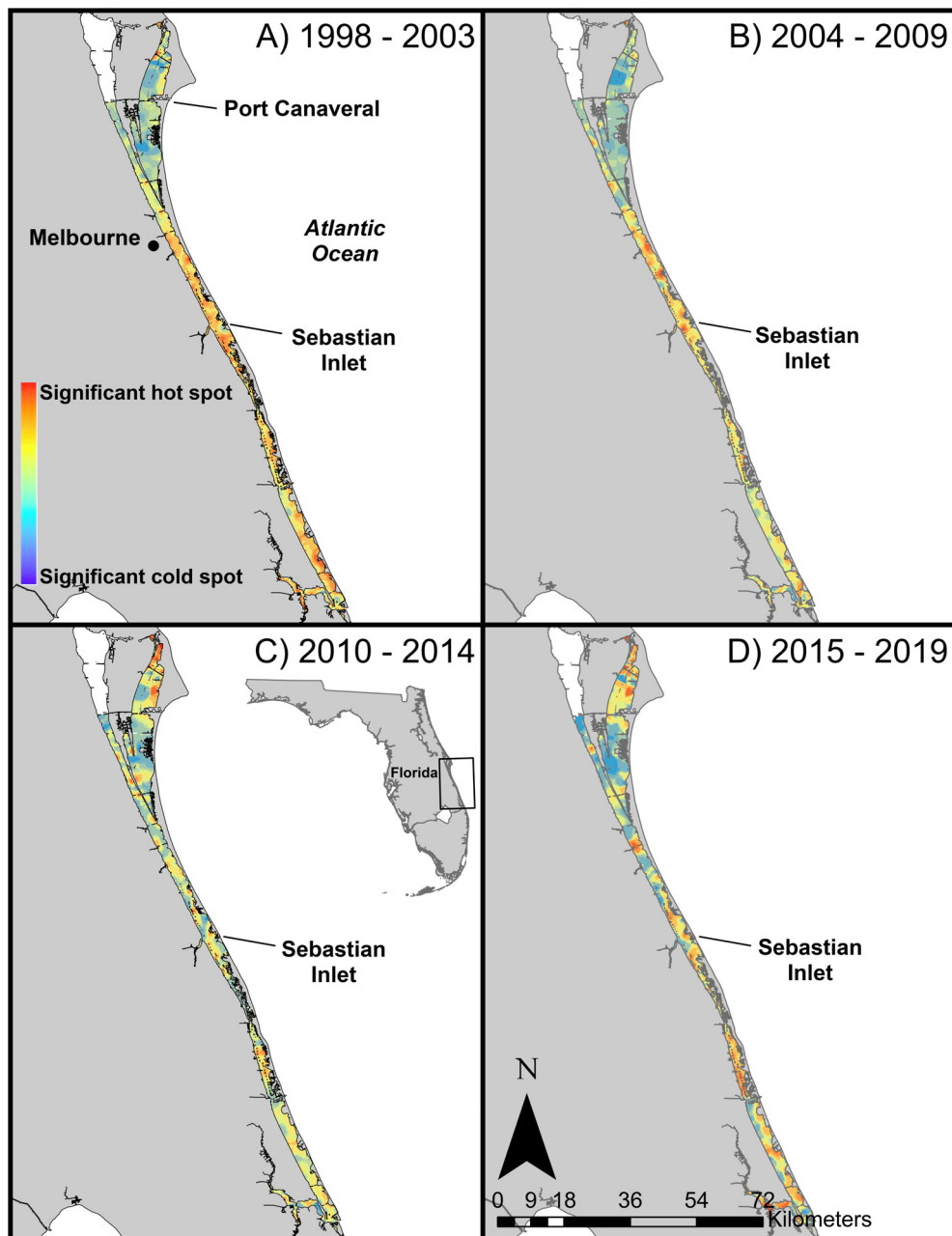
Fig. 4. Same as Fig. 3 but for adult sheepshead catch-per-unit-effort during (A) 1998–2003, (B) 2004–2009, (C) 2010–2014, and (D) 2015–2019

hot spot intensity there decreased from 1998–2014. By the 2010–2014 time period, several areas of the lower NIRL that had once been significant hot spots of YOY sheepshead had transitioned to significant cold spots. However, higher YOY sheepshead abundance partly recovered during 2015–2019 near Sebastian Inlet and the southern half of the Banana River Lagoon.

3.3. Environmental analyses

Environmental regimes in the NIRL proved to be dynamic over the 22 yr study period, across the 9818 sampling sites with available water condition data. From 1998–2019, mean annual water temperature increased approximately 0.9°C (Fig. 5). Annual minimum temperature also increased, by 1.5°C, while
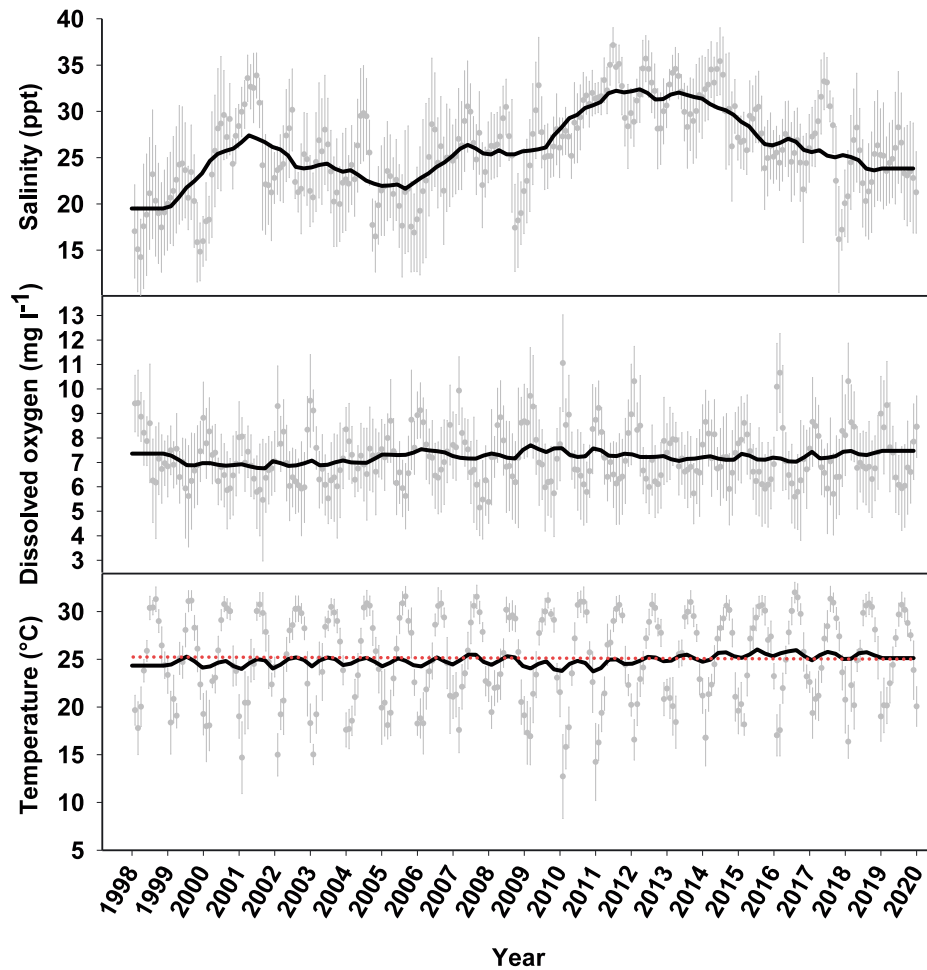
Fig. 5. Salinity, dissolved oxygen, and water temperature in the northern Indian River Lagoon, Florida, 1998–2019. Grey dots: monthly mean condition; grey error bars: SE; black line: a smoother utilizing a nearest neighbor rolling average; red dotted line: median temperature recorded from 1998–2019

maximum temperatures remained static at approximately 34°C. Mean annual dissolved oxygen increased slightly by approximately 0.3 mg l^{-1}. Mean salinity increased by 7.6 ppt during the study, peaking in 2011 with an annual mean of 32.1 ppt. Mean salinity remained >31 ppt until 2015, when it began to decrease, and had reached 24.4 ppt by 2019.

Regarding PCA results, differences in minimum and winter average temperature explained the most variation in the first principal component, while maximum temperature and dissolved oxygen provided the most variation in the second (Fig. 6A, Table S1). The later years of the study, from 2015, were associated with higher minimum and winter average temperatures. Clustering of years with higher abundance of sea bream were associated with generally warmer winter regimes with higher annual minimum temperatures. The years of greater sea bream abun-

dance also shared similar mean annual salinity regimes (24–26 ppt) but varied across a range of dissolved oxygen availability. No clear trends in abundance of adult sheepshead related to environmental metrics in the PCA were apparent based on yearly CPUE data from 183 m seines.

SAV composition and coverage changed in the NIRL. Peak seagrass cover at sampling sites in the NIRL was observed at the beginning of the study period in 1998 (162 923 m^2), which was followed by a sharp decline in seagrass, resulting in a low of 1022 m^2 in 2012, following a large-scale harmful algal bloom (Lopez et al. 2021). After 2012, cyclic periods of partial recovery and decline resulted in a net reduction in seagrass area of 98.4 % in areas sampled, compared with the 1998 peak (Fig. 7). Despite these drastic declines, seagrasses remained the dominant SAV type until 2019. Shifts in *Caulerpa* cover-
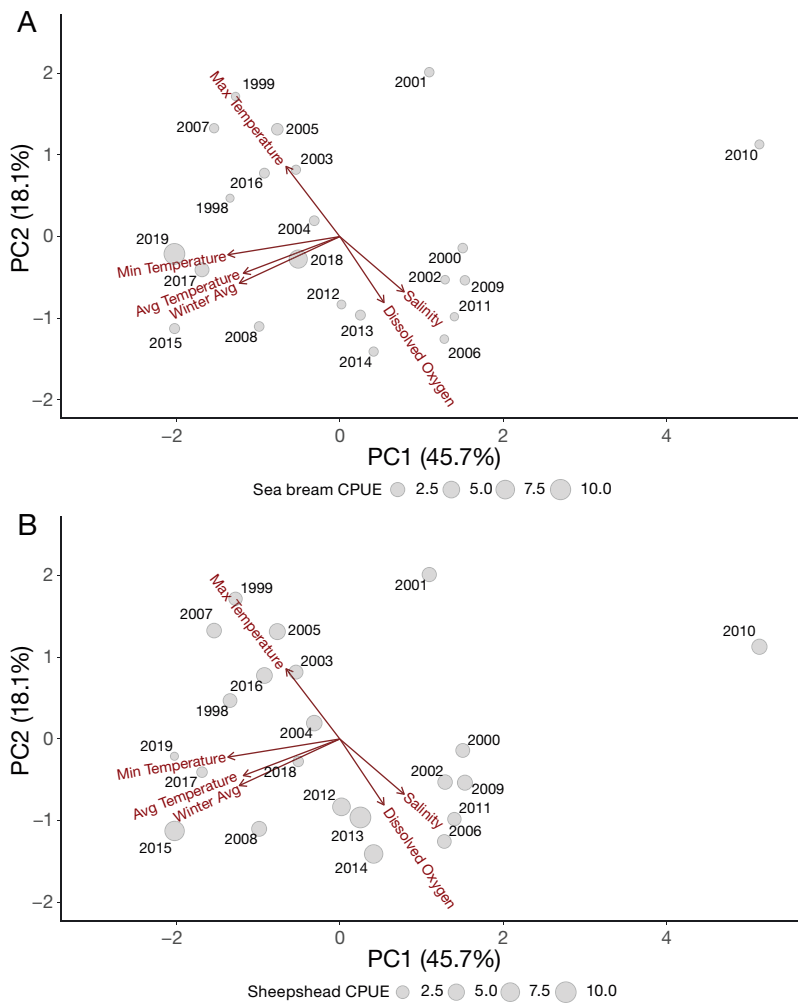
Fig. 6. Principal component analysis on water quality data in the Indian River Lagoon, Florida, 1998–2019, with bubble-plot overlay of catch-per-unit-effort of (A) sea bream and (B) sheepshead. Larger-diameter points indicate greater catch

age and relative dominance were cyclic, with 3 periods of short-term increases before 2015. *Caulerpa* area then increased through 2019. Maximum coverage of *Caulerpa* was 4560 m^2 in 2004, constituting a mean of 19% of the total SAV at sampled sites in the NIRL that year. In 2019, *Caulerpa* became a more dominant component of SAV. When compared to seagrass species, *Caulerpa* had a mean of 54% as a component of SAV species found at sampling sites. The change in percent composition by *Caulerpa* accounted for more than half the variation in adult sea bream (r^2 = 0.73, Fig. S4A) and adult sheepshead (r^2 = 0.53) mean annual abundance (Fig. S4B). Sea bream abundance was positively correlated with increased *Caulerpa* percentage. Conversely, sheepshead abundance was negatively correlated with in-

creased *Caulerpa*, where reductions in adult sheepshead were associated with increased loss of the seagrass component of SAV. *Caulerpa* was present at 332 of 2991 of the 183 m haul seine sampling sites at which sheepshead were captured but at only 35 of the 202 sites at which sea bream were captured.

The most influential predictor of sea bream abundance in the NIRL was subregion of capture (*F* = 215.54, p < 0.001). The lower NIRL subregion, adjacent to the SIRL and near Sebastian Inlet, accounted for 93.5% of the 4517 sea bream captured during the core years of abundance (2014–2019). Abundance of sea bream was significantly greater (p < 0.001) in this subregion than in any other NIRL subregion. Temperature was also identified as a significant (*F* = 6.51, p = 0.001) predictor of abundance for sea bream (Table 1).

Several spatial, temporal, and environmental variables significantly affected sheepshead abundance (Table 1). The most influential predictor of adult sheepshead abundance was subregion of capture (*F* = 215.54, p < 0.001; Table 1). Of all adult sheepshead captured, 58.7% were captured in the northern terminus of the Banana River Lagoon, in or near the John F. Kennedy Space Center. Tukey-Kramer post hoc comparisons revealed that sheepshead were significantly more abundant in this subregion (p < 0.001) than in any other subregion. Adult sheepshead were most often collected in habitats with SAV (82.4%, p = 0.001), sandy substratum (84.2%, p < 0.001), and mangrove-associated shoreline (62.1%, p < 0.001) throughout the NIRL. Post hoc comparisons of shoreline type revealed that mangroves were only significantly different from terrestrial vegetated shorelines in their predictive power (p < 0.001). Water temperature was a significant predictor of abundance of adult sheepshead (*F* = 17.83, p < 0.001; Table 1).

As with adult sheepshead, the most influential predictor of sheepshead YOY abundance was subregion of capture (*F* = 167.41, p < 0.001; Table 1). Estuarine waters adjacent to Sebastian Inlet, which contain the only permanent inlet access to the Atlantic Ocean in the lower NIRL, accounted for 89.8% (p < 0.001) of all
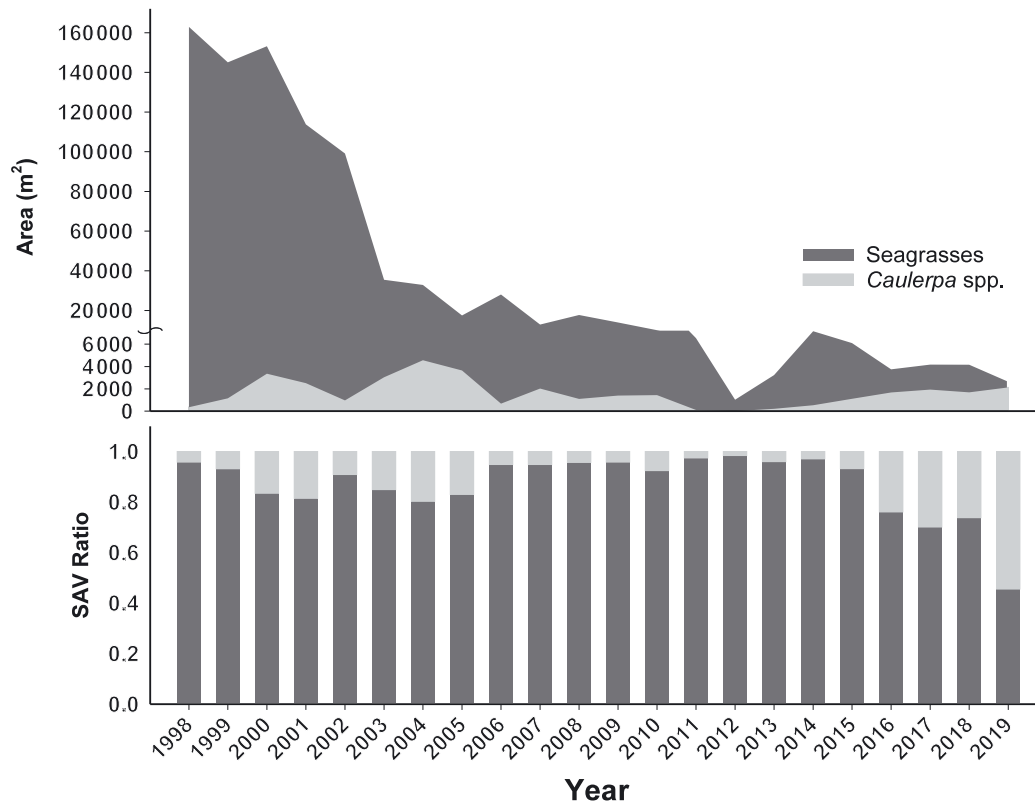
Fig. 7. Area of total coverage and ratio of mean annual submersed aquatic vegetation (SAV) coverage (seagrasses to *Caulerpa* spp.) at sampling sites in the Indian River Lagoon, Florida, 1998−2019

Table 1. Results of generalized linear modeling (GLIMMIX; SAS) of the effect of temporal, spatial, habitat, and physicochemical metrics on the catch-per-unit-effort (no. of ind. set^{-1}) of sheepshead and sea bream during long-term monitoring (1998−2019). Sea bream model is a reduced time series (2014−2019). Significance for model inclusion (in **bold**) set at p = 0.05; SAV: submersed aquatic vegetation

	Model variable	Sheepshead ≥242 mm SL 183 m haul seine			Sheepshead ≤40 mm SL 21.3 m bay seine			Sea bream ≥80 mm SL 183 m haul seine		
		df	F	p	df	F	p	df	F	p
Class variables	Sub-region	3	215.54	**<0.001**	2	156.13	**<0.001**	3	41.36	**<0.001**
	Substratum	1	13.26	**<0.001**	2	25.25	**<0.001**	3	2.14	0.093
	SAV presence	1	10.58	**0.001**	1	36.71	**<0.001**	1	0.02	0.878
	Year	21	7.51	**<0.001**	21	5.33	**<0.001**	5	21.28	**<0.001**
	Shoreline type	4	5.7	**<0.001**	4	0.71	0.583	7	1.88	0.069
	Month	11	4.12	**<0.001**	6	39.60	**<0.001**	11	3.31	**<0.001**
	Shoreline/offshore set	−	−	−	1	11.37	**0.001**	−	−	−
Covariates	Temperature	1	17.83	**<0.001**	1	0.6	0.438	1	6.51	**0.010**
	Salinity	1	3.16	**0.076**[a]	1	1.6	0.203	1	0.64	0.423
	Depth	1	0.49	0.484	1	0.2	0.607	1	3.51	**0.061**[a]

[a]Included non-significant covariate that contributed to best model fit by AIC

YOYs captured in the entire NIRL. YOY were associated with sand substratum (58.3%, p < 0.001) and SAV (84.2%, p < 0.001) habitat types throughout the NIRL. Shoreline type was not a significant variable for YOYs and was dropped from the final model run, but deployment orientation of the 21.3 m seine with regard to shoreline proximity was significant (p = 0.001). Sheepshead YOY were significantly more abundant in hauls directly on shorelines (p < 0.001) than in nearshore hauls not directly on shorelines.

4. DISCUSSION

Trends in long-term abundance and spatial dynamics of sea bream and sheepshead were related to multiple environmental factors and ecological changes in the IRL ecosystem. The abundance increases and spatial expansion of the sea bream population in the NIRL were likely related to changes in abiotic regimes, including water temperature and salinity, evident during the 22 yr of this study. Shifts in SAV involving declines in seagrasses and the proliferation of *Caulerpa* related to anthropogenic influences also likely alter the dynamics of sheepshead in the IRL.

Increasing water temperatures in the IRL associated with climate change are likely facilitating the poleward expansion of sea bream. In range expansions of warm-water species induced by climate change, the leading spatial edge of the expansion often does not keep pace with increasing temperature. Confounding non-climatic drivers and time lags can reduce our ability to directly tie warming to a range expansion (Fredston-Hermann et al. 2020). However, we observed warming of IRL waters, suggesting a trend toward milder winters in the system. Warmer minimum water temperatures were observed in the NIRL beginning approximately in 2015, and substantial increases in the seabream population followed 2 yr later. Increased annual temperature minima may be facilitating the spread of sea bream into the NIRL, as they are most abundant in tropical areas, typically with high sea surface temperatures (Chavance et al. 1984, Kendall et al. 2021). Temperature was a significant predictor of abundance for sea bream, and increased minimum and winter temperature regimes were associated in the PCA with the years of greatest abundance. Community assemblages in Northern Hemisphere temperate–tropical biogeographical transition zones, such as the IRL, are strongly influenced by annual temperature minima (Osland et al. 2021). Extreme cold events are becoming less frequent, enabling the poleward spread, survival, and proliferation of tropical species in affected regions (Purtlebaugh et al. 2020, McClenachan et al. 2021, Osland et al. 2021). Additionally, the documented shift in sea bream abundance aligns with previous evidence from FWC-FWRI FIM data of broadscale tropicalization of fish assemblages in the NIRL (Troast et al. 2020). Higher annual minimum temperatures may be improving the habitat suitability of the NIRL for sea bream by decreasing the frequency and intensity of thermal disturbances. However, it is currently unknown if increasing tem-

peratures are facilitating the survival of sea bream YOY or the immigration of adults into the NIRL. Chavance et al. (1984) collected sea bream larvae across a large temperature range (22–29°C) and found no evidence for a relationship between water temperature and larval abundance. Given that we also did not collect many YOY during 2016–2019 despite increasing annual minimum temperatures, there are likely more important drivers of sea bream larval production and survival than temperature. Kendall et al. (2021) observed increased movement of acoustically tagged sea bream in winter months, suggesting that water temperatures may influence the movement of adults across coastal regions.

The observed increases in salinity in the NIRL may be facilitating the rise of sea bream, which is most abundant in high-salinity waters, such as Biscayne Bay (Florida) and the Caribbean Sea (Chavance et al. 1984, Hammerschlag et al. 2010). Salinity also drives increased local abundance of sea bream in tropical estuarine lagoons, with lower-salinity pulses from elevated freshwater inputs correlating with decreased sea bream abundance (Ramos-Miranda et al. 2005). However, short-term declines in salinity began in 2015, when sea bream abundance actually began to increase, and if salinity were the primary driver of sea bream abundance in the NIRL, a sharp decrease would be expected in light of dropping salinity levels. These results suggest that other concurrent changes in environmental regimes are more important drivers for abundance and distribution shifts for this species.

Changes in SAV percent cover resulting from mass seagrass die-offs and subsequent macroalgal blooms during 2010–2019 (Lapointe et al. 2018, 2020, Morris et al. 2022) may be influencing sparid population dynamics in the NIRL. During early life-history stages, sheepshead can rely on seagrass meadows for refuge from predation, foraging, and relief from competition with adults that also occupy hard-bottom habitats (Jennings 1985, Sedberry 1987, Ballenger 2011). The near-total or total loss of seagrass cover in many areas of the NIRL has undoubtedly had negative impacts on seagrass-dependent fauna, resulting in severe declines in abundance and shifts in species composition (Paperno et al. 2020, Adams et al. 2022). High seagrass mortality has been linked to similar faunal declines in other estuaries. In 2 Massachusetts estuaries, Hughes et al. (2002) recorded drastic differences in the biomass, abundance, and diversity of fishes between sites with high seagrass density and bare sites that were previously covered by seagrass. Reed & Hovel (2006) reported experimental evidence

for a threshold effect of seagrass loss on dependent faunal communities, as declines in diversity and abundance were apparent only in high-seagrass-mortality treatments. In our study, the presence of SAV was a significant factor influencing the abundance of both adult and YOY sheepshead. Severe loss of seagrass habitat and increased dominance of *Caulerpa* indicate that as seagrass became less dominant, sheepshead abundance also declined. Thus, the seagrass component of SAV is likely an important environmental component influencing sheepshead abundance. Hot spot analysis illustrated a shift in the location of greatest sheepshead abundance away from the lower NIRL subregion northward to the Banana River Lagoon (Fig. 1). During 2013–2015, the Banana River Lagoon experienced a greater area of short-term recovery of seagrasses than did the lower NIRL (Morris et al. 2021). This spatial shift suggests that sheepshead hot spots shifted toward better available seagrass habitat during this period. The timing of this hot spot shift and short-term seagrass recovery coincided with a time of increased sheepshead abundance in the Banana River Lagoon. Following this short-term recovery, seagrass coverage again declined in the Banana River Lagoon (Morris et al. 2021), and sheepshead abundance began a mirrored decline that resulted in the lowest abundance estimate in 22 yr of monitoring. The northern terminus of the Banana River Lagoon, encompassed by the John F. Kennedy Space Center, was identified in GLMs as the strongest predictor of sheepshead abundance. Seagrass losses may also have limited the amount of suitable settlement habitat available to sheepshead, bottlenecking juvenile survivorship. However, abundances of YOY sheepshead varied throughout the study period, so the exact trajectory of their recruitment is still not fully understood.

The relationship between the abundance of sea bream and the increase in relative dominance of *Caulerpa* was difficult to elucidate; 83% of adult sea bream were captured in areas devoid of *Caulerpa* cover. In GLM analysis, the presence of SAV was not found to be a significant predictor of sea bream abundance. Yet *Caulerpa* percent composition was positively correlated with sea bream abundance and explained a large proportion of the variation in catch data ($r^2 = 0.73$).

In other estuarine systems, the colonization of seagrass-dominated habitats by *Caulerpa* has led to changes in nursery function, grazing, trophic structure, and ichthyofaunal assemblages that have benefited local sparids, including *Diplodus annularis* and *D. sargus* (Francour et al. 1995, Amade & Lemée

1998, York et al. 2006, Vázquez-Luis et al. 2008, Felline et al. 2012, Deudero et al. 2014). The role of *Caulerpa* as sea bream forage or habitat is unknown for the IRL and requires further exploration. We emphasize caution in drawing conclusions about *Caulerpa*'s role in the observed increased sea bream abundance in the NIRL. *Caulerpa* exhibits positive growth responses to both increased salinity (Theil et al. 2007) and increases in minimum annual temperatures (Terrados & Ros 1992). This positive correlation of sea bream abundance to increasing *Caulerpa* could be the result of similar relationships between this macroalgal species and changing environmental variables.

The environmental changes occurring in the NIRL may be beneficial for sea bream, but the influx of this closely related tropical sparid may be contributing to the barriers for recovery of both adult and YOY sheepshead. Throughout most of their geographic range, sheepshead feed on invertebrates with plant matter included. However, in the NIRL, the diet of adult sheepshead consists mostly of macrophytes, including algae and seagrasses, with a lesser volume of invertebrate prey (Cutwa & Turingan 2000, Heil 2017, Reeves et al. 2019). The diet of NIRL sheepshead may make them especially susceptible to intense competitive interactions with adult sea bream, which also feed primarily on macrophytes (Randall 1967, Vaughan 1978, Vega-Cendejas et al. 1994, Hammerschlag et al. 2010). The extent of higher sheepshead abundance in the NIRL and the frontier of expanding sea bream still afford some spatial separation, but as sea bream continue to expand northward they will likely encroach further into sheepshead habitats in the NIRL, and, by extension, continued poleward expansion by sea bream may further influence local sheepshead populations.

Heightened competition in ecological communities resulting from climate change has been well documented (Helland et al. 2011, Urban et al. 2012, Zarnetske et al. 2012, Everling 2021), but the competitive effects of poleward migrating herbivores on native herbivores in estuarine systems is not well understood. Despite this, many scientists hypothesize that as tropical species move poleward, competition with native species is inevitable (Zarnetske et al. 2012, Vergés et al. 2014a, Heck et al. 2015). In the case of the NIRL specifically, competition between these congeners is likely as sheepshead are common from Nova Scotia to Brazil, so no commensurate poleward shift in their distribution is expected in the near future. Additionally, if sea bream abundance continues to increase and the species continues to expand

northward in the NIRL, the fate of local seagrasses may be similar to that of the foundation species observed in other systems experiencing tropicalization (Ling 2008, Kelkar et al. 2013, Vergés et al. 2014a, 2016): the influx of an additional grazer could compound the pressures associated with earlier seagrass die-offs, leaving in question the future of NIRL seagrasses and their dependent fauna. Little is known regarding the feeding ecology of these sparids in the NIRL; however, preliminary work suggests that the diets of sea bream and sheepshead heavily overlap (A. R. Searles et al. unpubl. data). Further work investigating the dietary preferences of these congeners is necessary to quantify the direct competitive impact that sea bream might have on local sheepshead populations and the ecosystem-level influence this newly arrived tropical herbivore might exert on the NIRL via direct grazing of seagrasses and other macrophyte species.

After the recent discovery in the IRL of individuals possessing morphological characteristics of both sea bream and sheepshead, Seyoum et al. (2020) documented hybridization between these congeners. To our knowledge, this was the first time that hybridization had been observed between these species. Declining sheepshead abundance may also, in part, result from burdens imposed by hybridization, as interbreeding is known to increase competition, stunt population growth rates needed to replace biomass, and reduce reproductive output (Allendorf et al. 2013, Seyoum et al. 2020). In some cases, interbreeding between closely related species can result in the full replacement of parental populations by hybrids via genetic introgression (Anderson 1949, Rosenfield et al. 2004). Populations inhabiting anthropogenically disturbed systems that have increased contact after periods of limited gene flow are especially vulnerable (Rosenfield et al. 2004). Since these hybrids were discovered in 2005, observations of the hybrids have not increased significantly during FIM sampling, suggesting that hybridization is not the sole cause of sheepshead decline in the NIRL population but rather that it compounds other changing interactions between sheepshead and their environment. Furthermore, the temporal and spatial separation of sea bream and sheepshead population dynamics suggest that sea bream are more likely to be a hindrance to sheepshead recovery than the sole driver of the fish's decline.

Our study provides robust evidence to suggest that sea bream have extended their distribution northward, contributing to the tropicalization of local species assemblages in the NIRL. This expanding population has likely been facilitated by warming winter water temperatures and changes in habitat characteristics associated with anthropogenic degradation. These tropical herbivores feed heavily on macrophytes, which may pose an additive threat to the already sparse and declining seagrasses and, by extension, the seagrass-dependent fauna of the NIRL. Furthermore, geographic expansion of sea bream in the NIRL may negatively influence the local sheepshead population via hybridization and resource competition. Sheepshead have already declined significantly in certain regions of the NIRL in recent years. Research focusing on the reproductive biology and the trophic niches of these congeners is needed to improve our understanding of how sea bream may impact the local sheepshead population and the broader IRL system in the near future. Long-term monitoring coupled with directed studies designed to understand the impact of habitat loss on adult and YOY sheepshead in the NIRL are crucial to informing management efforts aimed at bolstering the resilience and stability of sheepshead and its important fishery. Effective long-term monitoring also allows for proactive assessment of potential needs for management actions for unregulated species like sea bream that are undergoing poleward range expansion into previously unoccupied habitats. It is imperative that research efforts focus on understanding and mitigating threats to the health and resilience of local fishes, seagrasses, and other biological resources as anthropogenic pressures continue to impact the NIRL ecosystem.

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