

Long-Term Seagrass Decline and Spatial Reorganization of Blue Crabs in the Indian River Lagoon

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1 Long-Term Seagrass Decline and Spatial Reorganization of Blue Crabs in the Indian River Lagoon

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5 **Abstract**

6 The Indian River Lagoon (IRL), one of North America's most biodiverse estuarine systems, has
7 undergone extensive ecological restructuring following widespread seagrass loss associated with nutrient
8 enrichment, the 2011-2012 superbloom event, and recurrent harmful algal blooms. Because blue crabs
9 (*Callinectes sapidus*) depend on structured and spatially continuous estuarine habitats during early
10 development, we examined whether long-term habitat loss was associated with changes in the spatial
11 organization of blue crabs across the lagoon. Using long-term fisheries-independent monitoring data from
12 the Florida Fish and Wildlife Conservation Commission and seagrass survey data from the St. Johns
13 River Water Management District, we quantified relationships among blue crab relative abundance, body
14 size, habitat cover, and climatic variability. Long-term trends indicated overall declines in both summer
15 seagrass percent cover and mean blue crab carapace width, although these changes were characterized by
16 substantial temporal variability and marked shifts after 2011. Low bottom-vegetation cover habitats
17 contained smaller and less abundant crabs than highly vegetated areas. Following the 2011-2012 seagrass
18 decline, blue crab populations became increasingly spatially reorganized, with persistent low-density
19 regions emerging in the northern region of the lagoon and areas of elevated blue crab relative abundance
20 concentrated in the southern lagoon. Empirical orthogonal function analysis of long-term seagrass cover
21 data showed that a single basin-wide mode explained 64.8% of habitat variability and corresponded with
22 rainfall variability and regional climatic oscillations. Although local water-quality variables explained
23 relatively little variation in blue crab abundance, blue crab abundance and size structure remained
24 strongly associated with vegetated habitat availability. These findings suggest that seagrass loss and
25 habitat restructuring were associated with large-scale spatial reorganization of blue crabs. Because
26 movement among habitat patches was not measured directly, connectivity is interpreted here as the spatial
27 continuity and persistence of vegetated nursery habitat rather than demographic or dispersal connectivity.

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32 River Lagoon

33 34 **Introduction**

35 Estuaries function as interconnected habitat mosaics in which ecological connectivity influences the
36 persistence, productivity, and resilience of estuarine-dependent species (Elliot & Whitfield, 2025;
37 Woodland et al., 2019). Many estuarine organisms rely on multiple habitats throughout their life cycle,
38 linking offshore, nearshore, and estuarine environments through ontogenetic migrations and trophic
39 interactions (Sheaves, 2009). Because of this, changes in habitat distribution and continuity can alter
40 ecological processes that support estuarine productivity (Peterson, 2003). Consequently, habitat loss has
41 emerged as a major concern in coastal ecosystems experiencing increasing anthropogenic and climatic
42 pressures (Thrush et al., 2008).

The blue crab, *Callinectes sapidus*, is a commercially and ecologically important estuarine-dependent species that supports multimillion-dollar fisheries throughout the western Atlantic Ocean (Cheng et al., 2022). Additionally, blue crabs function as important mesopredators within estuarine food webs (Hines et al., 1990). Their life cycle depends on connectivity among coastal and estuarine habitats. Adult females migrate to high-salinity waters to spawn, after which larvae are transported offshore and develop as plankton (Avyle & Fowler, 1984). Successful recruitment depends on water movement processes, including tides and coastal currents, that transport larvae back into estuaries (Forward et al., 2003). As juveniles transition to a nektonic lifestyle, they recruit into shallow vegetated nursery habitats where survival and growth are strongly influenced by habitat structure and refuge availability (Hines et al., 1995).

Vegetated habitats play a particularly important role during the juvenile and adolescent life stages. Seagrass meadows provide refuge from predation, support abundant prey resources, and enhance abundance, survival, and recruitment relative to unvegetated substrates (Wilson et al., 1990; Perkins-Visser et al., 1996; Hovel & Lipcius, 2001; Hovel & Fonseca, 2005; Hyman et al., 2023). However, nursery function depends not only on the presence of vegetated habitat but also on its spatial continuity across the landscape. Experimental and field studies have demonstrated that restructuring of seagrass habitat can reduce survival and recruitment potential by increasing predator exposure and disrupting refuge availability (Hovel & Lipcius, 2001, 2002; Mizerek et al., 2011). As a result, large-scale changes in the distribution and continuity of vegetated habitats have the potential to reorganize blue crab populations across estuarine landscapes by altering the availability and spatial arrangement of nursery habitat. In this study, nursery-habitat continuity refers to the spatial continuity and persistence of vegetated nursery habitats across lagoon regions, rather than direct larval dispersal connectivity. Direct larval dispersal and demographic exchange among habitat patches were not measured.

The Indian River Lagoon (IRL), Florida, is one of the most biodiverse estuarine systems in North America and provides a useful system for examining how large-scale habitat change is associated with estuarine nursery habitat continuity. The lagoon has undergone substantial ecological change in recent decades associated with nutrient enrichment, recurrent harmful algal blooms, and widespread seagrass loss (Barile, 2018; Freeman et al., 2019; FDEP, 2018). One of the most consequential disturbances occurred during the 2011-2012 “superbloom” event (St. Johns River Water Management District [SJRWMD], 2012), when prolonged phytoplankton blooms reduced water clarity and contributed to extensive seagrass mortality throughout portions of the lagoon. Assessments have estimated that approximately 58% of seagrass habitat, representing nearly 19,000 hectares, was lost between 2011 and 2019 (Morris et al., 2022). Similar responses have been documented in estuaries worldwide, where eutrophication promotes phytoplankton and macroalgal proliferation while reducing seagrass persistence through light limitation (Duarte et al., 1995; Sfriso et al., 2003; Waycott et al., 2009).

Nutrient enrichment can vary in response to changing climatic and hydrologic conditions. In Florida, rainfall patterns are strongly affected by the El Niño-Southern Oscillation (ENSO), which can alter freshwater inflow, nutrient delivery, and estuarine environmental conditions (Schmidt et al., 2001; Beckage et al., 2003). El Niño phases are generally associated with wetter conditions across peninsular Florida, increasing watershed discharge and nutrient transport to estuaries, while La Niña phases are typically associated with drier conditions and reduced freshwater inflow (Schmidt et al., 2001). Shifts in rainfall patterns change stormwater-driven freshwater inflow from the watershed, which influences

85 salinity regimes, nutrient inputs, and estuarine water quality. Elevated nutrient loading can stimulate
86 harmful algal blooms (HABs), particularly in estuaries characterized by restricted flushing and long water
87 residence times (Duarte et al., 1995; Barile, 2018; Freeman et al., 2019). These blooms reduce light
88 availability through increased phytoplankton biomass and turbidity, limiting photosynthesis and
89 contributing to declines in submerged aquatic vegetation (SAV), including seagrasses, that depend on
90 adequate light penetration for growth and persistence (Duarte et al., 1995; Waycott et al., 2009). Because
91 seagrass abundance is strongly influenced by environmental conditions such as salinity shifts and nutrient
92 loading, climate-mediated hydrologic variability has the potential to alter the spatial distribution and
93 continuity of vegetated nursery habitats across estuarine landscapes (Montagna et al., 2018).

94 Following extensive seagrass loss beginning in 2011 (Morris et al., 2022; Brewton & Lapointe, 2023),
95 *Caulerpa prolifera* expanded throughout the northern Indian River and Banana River, becoming the
96 dominant benthic cover in several monitoring segments by 2016 (Brewton & Lapointe, 2023). These
97 changes may represent more than simple habitat loss; they may reorganize the distribution and continuity
98 of nursery habitat across the estuary. Because blue crabs depend on vegetated nursery habitats for refuge
99 from predation and access to food resources during early development (Perkins-Visser et al., 1996; Hovel
100 & Lipcius, 2001, 2002; Hovel & Fonseca, 2005), the IRL provides a long-term observational setting for
101 evaluating how nearly three decades of environmental change (1996-2023) are associated with the spatial
102 organization of blue crab populations and the nursery habitats upon which they depend.

103 Previous studies have demonstrated that habitat restructuring can influence blue crab survival, abundance,
104 and recruitment at local and patch scales (Hovel & Lipcius, 2001, 2002; Mizerek et al., 2011). However,
105 it remains unclear whether habitat change occurring across an entire estuarine system produces
106 comparable responses at broader spatial scales. Most research has focused on comparisons among habitat
107 types or experimental manipulations of habitat structure, providing important insights into fine-scale
108 habitat use but offering a more limited understanding of how long-term changes in habitat distribution on
109 a decadal scale alter the spatial organization of estuary-dependent populations. This limitation is
110 particularly relevant in systems undergoing rapid environmental change, where habitat loss may not
111 simply reduce nursery area but may also reorganize the distribution and continuity of suitable habitat
112 across the landscape.

113 The IRL provides an opportunity to evaluate whether long-term habitat change is associated with the
114 spatial organization of blue crab populations at the system level. The combination of widespread seagrass
115 decline, expansion of macroalgal assemblages, and pronounced climatic variability creates a long-term
116 observational setting for examining how environmental change corresponds with habitat distribution and
117 associated population patterns through time. Integrating long-term fisheries-independent monitoring
118 (FIM) with basin-wide seagrass surveys further allows assessment of whether and how changes in
119 vegetated habitat correspond with shifts in blue crab abundance, size structure, and spatial distribution
120 across the lagoon.

121 This study evaluated whether long-term habitat change in the IRL was associated with the spatial
122 organization of blue crab populations across the estuary. We hypothesized that (1) widespread seagrass
123 decline would correspond with spatial reorganization of blue crab abundance and size structure across the
124 lagoon, (2) blue crab relative abundance and carapace width would be positively associated with
125 vegetated habitat cover and distribution despite widespread habitat restructuring, and (3) basin-scale

habitat variability would covary with shifts in ENSO and local rainfall, reflecting climate-associated changes in benthic vegetation. To test these hypotheses, we integrated 28 years of FIM data, seagrass surveys, and climate records to examine associations among seagrass change, blue crab demographics, and environmental variability throughout the IRL.

Methods

Study Area

The Indian River Lagoon (IRL) is a shallow, bar-built lagoonal estuary extending approximately 250 km along Florida's Atlantic coast and consisting of three interconnected sublagoon systems: Mosquito Lagoon, Banana River, and the Indian River (Figure 1). The lagoon supports extensive ecological and economic resources (The Balmoral Group, 2025), including seagrass communities, mangrove shorelines, and nursery habitat for numerous estuarine-dependent species. The lagoon has a mean depth of approximately 1.5 m, with most areas shallower than 2 m, and experiences a microtidal regime with tidal ranges generally less than 0.5 m due to limited exchange with the Atlantic Ocean through five tidal inlets (Smith, 1993; Liu et al., 1997). These physical characteristics result in relatively long water residence times and strong spatial heterogeneity in salinity, hydrology, nutrient dynamics, and benthic habitat composition.

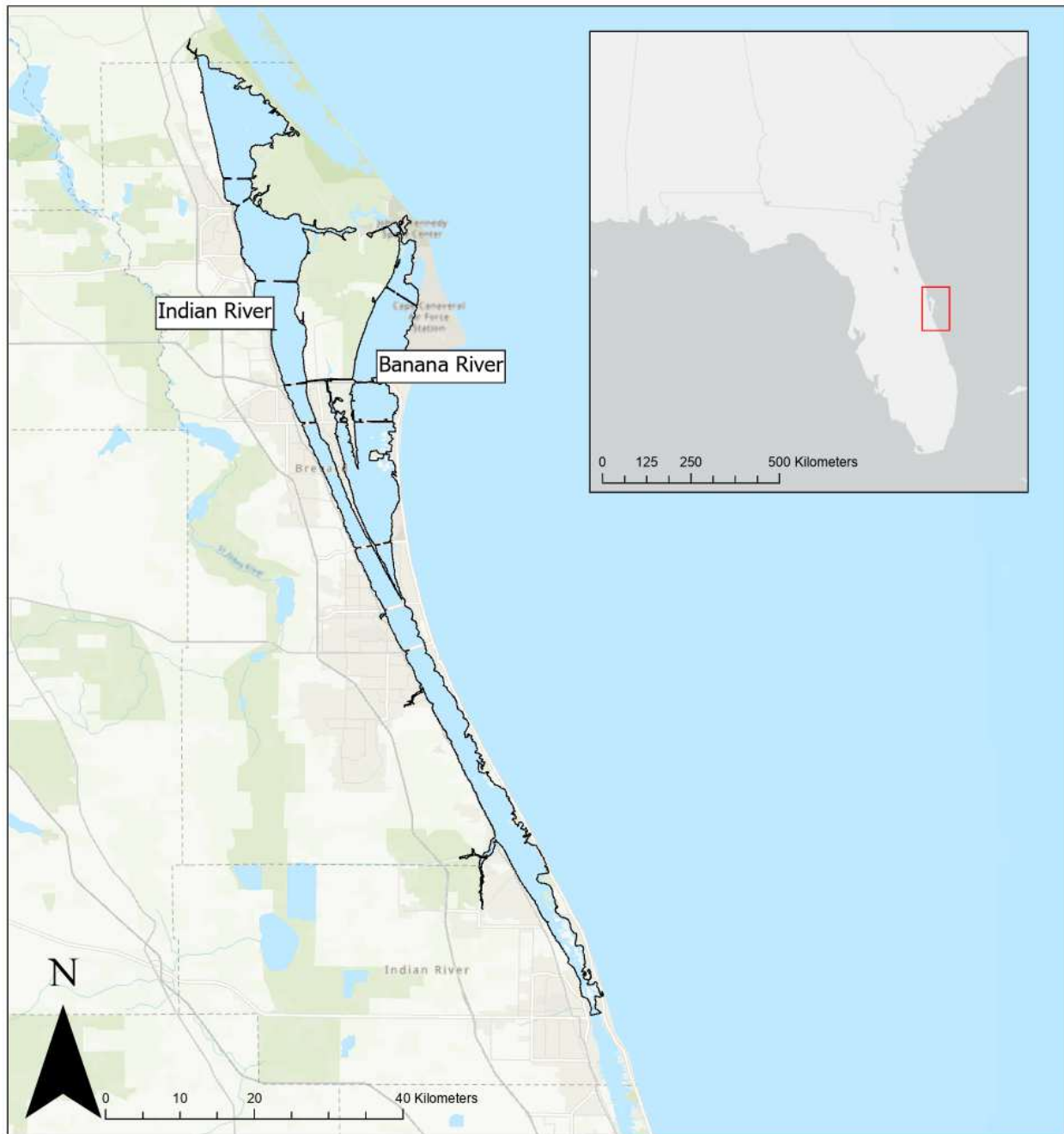


Figure 1. Regional context of the study area in the Indian River Lagoon along Florida’s east coast. The inset highlights the study area, extending from Banana River through northern Indian River, and shows its geographic extent within the broader southeastern United States.

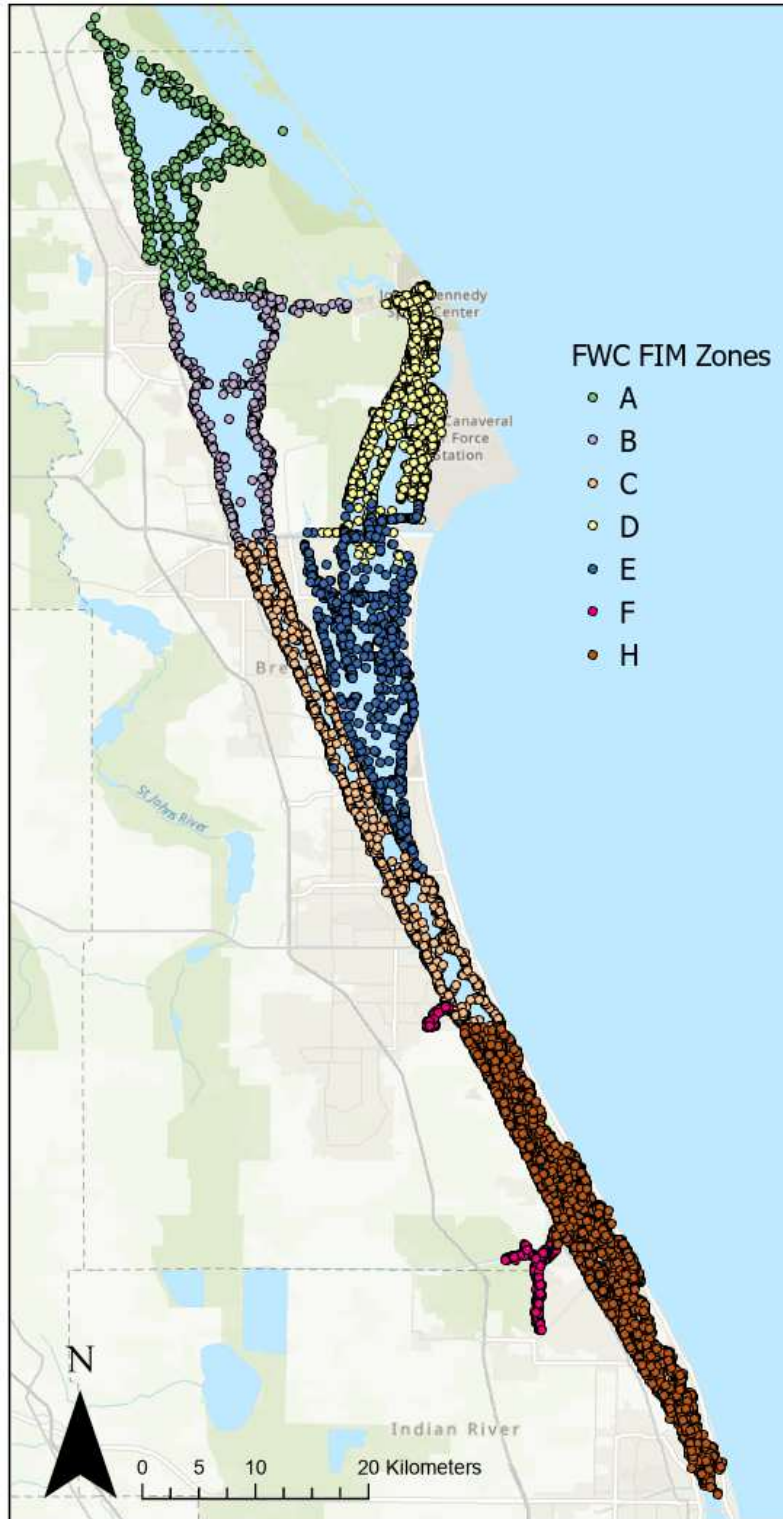
The watershed surrounding the IRL has also undergone substantial urbanization and land-use change over recent decades. Wastewater discharge, septic leachate, stormwater runoff, fertilizer application, and altered hydrology have contributed to elevated nitrogen and phosphorus concentrations, HAB events, and declining water clarity throughout portions of the lagoon (Barile, 2018; Freeman et al., 2019; FDEP, 2018). The 2011-2012 superbloom event, in particular, contributed to extensive seagrass mortality and

long-term reductions in seagrass cover throughout portions of the lagoon. These watershed influences have produced pronounced spatial and temporal variability in seagrass distribution across the lagoon, providing the environmental context for the present study.

Long-Term Ecological Datasets

To evaluate long-term relationships among blue crab populations, benthic habitat change, and environmental variability, we integrated fisheries-independent monitoring (FIM) data with seagrass monitoring datasets collected throughout the IRL. These complementary datasets provided information on blue crab demographic structure, seagrass dynamics, and environmental conditions across multiple regions of the lagoon over 28 years. Together, they allowed assessment of how changes in vegetated habitat distribution corresponded with shifts in blue crab abundance, body size, and spatial organization through time.

Blue crab demographic data were obtained from the Florida Fish and Wildlife Conservation Commission (FWC) Fisheries-Independent Monitoring (FIM) program, a long-term standardized fisheries survey designed to monitor estuarine and marine faunal communities throughout Florida. Blue crab observations were collected between 1996 and 2023 within the IRL using a combination of a 21.3m center-bag seine, an 183 m center-bag haul seine, and a 6.1 m otter trawl. Observations were obtained from FIM survey zones A-H (Figure 2). Variables extracted from the FIM database included the FIM variable NumAtSize, the number of blue crabs captured per standardized FIM sampling event, which was used as a measure of relative abundance (catch per unit effort; CPUE), carapace width (CW; mm), sex, geographic coordinates, sampling date, salinity, temperature, dissolved oxygen, pH, wind speed, and visually estimated bottom vegetation percent cover based on a visual estimate. Because multiple sampling gears were used by the FIM program, blue crab catches were standardized by gear-specific sampling effort following FWC FIM sampling protocols. Each gear was deployed using standardized procedures and sampled a defined area; blue crab CPUE was therefore calculated as the number of individuals captured divided by the corresponding area sampled, yielding a common relative-abundance metric of crabs m^{-2} . Standardized sampling areas were 140 m^2 for the 21.3-m bay seine, 68 m^2 for the 21.3-m river seine, 4,120 m^2 for the 183-m haul seine, and 518.8 m^2 for the 6.1-m otter trawl (Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 2019). Although standardization by sampled area accounts for differences in sampling effort among gears, potential differences in gear-specific catchability and size selectivity remain and should be considered when interpreting relative abundance patterns.



181

182 **Figure 2.** Sampling zones (A-H) used in the Florida Fish and Wildlife Conservation Commission
 183 (FWC) Fisheries-Independent Monitoring (FIM) program across the Indian River Lagoon from
 184 1996-2023. Each point represents a sampling site, and is color-coded by zone.

Seagrass data were obtained from the St. Johns River Water Management District (SJRWMD) long-term seagrass monitoring program, which has monitored seagrass communities throughout the Indian River Lagoon since 1994 (Figure 3). Occasional years in which individual monitoring transects were not surveyed were treated as missing observations and were not interpolated. Annual mean seagrass percent cover for each FIM zone was calculated using all available monitoring sites sampled during that year. Fixed transects are surveyed at least twice annually during summer and winter, corresponding to periods of maximum and minimum seagrass abundance, respectively, while a subset of transects is monitored monthly to capture seasonal variability. Surveys employ a standardized, non-destructive, quantitative transect-and-quadrat sampling protocol in which permanent transects extend approximately perpendicular to the shoreline, from the shoreline to the deep edge of the seagrass bed and are marked by permanently installed PVC stakes. At each sampling event, seagrass percent cover and associated benthic vegetation characteristics are quantified along each transect (SJRWMD, 2025).

For this study, summer seagrass observations were selected because they represent peak annual seagrass abundance and provide a consistent basis for evaluating interannual changes in seagrass distribution. Site-level seagrass percent cover was subsequently organized by FWC FIM zone and year for comparison with blue crab demographic data.

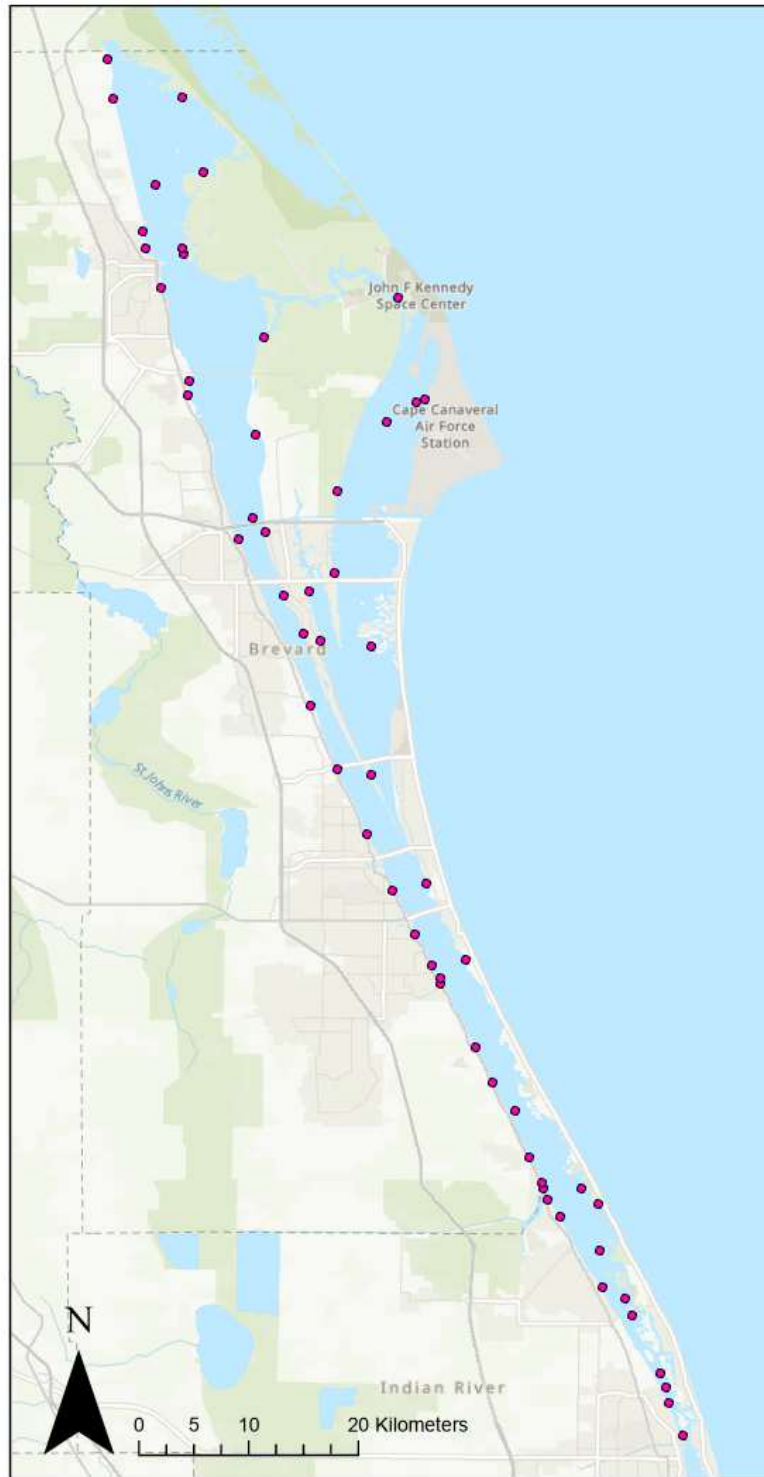


Figure 3. Fixed long-term seagrass monitoring stations within the Indian River Lagoon. Points represent sites sampled by the St. Johns River Water Management District (SJRWMD) for seagrass surveys from 1994-2024.

Both FWC and SJRWMD sampling locations were transformed into a common coordinate system (NAD 1983 StatePlane Florida East FIPS 0901) within ArcGIS Pro (Version 3.2; ESRI, Redlands, California, USA). Because the SJRWMD monitoring program employs fixed transects whereas the FWC FIM program uses a stratified-random sampling design, SJRWMD seagrass monitoring sites were assigned to their corresponding FIM survey zones. Seagrass percent cover was then subsequently summarized by FIM zone and year, allowing direct comparison with blue crab demographic data collected within the same spatial framework.

Spatial and Temporal Patterns of Blue Crab Demographic Structure

A series of spatial analyses was used to evaluate long-term spatial patterns in both seagrass beds and blue crab populations throughout the IRL. First, Kernel Interpolation with Barriers (KIB) was performed in ArcGIS Pro (Version 3.2; ESRI, Redlands, California, USA) to visualize spatial patterns in blue crab abundance and carapace width. KIB was chosen because the method incorporates physical barriers, such as water boundaries, that prevent interpolation across land masses and disconnected waterbodies, making it appropriate for elongated lagoonal estuaries characterized by restricted hydrologic connectivity. Interpolated surfaces were generated for three representative temporal periods: 1997-1999, representing conditions prior to widespread seagrass decline; 2007-2009, representing conditions immediately preceding the 2011-2012 superbloom; and 2015-2017, representing post-disturbance conditions following large-scale seagrass loss and habitat restructuring. These periods were selected to illustrate changes in blue crab spatial distribution before and after the major ecological transition within the IRL.

Getis-Ord Gi hotspot analyses were conducted separately for blue crab relative abundance (measured as catch per unit effort) and carapace width using spatially standardized FIM data pooled across the 1996–2023 study period. Local spatial relationships were defined using a K-nearest neighbors conceptualization (500 neighbors) with Euclidean distance and row standardization. The Getis-Ord Gi statistic was used to identify clusters of relatively high (hotspots) and low (coldspots) values based on local spatial autocorrelation. Statistical significance was evaluated using the False Discovery Rate (FDR) correction to account for multiple spatial comparisons (Getis & Ord, 1992; ESRI, 2024). Hotspot analyses were used to identify persistent regions of elevated or reduced demographic values throughout the lagoon.

Emerging Hotspot Analysis (EHA) was conducted using ArcGIS Pro space-time cube analyses to incorporate both spatial and temporal dimensions of blue crab distribution patterns. EHA identifies temporal trajectories of spatial clustering, including persistent, intensifying, diminishing, oscillating, and newly emerging hotspots and coldspots. These analyses were used to evaluate temporal changes in blue crab spatial organization throughout the study period.

Spatial and Temporal Patterns of Seagrass Habitat

Empirical Orthogonal Function (EOF) analysis and Principal Component Analysis (PCA) were used to evaluate dominant spatial and temporal patterns in seagrass cover throughout the IRL. Annual summer seagrass percent-cover data from individual SJRWMD monitoring sites were organized into a site $\times$ year matrix, with monitoring sites represented spatially and survey years represented temporally. Missing values (<8% of the dataset) were imputed using the annual mean across monitoring sites, and the matrix was mean centered by subtracting each site's long-term mean. EOF decomposition was then performed

using Singular Value Decomposition (SVD) to identify dominant spatial patterns of seagrass variability across the lagoon. Spatial loadings were associated with the geographic coordinates of individual SJRWMD monitoring sites, while the corresponding principal component scores represented temporal variation in each EOF mode. EOF1 represented the dominant mode of seagrass variability and its associated PC1 time series was used to evaluate temporal variability in benthic habitat structure throughout the lagoon.

Annual rainfall and ENSO datasets were used to examine associations between climatic variability and annual seagrass cover patterns. Annual rainfall data from Titusville, Florida, obtained from the Florida Climate Center, were calculated as the mean monthly precipitation for each calendar year (January-December) and used as a partial proxy for regional inflow variability affecting the northern and central IRL. ENSO variability was evaluated using Oceanic Niño Index (ONI) data obtained from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center. Relationships between PC1 (representing the dominant temporal pattern in seagrass cover) and annual rainfall and ONI values were evaluated using Spearman rank correlations due to non-normality and potential nonlinear relationships among variables. Correlations were evaluated across the full study period and separately for years through 2010 and after 2010 to examine whether climate-habitat associations differed following the onset superbloom events beginning in 2010 in the IRL.

Blue Crab Demographic and Habitat Association Analyses

Generalized Additive Models (GAMs) were used to evaluate nonlinear relationships between blue crab demographic metrics and environmental variables. Models were developed using the mgcv package in R (Version 4.4.1; R Core Team, 2024) with restricted maximum likelihood (REML) smoothing parameter estimation. FIM response variables included blue crab relative abundance (NumAtSize) and carapace width (CW; mm). FIM predictor environmental variables included salinity, temperature, dissolved oxygen, pH, wind speed, and BottomVegCover. These variables were recorded concurrently with each biological sampling event and characterize local environmental conditions at the time of collection. BottomVegCover was estimated visually in the field as the percent cover of submerged bottom vegetation present at each sampling location. BottomVegCover values recorded within the FWC FIM dataset were categorized into four vegetation cover classes: Low (0-25%), Medium (>25-50%), High (>50-75%), and Very High (>75%). While these visual estimates provide an effective measure of local habitat conditions for evaluating relationships between blue crab demographics and vegetation at individual sampling events, they are not intended to quantify long-term changes in seagrass distribution or abundance. Consequently, analyses of basin-scale habitat change utilized the SJRWMD seagrass monitoring program, which employs standardized permanent transects and quantitative sampling methods specifically designed to monitor temporal changes in seagrass percent cover throughout the IRL.

Nonparametric Kruskal-Wallis tests were used to evaluate differences in blue crab relative abundance and carapace width among vegetation cover classes due to non-normality of the response variables. Pairwise differences among vegetation cover classes were subsequently evaluated using Dunn's post hoc tests with Benjamini-Hochberg corrections for multiple comparisons.

Long-term habitat-demographic relationships were evaluated by correlating annual seagrass percent cover derived from SJRWMD monitoring data with annual mean blue crab abundance and carapace width

obtained from the FWC FIM dataset. Relationships were evaluated at lagoon-wide and zone-specific spatial scales. Analyses were conducted across the full temporal record as well as within pre- and post-2012 periods following the 2011-2012 superbloom. Spearman rank correlations were used to evaluate associations among seagrass cover, blue crab abundance, and carapace width due to non-normality and potential nonlinear relationships among variables.

Results

Long-Term Benthic Habitat Change

Lagoon-wide mean summer seagrass cover at surveyed transects exceeded 30% at the survey transects during periods of relatively stable benthic vegetation from 1996 to 2010 but declined to less than 5% following the system-wide seagrass die-off during 2017-2023 (Figure 4).

Results of the Empirical Orthogonal Function (EOF) analysis demonstrated that a strong basin-wide temporal signal dominated annual seagrass cover change within the IRL. EOF1 accounted for 64.8% of total variance in the site-by-year seagrass cover matrix, substantially exceeding the variance explained by subsequent modes (EOF2 = 5.8%, EOF3 = 4.1%, EOF4 = 3.6%, EOF5 = 2.9%) (Figure 4). Temporal patterns in EOF1 captured major shifts in lagoon-wide seagrass cover, with pronounced increases in the early 2000s and after 2011. Spatial loadings associated with EOF1 were coherent across nearly all monitoring locations, indicating that a similar pattern occurred at a basin-wide scale rather than being restricted to individual regions. Strong negative loadings were concentrated within the northern and central lagoon regions. PC1 was negatively correlated with seagrass percent cover, with lower PC1 values corresponding to periods of relatively high seagrass abundance and higher PC1 values corresponding to periods of reduced seagrass cover.

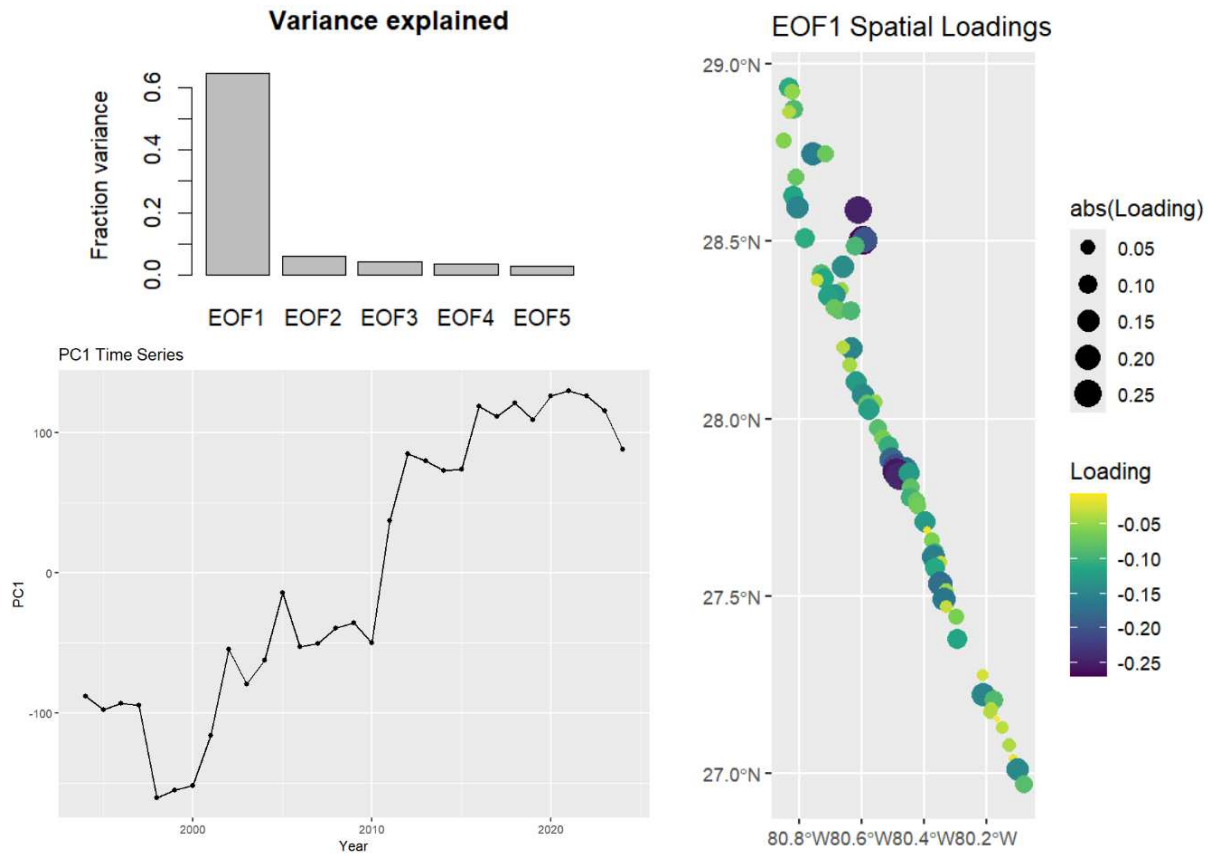


Figure 4. Variance explained by the first five empirical orthogonal functions (EOF1-EOF5) for seagrass time series across the IRL. EOF1 accounted for 64.8% of total variance, representing the dominant basin-wide temporal signal. The spatial loading map (right) illustrates broadly coherent negative loadings throughout the lagoon, reflecting a system-wide transition away from seagrass dominance. The associated PC1 time series (bottom left) captures long-term variability in seagrass cover, including the post 2011 seagrass decline.

Relationships Among Seagrass PC1, Rainfall, and ONI

PC1 scores, representing the dominant temporal pattern in seagrass percent cover, were compared with annual rainfall and Oceanic Niño Index (ONI) values. Comparisons among PC1, annual rainfall, and the Oceanic Niño Index (ONI) showed that PC1 values remained relatively low during 2002-2009, when lagoon-wide seagrass cover was comparatively stable, and increased markedly following the 2011-2012 seagrass die-off, when seagrass cover declined throughout the lagoon (Figure 5). PC1 represented the dominant mode of temporal variability identified by the EOF analysis, with EOF1 explaining 64.8% of the total variance in seagrass cover.

Across the full study period, PC1 exhibited little monotonic association with either annual mean ONI (Spearman's $\rho = 0.044$, $p = 0.815$) or annual rainfall ($\rho = 0.061$, $p = 0.747$). When evaluated separately around the onset of widespread seagrass decline, the relationships remained weak. Through 2010, PC1

exhibited a weak positive association with ONI ($\rho = 0.201$, $p = 0.439$) and little association with annual rainfall ($\rho = 0.050$, $p = 0.854$). After 2010, PC1 exhibited a weak negative association with ONI ($\rho = -0.138$, $p = 0.637$) and little association with annual rainfall ($\rho = 0.004$, $p = 0.988$). Despite these weak monotonic relationships, visual comparison of the time series indicated periods of temporal correspondence between PC1 and alternating El Niño and La Niña phases, particularly before 2010 (Figure 5). PC1 and annual rainfall similarly exhibited periods of visual temporal correspondence before 2010 (Figure 6).

Annual rainfall variability also corresponded with EOF-derived habitat restructuring indices. PC1 values were positively associated with annual rainfall during portions of the study period prior to the superbloom event (Figure 6). Wetter years generally corresponded with elevated PC1 values, whereas drought periods aligned with comparatively lower PC1 phases. Some of the largest increases in PC1 occurred following dry periods within the Titusville rainfall record. PC1 variability corresponded with annual rainfall variability and ENSO oscillations throughout the study period. Because rainfall from a single Titusville station represents only part of the study system, it is interpreted as a partial regional proxy rather than a lagoon-wide measure of hydrologic forcing.

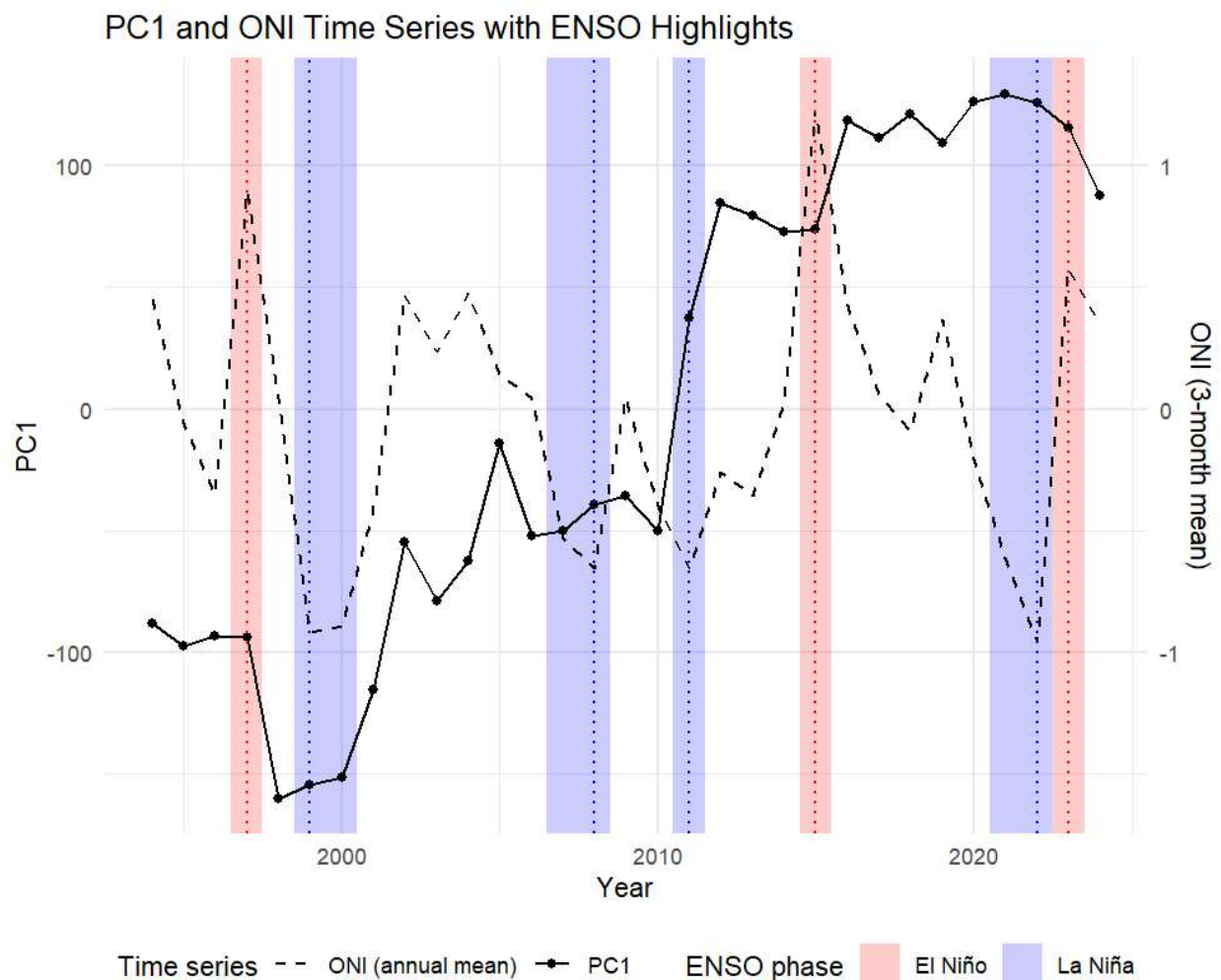


Figure 5. Time-series comparison of the first principal component (PC1; black solid line) and the Oceanic Niño Index (ONI; black dotted line) during 1996–2023, with shaded regions denoting El Niño (red) and La Niña (blue) events. Negative PC1 phases correspond with periods of greater lagoon-wide seagrass abundance, whereas positive PC1 phases align with intervals of reduced seagrass cover.

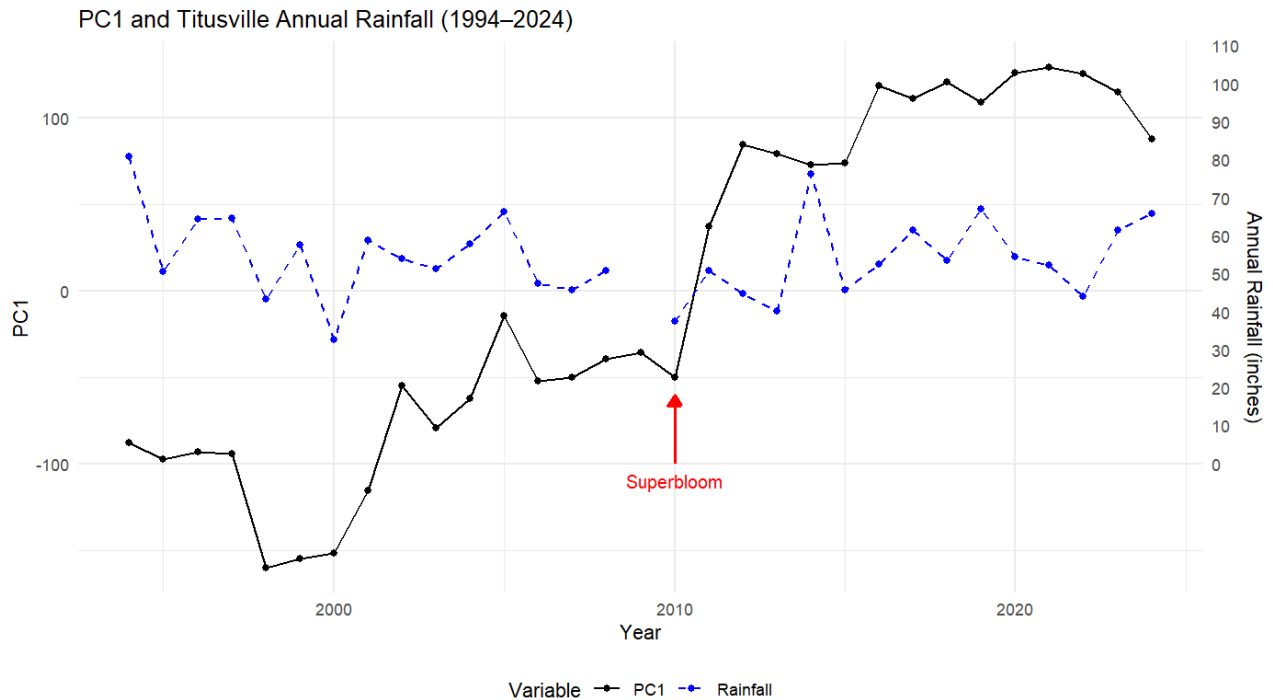


Figure 6. Time-series comparison of the first principal component (PC1) from the EOF analysis and average annual rainfall at Titusville, Florida during 1994–2024. The PC1 time series (black line, left axis) reflects lagoon-wide variability in seagrass cover, while annual precipitation (blue dashed line, right axis) is used as a partial regional proxy for hydrologic variability affecting the northern Indian River Lagoon.

Spatial Reorganization of Blue Crab Demographic Structure

Spatial analyses revealed changes in blue crab abundance and size structure throughout the IRL during the study period. Kernel Interpolation with Barriers (KIB) (Figure 7), Getis-Ord Gi* hotspot analyses (Figure 8), and Emerging Hotspot Analyses (Figure 9) were consistent with increasing spatial heterogeneity in blue crab abundance and carapace width following widespread benthic habitat restructuring associated with post-2011 seagrass decline.

Kernel interpolation analyses identified persistent spatial contrasts between northern and southern lagoon regions throughout the study period (Figure 7). During earlier periods characterized by relatively greater seagrass continuity, blue crab abundance and carapace width exhibited broader spatial distributions across multiple lagoon regions. Following the 2011–2012 superbloom and associated seagrass collapse, higher

interpolated values became increasingly concentrated within portions of the southern lagoon, while northern regions exhibited lower abundance and body size values. The spatial contraction of high-density regions was particularly evident within the northern IRL and Banana River.

Getis-Ord Gi* hotspot analyses identified strong spatial clustering of demographic values throughout the lagoon (Figure 8). Persistent coldspots in blue crab relative abundance and carapace width occurred primarily within the northern portion of the study area, whereas hotspots were concentrated within southern portions of the study area near the Fort Pierce and Vero Beach regions. These hotspot patterns remained relatively consistent across multiple temporal periods.

Emerging Hotspot Analysis (EHA) showed that blue crab spatial clustering within the IRL varied through time (Figure 9). Persistent, intensifying, and diminishing hotspot patterns were observed across lagoon regions. Several northern lagoon regions transitioned toward persistent or emerging coldspot classifications during later portions of the study period, whereas portions of the southern lagoon maintained stable or intensifying hotspot conditions. Collectively, these spatial analyses indicate that clustering became increasingly concentrated within southern lagoon regions during the period of widespread benthic habitat restructuring.

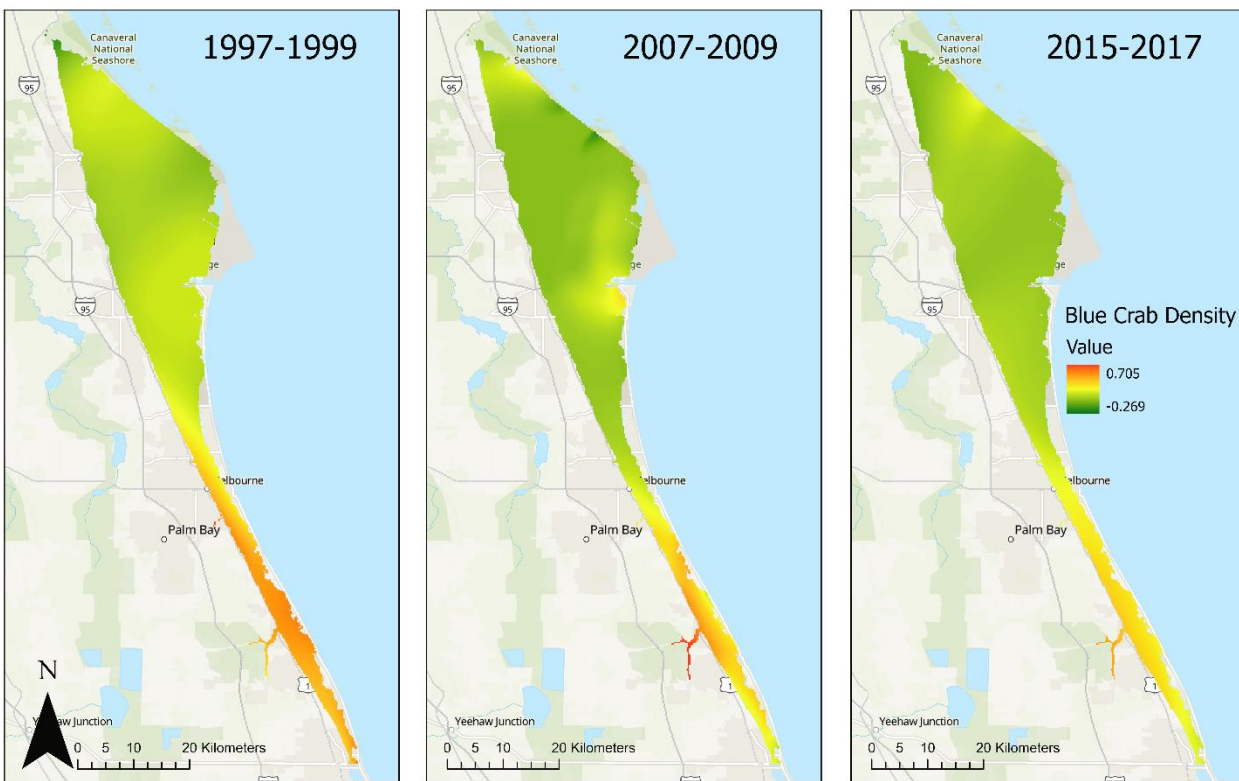
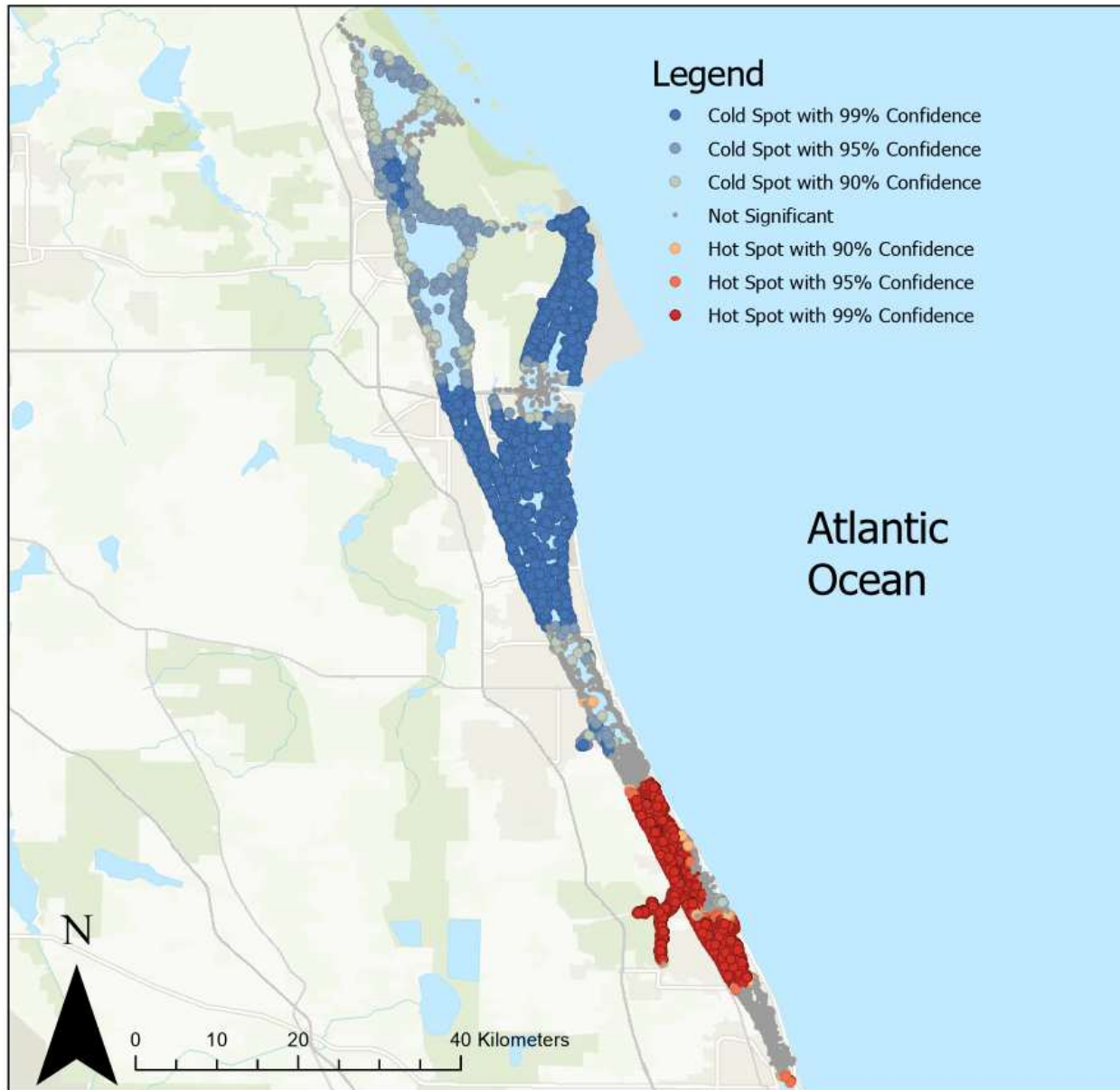


Figure 7. Kernel Interpolation with Barriers (KIB) maps showing interpolated blue crab density across the IRL for three representative time periods: 1997-1999, 2007-2009, and 2015-2017. The interpolation was constrained by lagoon boundaries, barrier islands, and inlets to minimize edge effects. Blue crab density declined over time, particularly in the Banana River and northern Indian River.



381

382 **Figure 8.** Getis-Ord G_i^* hotspot analysis of blue crab density during 1996-2023, showing
 383 clusters of high (hotspots) and low (coldspots) crab abundance within the study area of the
 384 Indian River Lagoon. Hotspots (red tones) occurred primarily within the southern portion of the
 385 study area, while coldspots (blue tones) occurred primarily in the northern portion of the study
 386 area.

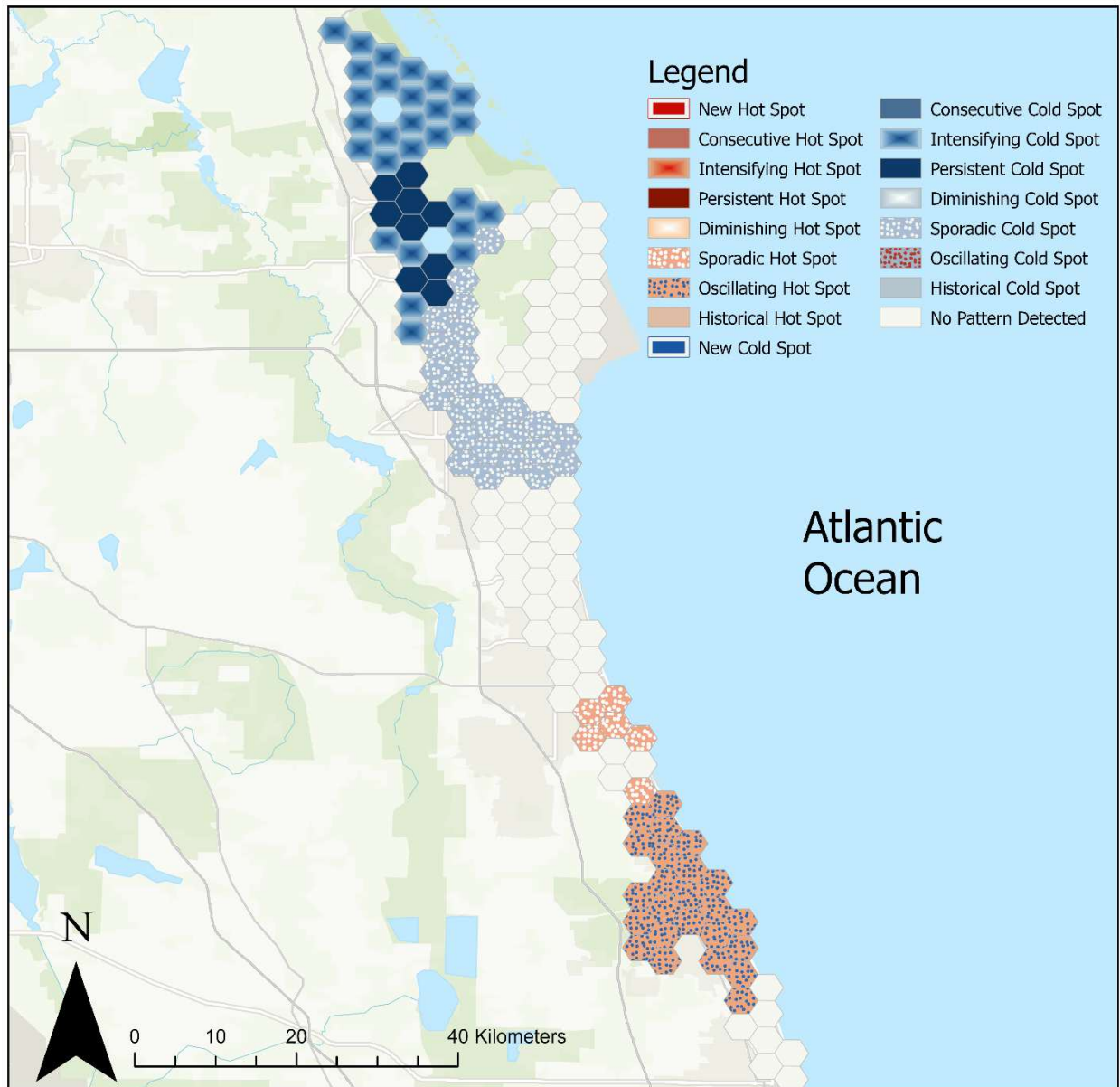


Figure 9. Emerging Hot Spot Analysis (EHA) of blue crab density (1996-2023) showing temporal patterns of hotspots and coldspots of crab abundance within the Indian River Lagoon. Persistent and intensifying hotspots (red tones) occurred in southern zones, whereas coldspots (blue tones) were concentrated in the northern lagoon, reflecting long-term spatial reorganization following seagrass decline and macroalgal expansion.

Environmental Drivers of Blue Crab Demographic Structure

Generalized Additive Models (GAMs) identified nonlinear relationships between blue crab demographic metrics and environmental gradients throughout the IRL (Figure 10, Figure 11). Environmental predictors

explained relatively little variation in blue crab abundance, whereas carapace width exhibited stronger relationships with environmental variables and vegetated habitat structure.

The abundance GAM explained 3.04% of the total deviance, indicating that the measured environmental variables collectively accounted for little variation in blue crab relative abundance (Table 1). Among the single-predictor models, pH explained the greatest proportion of deviance (2.40%; edf = 7.08, $F = 31.39$, $p = 1.09 \times 10^{-49}$), followed by dissolved oxygen (0.95%; edf = 3.90, $F = 20.48$, $p = 7.01 \times 10^{-20}$), bottom vegetation cover (0.84%; edf = 2.35, $F = 22.66$, $p = 7.17 \times 10^{-14}$), salinity (0.42%; edf = 4.03, $F = 8.67$, $p = 3.36 \times 10^{-8}$), wind speed (0.33%; edf = 1.91, $F = 14.17$, $p = 8.19 \times 10^{-8}$), and temperature (0.06%; edf = 2.72, $F = 1.39$, $p = 0.239$). The full model explained 3.04% of the deviance ($n = 7,520$), indicating that the measured environmental predictors collectively had limited explanatory power for blue crab relative abundance at the lagoon-wide scale.

The carapace width GAM explained 34.20% of the total deviance, indicating that the measured environmental variables collectively accounted for substantial variation in blue crab body size (Table 2). Among the single-predictor GAMs, bottom vegetation cover explained the greatest proportion of deviance (24.71%; edf = 8.71, $F = 276.31$, $p = 2.88 \times 10^{-457}$), followed by salinity (11.57%; edf = 8.55, $F = 179.05$, $p = 1.15 \times 10^{-318}$) and pH (11.22%; edf = 5.65, $F = 219.95$, $p = 1.49 \times 10^{-299}$). Temperature explained 4.23% of the deviance (edf = 7.55, $F = 63.11$, $p = 1.79 \times 10^{-107}$), followed by dissolved oxygen (2.12%; edf = 6.84, $F = 31.99$, $p = 1.05 \times 10^{-49}$) and wind speed (1.38%; edf = 7.87, $F = 18.61$, $p = 2.03 \times 10^{-29}$). The full model explained 34.20% of the deviance ($n = 7,520$), indicating that the measured environmental variables collectively accounted for substantial variation in blue crab carapace width, with bottom vegetation cover explaining the greatest proportion of deviance when considered individually.

GAM smooths (outliers removed): NumAtSize vs environmental predictors

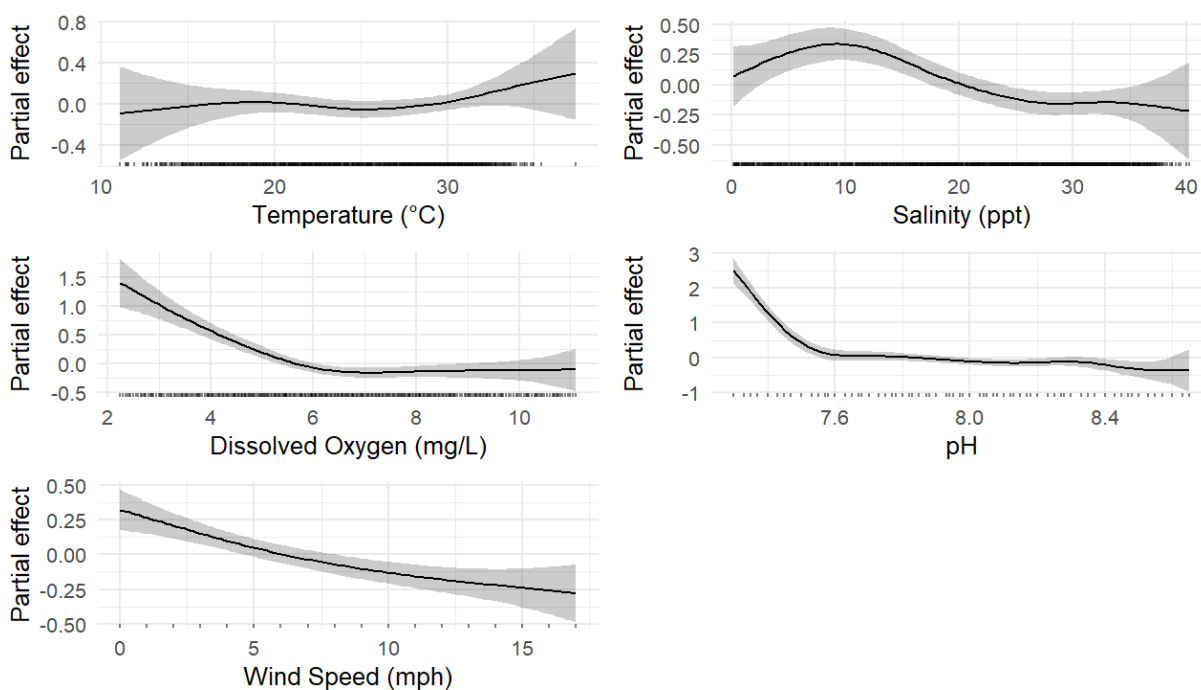
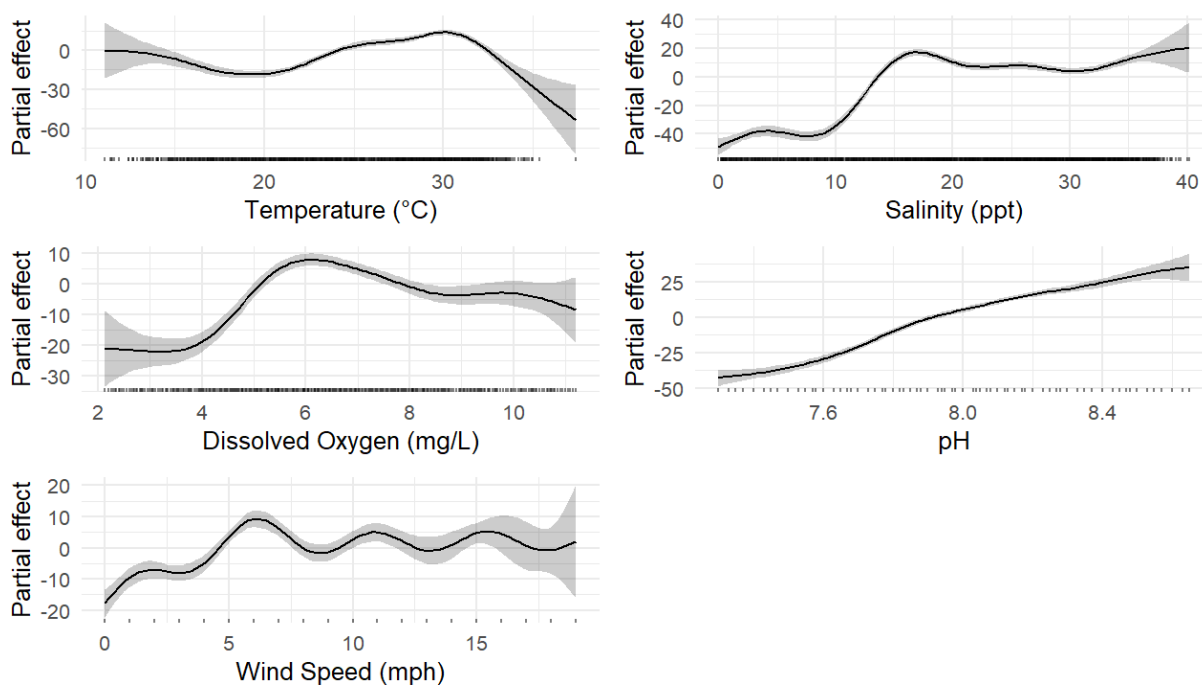


Figure 10. Partial effect smooths from Generalized Additive Models (GAMs) showing the nonlinear relationships between blue crab abundance (NumAtSize) and environmental predictors (temperature, salinity, dissolved oxygen, pH, and wind speed. Solid lines represent estimated smooth functions with 95% confidence intervals (gray shading). Patterns indicate nonlinear and threshold responses across environmental gradients.

Table 1. Summary of GAM smooth terms for blue crab abundance (NumAtSize) vs. environmental predictors. Reported statistics include estimated degrees of freedom (edf), F-value, p-value, deviance explained, and sample size.

Predictor	edf	Ref. df	F-value	p-value	Deviance explained (%)	N
Temperature	2.72	3.43	1.39	2.39e-1	0.06	10,986
Salinity	4.03	4.99	8.67	3.36e-8	0.42	10,995
Dissolved oxygen	3.90	4.85	20.48	7.01e-20	0.95	10,703
pH	7.08	8.10	31.39	1.09e-49	2.40	10,614
Wind speed	1.91	2.40	14.17	8.19e-8	0.33	10,456
Bottom vegetation cover	2.35	2.82	22.66	7.17e-14	0.84	7,603
Full model	—	—	—	—	3.04	7,520

GAM smooths (outliers removed): CW vs environmental predictors



429

430 **Figure 11.** Partial effect smooths from Generalized Additive Models (GAMs) showing the
 431 nonlinear relationships between blue crab carapace width (CW) and environmental predictors
 432 (temperature, salinity, dissolved oxygen, pH, and wind speed). Solid lines represent estimated
 433 smooth functions with 95% confidence intervals (gray shading). Patterns indicate nonlinear and
 434 threshold responses across environmental gradients.

435 **Table 2.** Summary of GAM smooth terms for blue crab carapace width (CW) vs. environmental
 436 predictors. Reported statistics include estimated degrees of freedom (edf), F-value, p-value,
 437 deviance explained, and sample size.

Predictor	edf	Ref. df	F- value	p-value	Deviance explained (%)	N
Temperature	7.55	8.47	63.11	1.79e-107	4.23	12,294
Salinity	8.55	8.94	179.05	1.15e-318	11.57	12,303
Dissolved oxygen	6.84	7.92	31.99	1.05e-49	2.12	12,011
pH	5.65	6.78	219.95	1.49e-299	11.22	11,857
Wind speed	7.87	8.44	18.61	2.03e-29	1.38	11,886
Bottom vegetation cover	8.71	8.97	276.31	2.88e-457	24.71	7,603
Full model	—	—	—	—	34.20	7,520

438 *Vegetation Structure and Blue Crab Demographics*

439 Blue crab relative abundance varied among BottomVegCover categories (Kruskal-Wallis $\chi^2 = 119.54$, df
 440 = 3, $p = 2.2 \times 10^{-16}$) (Table 3). Mean relative abundance generally increased with vegetation cover, with
 441 the highest values occurring in Very High vegetation habitats (>75% BottomVegCover) and the lowest
 442 values occurring in Low vegetation habitats (0–25% BottomVegCover). Dunn's post hoc comparisons
 443 provided strong evidence of differences between Low bottom vegetation habitats and the Medium
 444 (adjusted $p = 7.66 \times 10^{-11}$), High (adjusted $p = 1.69 \times 10^{-10}$), and Very High (adjusted $p = 1.39 \times 10^{-16}$)
 445 vegetation classes. Comparisons of Very High vegetation habitats with Medium (adjusted $p = 0.016$) and
 446 High (adjusted $p = 0.020$) vegetation habitats also indicated differences between these classes, whereas
 447 High and Medium vegetation habitats exhibited little evidence of a difference (adjusted $p = 0.908$).

448 Carapace width varied among vegetation cover categories (Kruskal-Wallis $\chi^2 = 2367.6$, df = 3, $p = 2.2 \times$
 449 10^{-16}) (Table 4). Mean carapace width increased progressively with vegetation cover, with the smallest
 450 individuals occurring in Low vegetation habitats and the Medium (adjusted $p = 6.07 \times 10^{-32}$), High
 451 (adjusted $p = 5.99 \times 10^{-31}$), and Very High (adjusted $p = 5.23 \times 10^{-32}$) vegetation classes. Dunn's post hoc
 452 comparisons provided strong evidence of differences between Low vegetation habitats and each of the
 453 other vegetation classes. Comparisons of Very High vegetation habitats with both Medium (adjusted $p =$
 454 3.21×10^{-17}) and High (1.04×10^{-17}) vegetation habitats also indicated differences in carapace width. In
 455 contrast, carapace widths were similar between High and Medium vegetation categories (adjusted $p =$
 456 0.888). Collectively, these results indicate that habitats with greater vegetation density supported both
 457 higher abundance and larger body sizes throughout the lagoon.

458 **Table 3.** Dunn's post hoc pairwise comparisons of blue crab abundance (NumAtSize) among
 459 bottom vegetation cover categories following a Kruskal-Wallis test. Z-statistics and Benjamini–
 460 Hochberg adjusted p-values are shown for each comparison.

Comparison	Z statistic	Adjusted p value
High - Low	-6.49	1.69e-10
High - Medium	0.12	9.08e-01
Low - Medium	6.67	7.66e-11
High - VeryHigh	-2.40	1.99e-02
Low - VeryHigh	8.48	1.39e-16
Medium - VeryHigh	-2.56	1.59e-02

461 **Table 4.** Dunn's post hoc pairwise comparisons of blue crab carapace width (CW) among
 462 bottom vegetation cover categories following a Kruskal-Wallis test. Z-statistics and Benjamini–
 463 Hochberg adjusted p-values are shown for each comparison.

Comparison	Z statistic	Adjusted p value
High - Low	11.63	5.99e-31
High - Medium	-0.14	8.88e-01
Low - Medium	-11.86	6.07e-32
High - VeryHigh	-8.62	1.04e-17
Low - VeryHigh	-42.76	5.23e-32

Medium - VeryHigh	-8.46	3.27e-17
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Long-Term Relationships Between Seagrass Cover and Blue Crab Demographic Metrics

Long-term comparisons among seagrass cover and blue crab demographic metrics showed temporal covariation between benthic habitat structure and blue crab populations throughout the IRL. Relationships among annual seagrass percent cover, blue crab relative abundance, and carapace width varied substantially during the study period, with pronounced changes occurring following the 2011–2012 superbloom and associated seagrass collapse.

Annual mean blue crab relative abundance generally declined alongside reductions in lagoon-wide seagrass cover throughout the study period. Periods characterized by relatively high seagrass cover during the late 1990s and early 2000s corresponded with comparatively elevated relative abundance throughout the lagoon, whereas years following widespread seagrass decline exhibited greater variability and reduced relative abundance across several lagoon regions. Although annual blue crab relative abundance exhibited only a weak overall temporal decline (-0.0053 CPUE yr^{-1} ; $R^2 = 0.04$), summer seagrass cover declined consistently throughout the study period (-1.097% yr^{-1} ; $R^2 = 0.883$), reflecting substantial long-term loss of structured benthic habitat.

Mean carapace width also generally declined during periods characterized by reduced benthic vegetation throughout the study period (Figure 12). Before the superbloom event in the early 2010s, periods of relatively continuous seagrass cover were associated with larger mean body sizes throughout much of the lagoon. Following large-scale habitat restructuring, carapace width became increasingly variable across regions, with several northern lagoon areas exhibiting persistent reductions in mean body size. Across the full study period, mean carapace width declined by 1.024 mm yr^{-1} ($R^2 = 0.333$), indicating a gradual reduction in body size through time.

Zone-level comparisons further demonstrated considerable spatial heterogeneity in habitat demographic relationships throughout the lagoon. Northern lagoon regions experiencing the greatest losses of seagrass generally exhibited larger declines in blue crab relative abundance and carapace width than portions of the southern IRL, where vegetated habitats remained comparatively more persistent. These regional differences were evident in the zone-specific time series, which showed steeper declines in seagrass cover and more pronounced changes in blue crab demographic metrics in northern FIM zones than in southern portions of the lagoon.

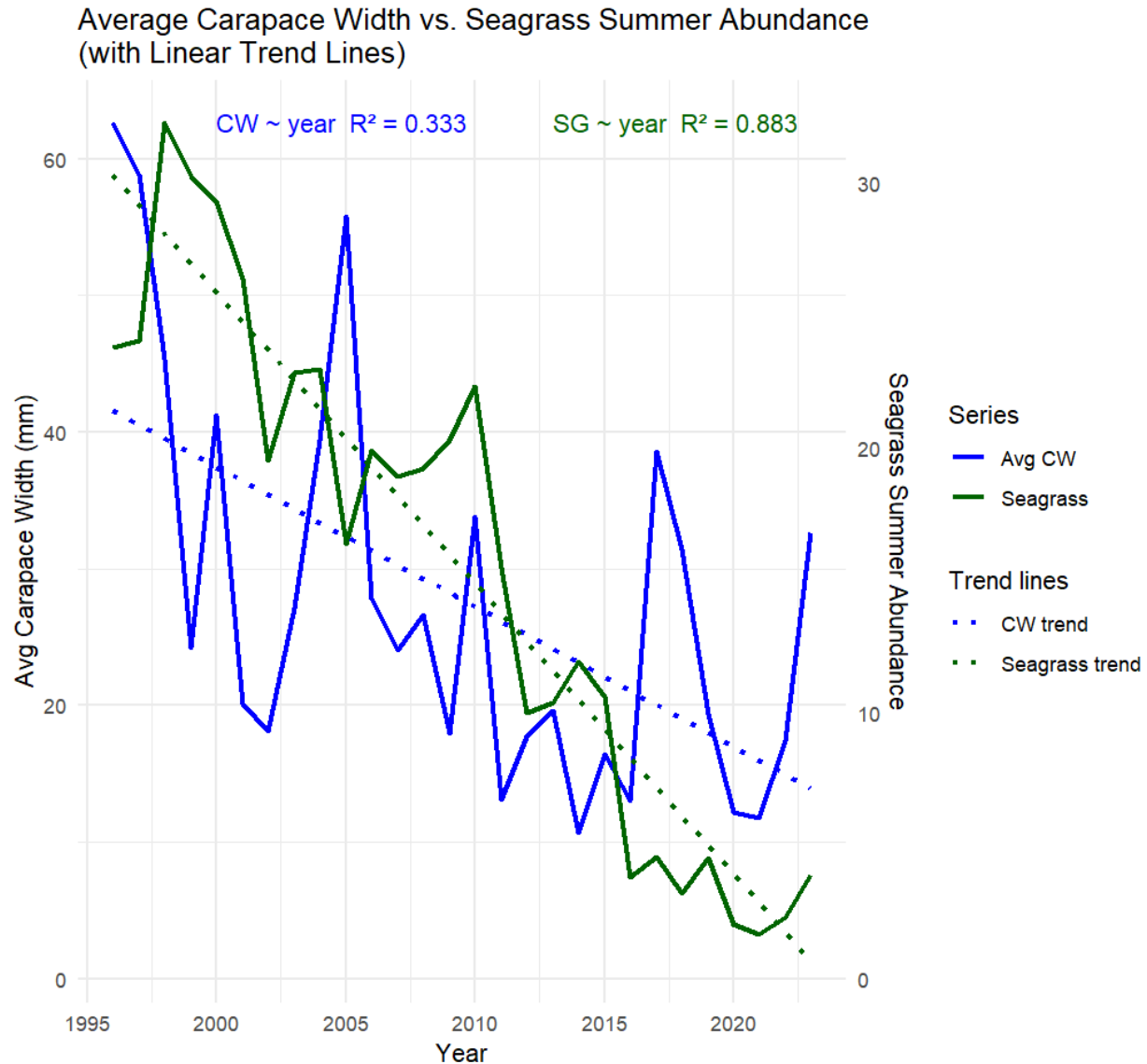


Figure 12. Long-term trends in average blue crab carapace width (CW; blue line, left axis) from the FIM dataset and summer seagrass percent cover (green line, right axis) from the SJRWMD long-term seagrass monitoring program across the Indian River Lagoon, 1996-2023. Dotted lines represent descriptive linear trend fits for each time series.

Discussion

Habitat Restructuring and Spatial Reorganization of Blue Crab Populations

This study demonstrates that long-term habitat change within the Indian River Lagoon (IRL) corresponded with substantial reorganization of blue crab populations across the estuarine landscape (Hovel & Lipcius 2001, 2002; Sheaves et al. 2009). The strongest evidence for basin-scale habitat change emerged from the EOF analysis, in which EOF1 explained 64.8% of total variance in seagrass cover and

the first five EOF modes explained 81.3% of total variance. These results indicate coherent temporal variation across much of the lagoon rather than through isolated local changes, consistent with the lagoon-wide habitat restructuring documented following widespread seagrass decline (Morris et al. 2022; Brewton & Lapointe 2023). The temporal trajectory of EOF1 further shows that the most pronounced shifts in habitat structure occurred during periods of major seagrass decline, particularly after the 2011-2012 superbloom event.

Spatial analyses indicate that blue crab distributions changed during the period of habitat restructuring rather than declining uniformly throughout the lagoon. Kernel interpolation and hotspot analyses revealed persistent northern coldspots and southern hotspots in both abundance and carapace width following widespread seagrass loss. Emerging Hotspot Analysis further demonstrated that these patterns remained dynamic through time, with some regions transitioning toward persistent coldspot conditions while others maintained stable or intensifying hotspots. Collectively, these findings suggest that habitat degradation was associated with reorganization of blue crab populations and that potential nursery function may have become concentrated within regions that retained relatively persistent, vegetated habitat (Beck et al. 2001; Hovel & Lipcius 2001, 2002; Thrush et al. 2008; Sheaves et al. 2009; Woodland et al. 2019).

Previous studies have demonstrated that habitat restructuring influences blue crab survival and distribution at relatively small spatial scales. In experimental seagrass landscapes, Hovel and Lipcius (2001) found that blue crab survival depended jointly on seagrass patch size and shoot density, demonstrating that habitat complexity and landscape structure interact to influence predation risk. Expanding on this work, Hovel and Lipcius (2002) showed that patch isolation, structural complexity, seasonal changes in seagrass configuration, and crab density collectively influenced survival and abundance, emphasizing that habitat restructuring cannot be considered independently of habitat connectivity and temporal variation. Our study extends these findings from individual habitat patches to an entire estuarine ecosystem by demonstrating that long-term habitat restructuring corresponded with basin-scale reorganization of blue crab relative abundance and body size. Rather than examining how habitat restructuring influences survival within individual seagrass patches, our analyses indicate that widespread seagrass loss and habitat restructuring corresponded with changes in the spatial distribution of blue crabs across the Indian River Lagoon over nearly three decades. However, because movement, dispersal, and exchange among habitat patches were not measured, this study does not directly quantify functional connectivity but instead infers changes in nursery habitat organization from long-term spatial patterns in habitat and blue crab distributions.

Climatic and Watershed Associations with Habitat Change

EOF-derived habitat indices exhibited periods of visual correspondence with annual rainfall variability and ENSO oscillations. However, these patterns did not result in significant monotonic relationships between PC1 and either annual rainfall or ONI across the full study period or when evaluated separately through and after 2010. Positive ONI phases sometimes coincided with declines in PC1, whereas negative ONI phases sometimes coincided with elevated PC1 values. These patterns therefore suggest that climatic variability only explain a part of long-term seagrass variability across the IRL.

Although the correlations observed in this study do not demonstrate a direct relationship between annual climatic variability and PC1, watershed-estuary coupling provides a plausible mechanism through which

climatic variability can influence benthic habitat conditions in the IRL. Rainfall influences freshwater inflow, nutrient transport, turbidity, and residence time throughout the IRL. Under eutrophic conditions, increased nutrient loading and reduced water clarity can suppress seagrass persistence while promoting phytoplankton blooms and opportunistic primary producers. The widespread seagrass decline associated with the 2011-2012 superbloom represents one of the clearest examples of this process within the lagoon.

These findings are consistent with previous studies identifying nutrient enrichment as a primary driver of ecological degradation in the Indian River Lagoon. Barile (2018) demonstrated that nitrogen enrichment derived from human wastewater sources was widespread throughout the lagoon, with elevated $\delta^{15}\text{N}$ values indicating increasing nitrogen loading during wetter years, suggesting that rainfall-driven watershed runoff can enhance nutrient delivery to the estuary. Similarly, Freeman et al. (2019) described how urbanization and watershed development increase sediment and nutrient runoff, promoting harmful algal blooms, reduced water clarity, and ultimately seagrass decline through light limitation. These regional observations are consistent with broader conceptual and global studies showing that nutrient enrichment drives shifts from seagrass-dominated communities to macroalgal and phytoplankton-dominated systems (Duarte et al., 1995), contributing to widespread seagrass loss in coastal ecosystems worldwide (Waycott et al., 2009). Previous studies therefore provide a mechanistic basis for the periods of temporal correspondence observed in this study between climatic variability and seagrass dynamics. However, the weak correlations between PC1 and both annual rainfall and ONI indicate that these broad annual climate metrics alone do not consistently account for long-term seagrass variability. Climatic and hydrologic processes may instead interact with nutrient enrichment, water clarity, residence time, and other local or lagged processes that were not directly evaluated here.

The weak relationships between PC1 and the climatic variables should also be interpreted in the context of the temporal and spatial resolution of the datasets. Annual rainfall from a single Titusville station provides only a partial proxy for hydrologic conditions across the approximately 250-km lagoon, and annual averaging of both rainfall and ONI may obscure seasonal, event-scale, or lagged relationships with seagrass dynamics.

Blue Crab Demographic Responses to Habitat Change

Although habitat restructuring corresponded with substantial changes in blue crab spatial organization, demographic responses differed between abundance and body size. Environmental variables explained only 3.04% of deviance in abundance but explained 34.20% of deviance in carapace width, suggesting that body size may be more closely associated with measured habitat and environmental conditions than abundance alone. This distinction is important because abundance can be influenced by numerous factors, including recruitment variability, movement, gear effects, and sampling conditions, whereas size structure may provide a complementary indication of habitat quality.

Vegetation density emerged as one of the most consistent correlators of blue crab demographic structure. Abundance differed among BottomVegCover categories ($\chi^2 = 119.54$, $df = 3$, $p = 2.2 \times 10^{-16}$), with the greatest abundance in Very High vegetation habitats and the lowest abundance in Low vegetation habitats. Similarly, carapace width differed strongly among vegetation classes ($\chi^2 = 2367.6$, $df = 3$, $p = 2.2 \times 10^{-16}$), with the largest crabs occurring in habitats characterized by the greatest vegetation cover. These relationships remained evident despite widespread habitat change throughout the lagoon.

The strong association between vegetation cover and demographic structure is consistent with previous studies demonstrating the importance of vegetated habitats for blue crab refuge, survival, and recruitment (Perkins-Visser et al., 1996; Hovel & Lipcius, 2001; Hovel & Fonseca, 2005). Vegetated habitats provide protection from predation while also supporting prey availability and foraging opportunities. The persistence of these relationships throughout the study period suggests that habitat quality remained closely linked to vegetation density even as the broader habitat mosaic was reorganized.

Long-term comparisons between seagrass abundance and blue crab demographics further support this interpretation. Descriptive patterns suggested stronger positive relationships were generally observed between seagrass cover and both abundance and carapace width before the 2011-2012 seagrass decline. Following habitat restructuring, these relationships appeared weaker and more spatially variable, suggesting that blue crab distributions became less closely aligned with historical seagrass distribution patterns as habitat organization changed across the lagoon.

Study Limitations

This observational analysis does not establish that seagrass loss caused blue crab redistribution. The fisheries and seagrass programs used different sampling designs and spatial supports, and the blue crab record combined multiple gear types. Habitat connectivity was inferred from vegetation continuity and spatial demographic patterns rather than measured through movement, dispersal, or exchange among patches. In addition, rainfall from a single Titusville station is only a partial proxy for hydrologic forcing across the lagoon. These limitations should be considered when interpreting causal, climate-driver, and nursery-refugium claims.

Management and Habitat-Continuity Implications

The results of this study suggest that habitat continuity and spatial organization may be as important as total habitat area when evaluating nursery habitat function within estuarine ecosystems (Beck et al., 2001; Thrush et al., 2013). Although seagrass abundance declined substantially throughout the IRL, blue crab demographic patterns did not change uniformly across the lagoon. Instead, hotspots became increasingly concentrated within regions that maintained relatively persistent, vegetated habitat, indicating that the distribution and continuity of vegetated habitat may influence demographic organization at ecosystem scales. This interpretation is consistent with studies demonstrating that blue crab survival and abundance are influenced not only by habitat amount but also by habitat restructuring, patch isolation, and structural complexity (Hovel & Lipcius, 2001, 2002; Mizerek et al., 2011; Hovel & Fonseca, 2005).

These findings have important implications for restoration and management. Traditional restoration efforts often emphasize recovery of total seagrass acreage, but the present results suggest that the spatial continuity and distribution of vegetated habitat should also be considered when evaluating nursery habitat function (Beck et al., 2001; Morris et al., 2022). Management strategies may therefore benefit from considering the spatial distribution of vegetated habitat in addition to total habitat area, thereby maintaining structurally complex nursery habitats that support blue crab refuge, foraging, and recruitment (Perkins-Visser et al., 1996; Hovel et al., 2005). Persistent southern hotspots identified in this study may represent areas where relatively stable vegetated habitat continues to support productive nursery function, consistent with observations that persistent seagrass patches within the IRL occur in discrete

environmental settings rather than being uniformly distributed throughout the lagoon (Morris et al., 2022). Conversely, persistent northern coldspots may represent priority areas for habitat restoration, water-quality improvement, and long-term ecological monitoring as seagrass recovery efforts continue throughout the estuary (Barile, 2018; Freeman et al., 2019).

More broadly, this study demonstrates that estuarine degradation may manifest not only through habitat loss but also through reorganization of habitat patterns across the landscape. As eutrophication, climatic variability, and watershed development continue to alter coastal ecosystems worldwide, understanding how these stressors affect habitat continuity will become increasingly important for conserving estuarine-dependent species. By integrating long-term habitat monitoring, fisheries-independent surveys, climate records, and spatial analyses, this study shows that habitat change can be accompanied by large-scale reorganization of nursery habitat patterns and associated populations across an entire estuarine ecosystem.

Conclusion

Long-term habitat change within the Indian River Lagoon (IRL) corresponded with substantial reorganization of blue crab populations across the estuarine landscape. Basin-wide seagrass decline after the 2011-2012 superbloom was associated with changes in the spatial distribution of blue crabs, including persistent northern coldspots, concentration of southern hotspots, and increased spatial heterogeneity throughout the lagoon. Habitat restructuring also showed temporal associations with climatic variability and rainfall. Despite widespread ecological change, abundance and carapace width remained strongly associated with vegetated habitats, with greater vegetation cover corresponding to higher abundance and larger individuals.

These findings indicate that environmental change may affect estuarine-dependent species not only through habitat loss, but also through reorganization of habitat distribution and spatial population structure. The IRL provides an example of how eutrophication, climatic variability, and habitat restructuring may interact to reshape nursery habitat patterns at ecosystem scales. As coastal ecosystems continue to experience increasing anthropogenic and climatic pressures, conserving and restoring vegetated habitat mosaics may help maintain nursery function, fisheries productivity, and ecological resilience.

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References

661 Barile, P. J. (2018). Widespread sewage pollution of the Indian River Lagoon system, Florida (USA)
 662 resolved by spatial analyses of macroalgal biogeochemistry. *Marine Pollution Bulletin*, 128, 557–574.
 663 <https://doi.org/10.1016/j.marpolbul.2018.01.046>

664 Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B.,
 665 Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., & Weinstein, M. P. (2001). The
 666 Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and
 667 Invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the
 668 factors that create site-specific variability in nursery quality will improve conservation and management
 669 of these areas. *BioScience*, 51(8), 633–641. [https://doi.org/10.1641/0006-](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2)
 670 [3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2)

671 Beckage, B., Platt, W. J., Slocum, M. G., & Panko, B. (2003). Influence of the El Niño Southern
 672 Oscillation on fire regimes in the Florida everglades. *Ecology*, 84(12), 3124–3130.
 673 <https://doi.org/10.1890/02-0183>

674 Brewton, R. A., & Lapointe, B. E. (2023). The green macroalga *Caulerpa prolifera* replaces seagrass in a
 675 nitrogen enriched, phosphorus limited, urbanized estuary. *Ecological Indicators*, 156, 111035.
 676 <https://doi.org/10.1016/j.ecolind.2023.111035>

677 Cheng, S. L., Tedford, K. N., Smith, R. S., Hardison, S., Cornish, M. R., & Castorani, M. C. (2022).
 678 Coastal vegetation and bathymetry influence blue crab abundance across spatial scales. *Estuaries and*
 679 *Coasts*, 45(6), 1701–1715. <https://doi.org/10.1007/s12237-021-01039-5>

680 Duarte, C. M. (1995). Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia*,
 681 41(1), 87–112. <https://doi.org/10.1080/00785236.1995.10422039>

682 Elliott, M., & Whitfield, A. K. (2025). Science and management achieving connectivity, coherence and
 683 equivalence to ensure the health of Estuarine Fish Communities. *Estuarine, Coastal and Shelf Science*,
 684 314, 109133. <https://doi.org/10.1016/j.ecss.2025.109133>

685 Florida Department of Environmental Protection (FDEP). (2018). *Total Maximum Daily Loads for the*
 686 *Indian River Lagoon Basin*. [https://floridadep.gov/dear/water-quality-restoration/content/nutrient-basin-](https://floridadep.gov/dear/water-quality-restoration/content/nutrient-basin-management-action-plans)
 687 [management-action-plans](https://floridadep.gov/dear/water-quality-restoration/content/nutrient-basin-management-action-plans) Accessed October 3, 2025.

688 Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute. (2019).
 689 Fisheries-Independent Monitoring Program: Procedure manual.

690 Forward, R. B., Tankersley, R. A., & Welch, J. M. (2003). Selective tidal-stream transport of the blue
 691 crab *Callinectes sapidus*: An overview. *Bulletin of Marine Science*, 72(2), 347–365.

692 Freeman, L. A., Corbett, D. R., Fitzgerald, A. M., Lemley, D. A., Quigg, A., & Steppe, C. N. (2019).
 693 Impacts of urbanization and development on estuarine ecosystems and water quality. *Estuaries and*
 694 *Coasts*, 42(7), 1821–1838. <https://doi.org/10.1007/s12237-019-00597-z>

695 Hines, A., Haddon, A., & Wiechert, L. (1990). Guild structure and foraging impact of blue crabs and
696 epibenthic fish in a sub-estuary of Chesapeake Bay. *Marine Ecology Progress Series*, 67, 105–126.
697 <https://doi.org/10.3354/meps067105>

698 Hines, A. H., Wolcott, T. G., González-Gurriarán, E., González-Escalante, J. L., & Freire, J. (1995).
699 Movement patterns and migrations in crabs: Telemetry of juvenile and adult behaviour in *Callinectes*
700 *sapidus* and *Maja squinado*. *Journal of the Marine Biological Association of the United Kingdom*, 75(1),
701 27–42. <https://doi.org/10.1017/S0025315400015174>

702 Hovel, K. A., & Fonseca, M. (2005). Influence of seagrass landscape structure on juvenile blue crab
703 habitat-survival function. *Marine Ecology Progress Series*, 300, 179–191.
704 <https://doi.org/10.3354/meps300179>

705 Hovel, K. A., & Lipcius, R. N. (2001). Habitat fragmentation in a seagrass landscape: Patch size and
706 complexity control blue crab survival. *Ecology*, 82(7), 1814–1829. [https://doi.org/10.1890/0012-9658\(2001\)082\[1814:HFIASL\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1814:HFIASL]2.0.CO;2)

707

708 Hovel, K. A., & Lipcius, R. N. (2002). Effects of seagrass habitat fragmentation on juvenile blue crab
709 survival and abundance. *Journal of Experimental Marine Biology and Ecology*, 271(1), 75–98.
710 [https://doi.org/10.1016/S0022-0981\(02\)00043-6](https://doi.org/10.1016/S0022-0981(02)00043-6)

711 Hyman, A., Chiu, G., M. S. Seebo, Smith, A., Saluta, G., & R. N. Lipcius. (2023). Ontogenetic patterns in
712 juvenile blue crab density: effects of habitat and turbidity in a Chesapeake Bay tributary. *Marine Ecology*.
713 *Progress Series*. <https://doi.org/10.3354/meps14490>

714 Liu, J. T., Zarillo, G., & Surak, C. R. (1997). The influence of river discharge on hydrodynamics and
715 mixing in a subtropical lagoon. *Journal of Coastal Research*, 13(4), 1016–1034.
716 [https://doi.org/10.1016/S0967-0653\(98\)80018-5](https://doi.org/10.1016/S0967-0653(98)80018-5)

717 Mizerek, T., Regan, H., & Hovel, K. (2011). Seagrass habitat loss and fragmentation influence
718 management strategies for a blue crab *Callinectes sapidus* fishery. *Marine Ecology Progress Series*, 427,
719 247–257. <https://doi.org/10.3354/meps09021>

720 Montagna, P. A., Hu, X., Palmer, T. A., & Wetz, M. (2018). Effect of hydrological variability on the
721 biogeochemistry of estuaries across a regional climatic gradient. *Limnology and Oceanography*, 63(6),
722 2465–2478. <https://doi.org/10.1002/lno.10953>

723 Morris, L. J., Hall, L. M., Jacoby, C. A., Chamberlain, R. H., Hanisak, M. D., Miller, J. D., & Virnstein,
724 R. W. (2022). Seagrass in a Changing Estuary, the Indian River Lagoon, Florida, United States. *Frontiers*
725 *in Marine Science*, 8. <https://doi.org/10.3389/fmars.2021.789818>

726 Perkins-Visser, E., Wolcott, T. G., & Wolcott, D. L. (1996). Nursery role of seagrass beds: Enhanced
727 growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology*
728 *and Ecology*, 198(2), 155–173. [https://doi.org/10.1016/0022-0981\(96\)00014-7](https://doi.org/10.1016/0022-0981(96)00014-7)

729 Peterson, M. S. (2003). A conceptual view of environment-habitat-production linkages in tidal river
 730 estuaries. *Reviews in Fisheries Science*, 11(4), 291–313. <https://doi.org/10.1080/10641260390255844>

731 Schmidt, N., Lipp, E., Rose, J., & Luther, M. (2001). ENSO Influences on Seasonal Rainfall and River
 732 Discharge in Florida. *Journal of Climate*, 14, 615–628. [https://doi.org/https://doi.org/10.1175/1520-0442\(2001\)014<0615:EIOSRA>2.0.CO;2](https://doi.org/https://doi.org/10.1175/1520-0442(2001)014<0615:EIOSRA>2.0.CO;2)
 733

734 Sfriso, A., Facca, C., & Ghetti, P. F. (2003). Temporal and spatial changes of macroalgae and
 735 phytoplankton in a Mediterranean coastal area: The Venice Lagoon as a case study. *Marine*
 736 *Environmental Research*, 56(5), 617–636. [https://doi.org/10.1016/s0141-1136\(03\)00046-1](https://doi.org/10.1016/s0141-1136(03)00046-1)

737 Sheaves, M. (2009). Consequences of ecological connectivity: The Coastal Ecosystem Mosaic. *Marine*
 738 *Ecology Progress Series*, 391, 107–115. <https://doi.org/10.3354/meps08121>

739 Smith, N. P. (1993). Tidal and nontidal flushing of Florida’s Indian River Lagoon. *Estuaries*, 16(4), 739.
 740 <https://doi.org/10.2307/1352432>

741 St. Johns River Water Management District (SJRWMD). (2025). *Seagrass (SJRWMD)*. SEACAR Data
 742 Discovery Interface, Office of Resilience and Coastal Protection, Florida Department of Environmental
 743 Protection. <https://data.florida-seacar.org/programs/details/3013>

744 St. Johns River Water Management District, Florida Fish and Wildlife Conservation Commission, Harbor
 745 Branch Oceanographic Institute at Florida Atlantic University, Bethune-Cookman University, & Nova
 746 Southeastern University. (2012). *Indian River Lagoon 2011 superbloom: Plan of investigation*.

747 The Balmoral Group. (2025). *Indian River Lagoon economic valuation 2025* (Indian River Lagoon
 748 National Estuary Program Technical Report No. 2025-02b). Indian River Lagoon National Estuary
 749 Program.

750 Thrush, S. F., Halliday, J., Hewitt, J. E., & Lohrer, A. M. (2008). THE EFFECTS OF HABITAT LOSS,
 751 FRAGMENTATION, AND COMMUNITY HOMOGENIZATION ON RESILIENCE IN ESTUARIES.
 752 *Ecological Applications*, 18(1), 12–21. <https://doi.org/10.1890/07-0436.1>

753 Van Den Avyle, M. J., & Fowler, D. L. (1984). Species Profiles: Life Histories and Environmental
 754 Requirements of Coastal Fishes and Invertebrates (South Atlantic). BLUE CRAB. FWS/OBS 82/11.19,
 755 vi, 16 p. : ill., map; 28 cm.

756 Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A.,
 757 Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., &
 758 Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems.
 759 *Proceedings of the National Academy of Sciences*, 106(30), 12377–12381.
 760 <https://doi.org/10.1073/pnas.0905620106>

761 Wilson, K. A., Able, K. W., & Heck, K. L., Jr. (1990). Predation rates on juvenile blue crabs in estuarine
 762 nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). *Marine Ecology Progress*
 763 *Series*, 58, 243–251. 10.3354/meps058243.

764 Woodland, R., Warry, F., Zhu, Y., Mac Nally, R., Reich, P., Jenkins, G., Brehm, D., & Cook, P. (2019).
765 Role of benthic habitat structure and riverine connectivity in controlling the spatial distribution and
766 ecology of Estuarine fish. *Marine Ecology Progress Series*, 630, 197–214.
767 <https://doi.org/10.3354/meps13116>

768 **Statements and Declarations**

769 *Competing Interests*

770 The authors declare that they have no competing interests.