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REVIEW ARTICLE

Development of modelling and mapping methods to predict spatial distributions and abundance of estuarine and coastal fish species life-stages in Florida

Peter J. Rubec[1] | **Christine E. Santi**[2] | **Jerald S. Ault**[3] | **Mark E. Monaco**[4]

[1] 2335 Murilla Way South, St. Petersburg, Florida, USA

[2] Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Center for Spatial Analysis, St. Petersburg, Florida, USA

[3] Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida, USA

[4] NOAA Marine Spatial Ecology Division, Silver Spring, Maryland, USA

Correspondence
Peter J. Rubec, 2335 Murilla Way South, St. Petersburg, FL, USA.
Email: peterrubec@cs.com

Abstract

Suitability modelling and mapping methods were developed to predict spatial distributions and population abundance of fish and macroinvertebrate species in Florida estuaries and coastal zones. Habitats were mapped in Pensacola Bay, Tampa Bay, and Charlotte Harbor using data from fisheries-independent monitoring. Starting in 1997, suitability functions from habitat suitability index models were linked to habitat grids to create seasonal maps for early-juvenile, juvenile, and adult life-stages. After 2003, habitat suitability models (HSM) were linked to seasonal habitat grids to create seasonal maps validated by reciprocal transfer of suitability functions between estuaries. A quantitative method was used with five factor models and models with fewer environmental factors for four species in 2005 and for 11 species by life-stages in 2009. In 2006, suitability functions transferred from Charlotte Harbor were linked with habitat grids for Rookery Bay and Fakahatchee Bay and HSM maps produced for three time periods to test transferability to estuaries lacking long-term monitoring. Analyses in 2012 demonstrated that HSM maps for Tampa Bay derived independently from earlier suitability functions were almost identical to HSM maps created using recent suitability functions. Salinity was the most significant environmental variable for predicting abundance in models for species life-stages in the Peace River and Charlotte Harbor, although nutrient concentrations from upriver may have influenced species' abundances associated with low (<5 psu) to moderate (5–10 psu) salinities. Population abundance estimates for Charlotte Harbor were derived from seasonal HSM maps created in 2019 and 2021. The 2021 paper compared changes in seasonal population numbers between Baseline and Minimum Flows associated with projected water withdrawals from the Peace River. Electronic logbooks were developed in 2001 and 2004 to collect data on shrimp fishing vessels and HSM maps for the West Florida Shelf created for 16 months in 2004–2005. Methodologies evolved as enabling technology became available.

KEYWORDS
estuarine management, freshwater inflow, habitat mapping, habitat suitability modelling

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1 | INTRODUCTION

As part of the Magnuson–Stevens Conservation and Management Act of 1996, the U.S. Congress mandated that the National Marine Fisheries Service (NMFS) develop guidelines to assist fisheries management councils nationwide in the creation of essential fish habitat regulations for fishery management plans and that the councils describe these habitats in text, tables, and maps (NMFS, 1996). Essential fish habitat (EFH) was defined as those waters and substrates necessary for spawning, breeding, feeding, or growth to maturity. It is the geographic area where a species occurs at any time during its life and comprises substrate and water column characteristics that focus on the species' distribution. The prescribed extent of EFH should be based on the amount of habitat necessary to maintain a managed species at a target production level that provides the maximum benefit to human society, including the catch of the species. In addition, the councils were required to identify habitat areas of particular concern. The Magnuson–Stevens Reauthorization Act required the councils to create fishery ecosystem plans to better relate fishery species and fisheries to their supporting ecosystems.

Early attempts to define linkages between fish and 'habitat' stem from the U.S. Fish and Wildlife Service (FWS) Habitat Evaluation Program that mostly studied freshwater and riparian environments (FWS, 1980a, 1980b, 1981). The habitat suitability index (HSI) modelling approach derives from ecological theory which states that the 'value' of an area of 'habitat' for the productivity of a given species is determined by habitat carrying capacity as it relates to density-dependent population regulation (FWS, 1981). Suitability indices have been used as input to HSI models to create suitability functions fitted across environmental gradients. When abundance data are used as input to the model, higher suitability values indicate that areas with higher relative abundance are 'more suitable habitat' (Bovee, 1986; Terrell, 1984). Suitability indices (SIs) multiplied by the amount of area constituting the index score can be used to determine habitat unit areas (HUAs) that quantify the spatial extent of suitable habitats (FWS, 1980b, 1981).

Fisheries managers do not have adequate information about estuarine and marine habitats to effectively manage recreational and commercial fisheries in the southern United States (Elliott et al., 2016; Rubec & McMichael, 1996). For many estuarine and marine species, what constitutes 'habitat' and how it relates to spatial variations in occurrence or abundance is not known. Rather than being a simple function of any single factor, areas of higher or lower species' abundance are typically dependent upon composites of several environmental factors.

The fishery management councils do review some EFH plans. However, stock assessments are still largely based on mortality matrices across years linked with time series of abundance. Stock assessment models are only recently being designed to include environmental factors and/or habitat information. They are not derived from spatial information in maps created using a geographic information system (GIS).

While the conclusions concerning stock assessments are still generally true, there are a growing number of scientists across research and management institutions and associated with fisheries agencies worldwide that see the need to support place-based management of coastal marine ecosystems (Young et al., 2007). There is growing awareness that the escalating crisis in marine ecosystems—from biodiversity losses and transformed food webs to marine pollution and warming waters—is in large part a failure of governance. Many scientists have advocated reforms centred on the idea of ecosystem-based management. To date, however, a politically and administratively feasible method for translating this attractive concept into an operational management practice has not emerged. A practical way to solve this problem features place-based management—a strategy that calls for integrated management of the full suite of human activities occurring in spatially demarcated areas identified through a procedure that takes into account biophysical, socioeconomic, and jurisdictional considerations.

Models and GIS can provide objective means to support fisheries management. Various statistical, modelling, and mapping approaches have been used to relate species' distributions and abundance to habitats at locations in estuaries and coastal zones worldwide. Spatial-temporal models have been developed to support (a) the placement of marine protected areas (Friedlander et al., 2007; Peterson et al., 2007), (b) the delineation of essential fish habitat (Trimoreau et al., 2013; Valavanis et al., 2004), and (c) ecosystem-based fisheries management (Elliott et al., 2016; Grandos-Diesseldorff 2009), marine spatial planning (Dineshbabu et al., 2019; Douvere 2008), and for other reasons important for fish species management and/or fisheries management (Franca & Cabral 2016; Huijelos et al., 2016; Mathiopoulos et al., 2015). But there is no consensus concerning the best modelling and mapping methods.

The papers reviewed herein developed habitat suitability models that related frequency of occurrence or abundance indices with associated environmental data and used GIS to map species' distributions and abundance in Florida estuaries and coastal zones. SIs associated with suitability functions scaled to the same maximum value (1 or 10) were used as input to HSI models. Gear-corrected (GC) catch-per-unit-efforts (GC-CPUEs) were used with habitat suitability models (HSMs). The HSM analyses involved development of multiple regression models to predict CPUEs in relation to environmental factors using generalized additive models (GAMs) or generalized linear models (GLMs and generalized linear modelling [GLIMs]). GC-CPUEs were graphed using the Statistical Analysis System (SAS) or the data visualization, dynamic linking, and analytic capabilities of SAS JMP not present in SAS.

2 | METHODS AND RESULTS

Methods for mapping habitats and modelling and mapping spatial distributions of fish and invertebrate species in Florida were initially developed by a committee comprised members from the Fish & Wildlife Research Institute (FWRI), NOAA Strategic Environmental Assessments Division, and the University of Miami. Since the spatial distributions and abundance of species life-stages change over time, the analyses have been conducted over various yearly intervals. As technologies evolved, we have used a variety of modelling and mapping approaches. The advantages and disadvantages of these approaches are discussed associated with the papers published by the first author from 1997 to present.

HSI models prior to 1997 were developed by others to support rapid decision-making using qualitative methods based on expert opinion. Many of the early HSI models developed for various species were not verified or validated with actual field data. Rigorous sampling designs that provide comprehensive temporal or spatial coverages were rarely employed. These problems have limited the development of quantitative HSI models capable of supporting fishery management strategies.

2.1 | Estuarine studies

FWRI currently conducts fisheries-independent monitoring (FIM) to collect fish abundance, water quality, and habitat type data in five of 18 larger estuaries (McMichael 1991; Nelson et al., 1997). We recognized the potential of habitat suitability models to predict the spatial distribution and relative abundance of a species life-stage in a similar nearby estuary lacking long-term fisheries monitoring. Models linked to GIS may provide a means of mapping species distributions in estuaries not currently surveyed by fisheries monitoring. Hence, we wanted to determine whether it was possible for suitability functions to be transferred from one estuary to another without significant loss of precision and biological interpretability.

2.2 | GIS software for suitability modelling

The Arc Macro Language code used to conduct HSI modelling in Pensacola Bay was developed by the NOAA-Strategic Environmental Assessments Division in 1997 to run with raster-based modules within the ArcInfo GIS. In 1998, FWRI's GIS staff rewrote the code in Avenue to run HSI models with the ArcView GIS Spatial Analyst extension. The code was further modified and refined during 1999 to display HSI maps along with a histogram and tables. The tables output from the model depicted observed mean SIs and predicted mean SIs within four predicted HSI zones. During 2000, the Avenue scripts were modified to facilitate running HSMs by creating GC-CPUEs. The Avenue scripts were rewritten as a Visual Basic application using Arc Objects to port the models to ArcGIS 8.3. The software installed on a computer allowed the user to select the estuary, habitat suitability model, species, life-stage, habitat factors, season, and years to produce either within or transfer maps (Figure 1). The scripts could run either HSI or HSM models.

2.3 | Pensacola Bay

2.3.1 | Habitat mapping

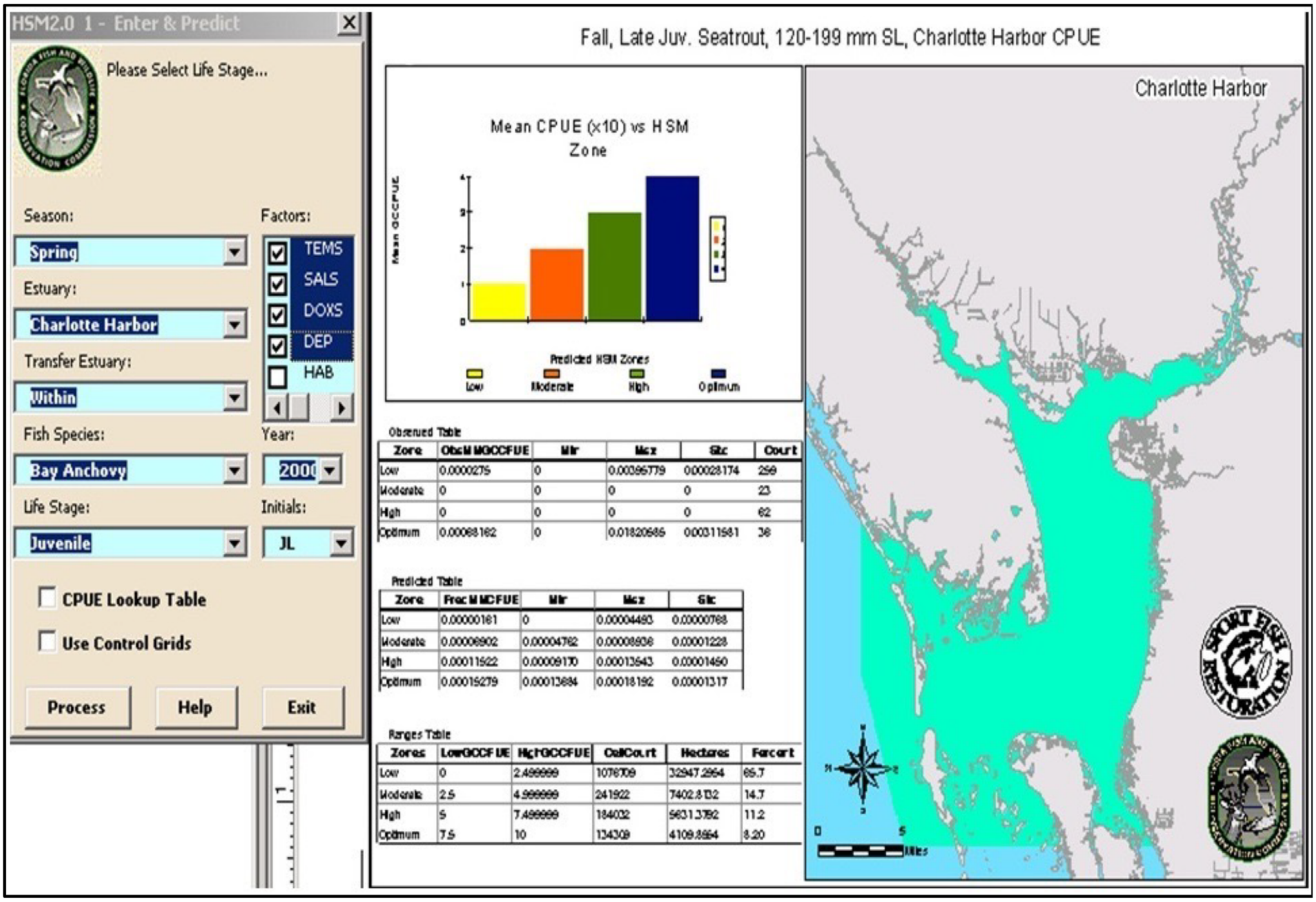
Continuous data that vary along a gradient, such as bathymetry, dissolved oxygen, salinity, and temperature, were acquired from the Florida Department of Natural Resources and the Environmental Protection Agency's EMAP Program (Christensen et al., 1997). The environmental data were independently mapped by georeferenced (latitude/longitude) sampling stations. The point data were interpolated into continuous, contoured surfaces using inverse distance weighting, and then rasterized into a grid format. Each grid was created with the same coordinate system, and cells among grids were aligned in geographic space to facilitate inter-grid processing. All grids had the same cell size of 1000 m^2. At this resolution, each environmental grid map in Pensacola Bay consisted of approximately 37,000 cells. Each environmental grid was then categorized: salinity was mapped in 5 g/L increments, water temperature in 2°C isotherms and, dissolved oxygen in 1 mg/L increments. Substrate was categorized using a modified Shepard's classification scheme and was classified as sand, silt, and clay. The distributions of submerged aquatic vegetation (SAV) and emergent vegetation (EV) were determined by aerial photography and digitized by the FWS. SAV and EV grid cells were classified as either present or absent.

2.3.2 | Habitat suitability index modelling

HSI models were developed for Pensacola Bay to examine relationships for frequency of occurrence of eastern oyster (*Crassostrea virginica*), white shrimp (*Litopenaeus setiferus*), and spotted seatrout (*Cynoscion nebulosus*) with hydrological and biological parameters (Christensen et al., 1997). Pensacola Bay was chosen as the test area because its hydrographic conditions were considered representative for most Gulf of Mexico estuaries. The first step in developing HSI models was to conduct a comprehensive data and literature search. This was combined with an expert review process to identify biological and environmental variables to include in the model. Salinity, water temperature, dissolved oxygen content, bathymetry, substrate type, and the presence or absence of SAV and EV were selected to model habitat suitability.

Hypothetical salinity scenarios were modelled to evaluate the impact of changes in freshwater inflow on the species being modelled in the Pensacola Bay system (Christensen et al., 1997). To accomplish this, baywide salinities were increased by 5 g/L for the high salinity time period. Likewise, baywide salinities were decreased by 5 g/L for the low salinity time period.

GIS technology was explicitly incorporated to produce a 'seascape' view of relative suitability of locations in geographic space through time. The ArcInfo 7.03 GRID module was used to conduct HSI modelling. The models were run during four time periods to address fluctuations in species distributions (Christensen et al., 1997). Representative periods for the Pensacola Bay HSI model were determined by characterizing salinity conditions in the estuary. Seasonal depth-averaged salinity was modelled from a subset of field salinity data collected between 1970 and 1994. Salinity time periods consisted of high salinity (September–November), decreasing salinity (December–January), low salinity (February–April), and increasing salinity (May–August). These periods represent the typical salinity conditions experienced under average freshwater inflow conditions. Water temperature was



Season: Spring

Estuary: Charlotte Harbor

Transfer Estuary: Within

Fish Species: Bay Anchovy

Life Stage: Juvenile

Factors:
☑ TEMS
☑ SALS
☑ DOXS
☑ DEP
☐ HAB

Year: 200

Initials: JL

☐ CPUE Lookup Table

☐ Use Control Grids

Observed Table

Zone	ObsMMGCCFUE	Min	Max	Std	Count
Low	0.0000275	0	0.00386779	0.00028174	259
Moderate	0	0	0	0	23
High	0	0	0	0	62
Optimum	0.00068162	0	0.01820686	0.00311581	38

Predicted Table

Zone	PredMMCFUE	Min	Max	Std
Low	0.00000161	0	0.00004483	0.00000768
Moderate	0.00006902	0.00004762	0.00008936	0.00001228
High	0.00011522	0.00009170	0.00013643	0.00001460
Optimum	0.00015279	0.00013684	0.00018192	0.00001317

Ranges Table

Zones	LowGCCFUE	HighGCCFUE	CellCount	Hectares	Percent
Low	0	2.499999	1076709	32947.2964	65.7
Moderate	2.5	4.999999	241922	7402.8132	14.7
High	5	7.499999	184032	5631.3782	11.2
Optimum	7.5	10	134309	4109.8864	8.20

FIGURE 1 Computer front-end created by Fish & Wildlife Research Institute geographic information system (FWRI GIS) staff in 2005 for running analyses in selected estuaries using pull-down menus to create within or transfer habitat suitability modelling maps. The pull-down menus selected the season, estuary, within/transfer suitability functions, species, life-stage, years, environmental factors, and initials of the analyst. The light green area indicated the area modelled. The system was capable of creating either habitat suitability index (HSI) maps or habitat suitability model (HSM) maps.

contoured for the same months as the salinity time periods to ensure temporal uniformity in the models.

2.3.3 | HSI maps

White shrimp and juvenile spotted seatrout HSI maps for Pensacola Bay exhibited great spatial and temporal sensitivity to fluctuating environmental parameters (Christensen et al., 1997). Highest suitability values were observed in EV and SAV habitats during the increasing salinity time period when water temperatures were at an optimum level. Suitability was moderate in the non-vegetated habitats throughout the rest of the bay. Low suitability was observed throughout the bay during the decreasing salinity time period, when temperatures declined to 10–14°C. Spotted seatrout have been observed to move to warmer waters of deep channels and depressions to avoid thermal stress in the winter.

Moderate HSI values for juvenile seatrout were observed baywide during the low and high salinity time periods as temperatures declined away from or increased towards the optima (Christensen et al., 1997). Similar patterns were observed with the adult seatrout HSI distributions. Optimum and high suitability was predicted for shallow, vegetated habitats during the increasing and high salinity time periods. Optimum and high suitability zones were more extensive for adults compared to juveniles. Approximately 90% of the bay was considered high or optimum habitat for adult seatrout during these time periods. Cooler temperatures during the decreasing and low salinity time periods resulted in moderate or low suitability throughout the unvegetated portions of the bay. Vegetated habitats in the lower portion of the bay were ranked as high suitability during the low salinity time period and moderate during the decreasing salinity time period.

2.3.4 | Model validation

Due to the lack of consistent and robust FIM data in Pensacola Bay, a qualitative assessment was conducted to validate the white shrimp and spotted seatrout models (Christensen et al., 1997). Local fisheries biologists and commercial fishermen compared the HSI maps to their collective expertise. Consensus was reached that the HSI maps portrayed a reasonable representation of potential distributions of white shrimp and spotted seatrout in the Pensacola Bay system. They concluded that the scenarios depicting potential effects of habitat change can be easily determined using HSI modelling in conjunction with GIS technology.

In order to test model performance and transferability, SI values developed in Pensacola Bay were applied to 10 years (1987–1996) of FIM data collected by the Texas Parks and Wildlife Department in Galveston Bay (Clark et al., 2002). Juvenile spotted seatrout CPUE data from Galveston Bay bag seine samples were used to test juvenile HSI model performance, while gill net samples were used to assess the adult HSI model from Pensacola Bay across suitability zones. Plotted linear regressions revealed increasing relationships between mean CPUEs from Galveston Bay and mean HSIs from Pensacola Bay across suitability zones for juvenile spotted seatrout bag seine data and adult gill net data, respectively.

2.4 | Tampa Bay and Charlotte Harbor

2.4.1 | Habitat mapping

Environmental data, collected by the FWRI FIM program, were aggregated across years (1996–2014) to ensure adequate sample sizes and interpolated with GIS using universal linear kriging to create seasonal habitat grids (surface and bottom) for salinity, temperature, and dissolved oxygen in Tampa Bay (TB) and in Charlotte Harbor (CH) (Rubec et al., 1999, 2001). Then, the surface and bottom habitat grids were averaged. Conventional seasons included fall (September–November), winter (December–February), spring (March–May), and summer (June–August). Depth was mapped by interpolation of NOAA bathymetry data. Bottom type was initially mapped using SAV and bare-bottom categories (Rubec et al., 1998a, 1998b). Later studies used sand, mud, and SAV distributions to map bottom type in each estuary (Rubec et al., 1999, 2001).

Recently, the seasonal habitat grids for CH were improved using data supplied by the Southwest Florida Water Management District (SWFWMD). The months comprising non-conventional seasons were chosen based on differences in freshwater inflows: fall (October–December), winter (January–March), spring (April–June), and summer (July–September) (Rubec et al., 2019, 2021). Non-conventional seasonal temperature, salinity, and dissolved oxygen grids were derived from FWRI FIM data (Rubec et al., 2019). Sand and mud polygons in CH were obtained from NOAA, and the distribution of SAV in CH was derived from aerial photography conducted by SWFWMD in 2012. Bathymetry data, from a sonar survey in CH conducted by Ping Wang in 2012 (University of South Florida, Department of Geology), were obtained from SWFWMD.

2.4.2 | Habitat suitability index modelling

Rubec et al. (1999) tested the hypothesis that it was possible to predict the geographic distribution of fish species by life-stage in estuaries lacking FIM using transferred SIs. SI functions for CH in the fall were created by fitting polynomial regressions to smooth-mean CPUEs by depth, by salinity and by temperature, and graphing mean CPUEs by bottom type; then scaling the CPUE functions to the same maximum value (10) in each estuary to create SI functions using SAS JMP. The HSI models integrated the environmental SIs across gear types. Then, SIs for each environmental variable output from the HSI model were assigned to cells associated with corresponding intervals in the CH habitat grids. ESRI's ArcView GIS Spatial Analyst module was used to average the SIs assigned to cells within the habitat grids to create a predicted HSI grid (Figure 2). The predicted HSI grid was partitioned into low to optimum zones to create a seasonal HSI map for early-juvenile spotted seatrout in the fall. Increasing observed mean CPUEs across predicted HSI zones within the CH map were used as a verification test. The process was repeated using independent SI functions transferred from TB assigned to the fall habitat grid layers for CH.

The CH HSI map for early-juvenile spotted seatrout in the fall, derived using SI functions associated with polynomial regressions and habitat grids from within CH, was not significantly different from the CH HSI map derived using SIs transferred from TB (Rubec et al., 1999). Grid cell frequencies in low to optimum zones were compared between within and transferred data. The HSI map in CH derived from transferred TB SIs was quite similar to the map based on within CH SI data. Most of the differences between the maps were in the low and moderate zones. The differences between the within and transfer maps for CH were ascribed to differences in the fitted functions for depth. Early-juvenile spotted seatrout occurred at greater depths in TB than were found in CH. Using these methods to create HSI maps for early-juvenile seatrout for the fall season in CH tended to confirm the hypothesis that it was possible to predict the geographic distribution of fish species by life-stage in estuaries lacking FIM using transferred SIs.

Similar methods were used to develop seasonal HSI models in 2001 to predict spatial distributions by other species life-stages and seasons in TB and in CH (Rubec et al., 2001, 2016d). Reciprocal transfer of SI functions between estuaries was conducted to test whether HSI modelling could be used to predict seasonal distributions of species life-stages in estuaries lacking FIM. FIM datasets for each estuary were analyzed from 1989 to mid-1997. The analyses produced HSI maps by life-stage (within and transfer) in the two estuaries for early-juvenile, juvenile, adult Spotted Seatrout; juvenile, adult Bay Anchovy; and juvenile, adult Pinfish. The derived SI functions for the environmental factors were plotted to compare similarity of the functions in each estuary. Similar seasonal HSI maps were derived by only using the factors associated with the most similar suitability functions.

To verify the reliability of seasonal HSI maps, observed mean CPUEs were plotted across four predicted HSI zones (Rubec et al., 2001). Analyses showed that fish densities increased from low to optimum zones

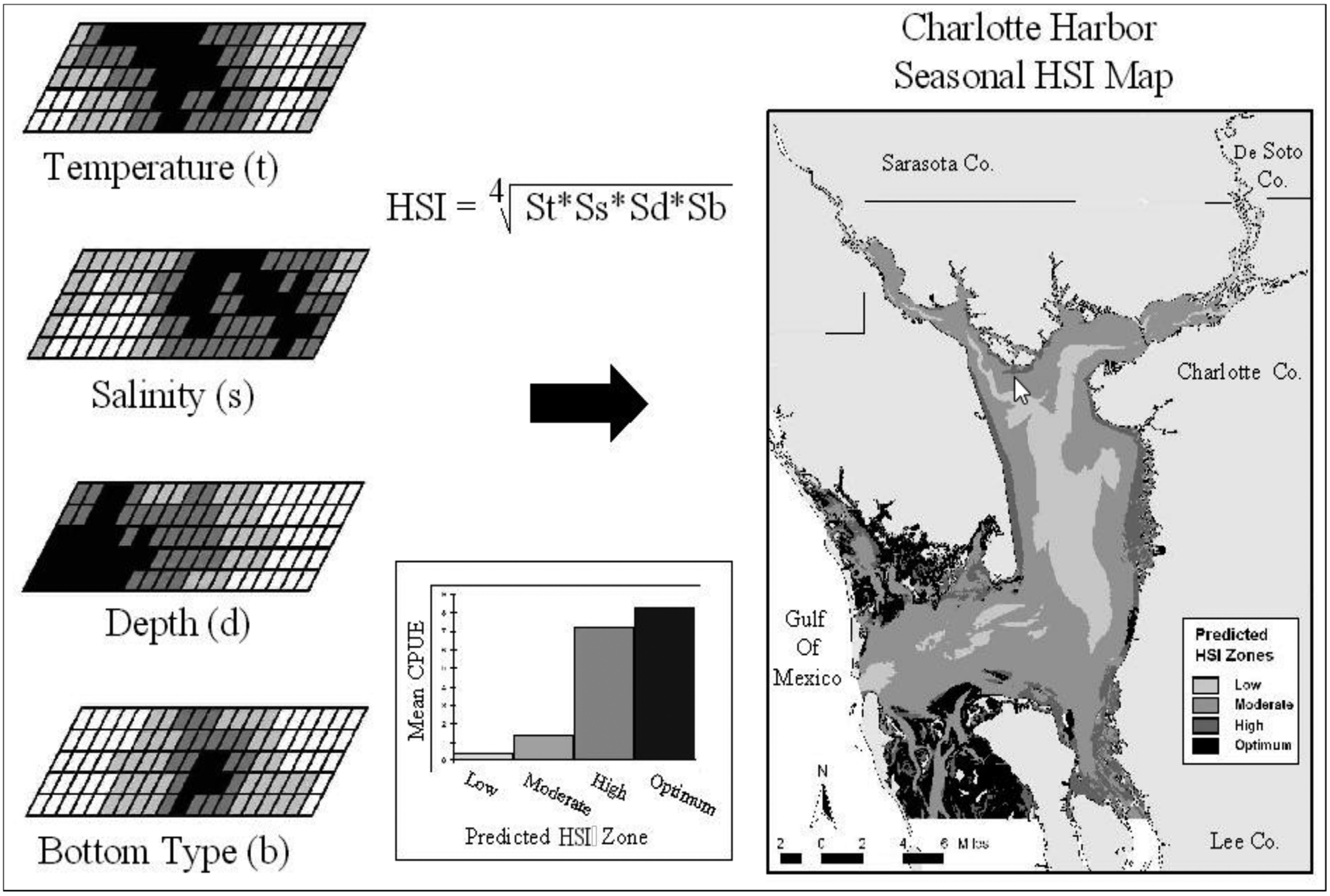


FIGURE 2 Drawing depicting geometric-mean computations of suitability indices (SIs) assigned to habitat layers to produce a predicted habitat suitability index (HSI) map. Computations were done with SIs in HSI models. Fitted SIs from splines and graphs across environmental gradients output from the models were assigned to cells in habitat grids for temperature, salinity, depth, and bottom type. Then, the SIs associated with the habitat grids were averaged within the cells.

for the majority of species life-stages examined. For CH, observed mean CPUEs increased across low to optimum HSI zones for 78.6% of the 28 predicted HSI maps produced using CH habitat grids and within SI functions. Similarly with SI functions transferred from TB, 82.1% of 28 cases showed increasing mean CPUEs across four HSI zones using seasonal CH habitat grids. In TB, increasing mean CPUEs occurred in 42.9% of 28 cases using seasonal TB habitat grids and SI functions from within TB. Increasing mean CPUEs occurred in 50% of 28 cases for HSI maps created from TB habitat grids and SI functions transferred from CH. Most of the low increasing CPUE scores in TB were associated with seasonal HSI maps for the life-stages of spotted seatrout. The low percentage of increasing CPUE scores in TB occurred because TB is deeper than CH, and the SI by depth functions transferred from CH did not account for this.

To test the similarity of within and transfer seasonal HSI maps, zone values (low to optimum) for within HSI maps were compared on a cell-by-cell basis with zone values of the corresponding HSI map for the same estuary derived from transferred SI functions (Rubec et al., 2001). Each pair of seasonal HSI maps were considered to be similar if ≥60% of the cells by zone were scored the same in the majority of the HSI zones. To evaluate whether the maps minimally identified the most suitable habitats associated with higher species life-stage abundances, differences between predictions of the 'optimum' zones by the two models were also computed. Better results were obtained when the similarity of optimum zones was compared. The similarity of within and transferred SI functions used with the HSI models accounted for the high similarity of predicted maps for juvenile Pinfish and for juvenile Bay Anchovy in each estuary. The dissimilarity of SI functions input into HSI models accounted for why other species life-stages had dissimilar HSI maps. Another issue was that annual data were used to create suitability functions associated with the HSI modelling (i.e., FIM data were not analyzed to create seasonal SI functions).

HSI models were developed for TB and CH (Rubec et al., 1998a, 1998b, 1999, 2001). Many of the HSI models published prior to 1998 were created using SI values derived from the literature and/or expert opinion (Rubec et al., 2001). The 2001 paper concluded that the HSI algorithm in its present format is a heuristic model useful for qualitative interpretations and may be inadequate for quantitative analysis and as a prediction tool. HSI models may be very useful in data-poor situations where some type of rapid management response is required. However, when fish abundance and environmental 'habitat' data of high spatial and temporal resolution are available, significant improvements in the development of predictive models of fish-habitat associations can be obtained by using more contemporaneous regression-based methods.

2.4.3 | Habitat suitability modelling

Kupschus (2003) developed GAMs using S-Plus to predict the spatial distributions of early-juvenile spotted seatrout ≤50 mm standard length in Tampa Bay, Charlotte Harbor, and Indian River Lagoon. GAMs were used to fit splines to CPUEs in relation to environmental variables within each estuary. The approach compared within CPUEs with transferred CPUEs (derived from FIM sampling data collected from January 1996 to December 1999) at station locations in each estuary. The GAMs created within each estuary were tested in terms of their transferability to the other estuaries. Only the Indian River Lagoon GAMs appeared to reliably predict CPUEs, when transferred to the other two estuaries. This could be due to differences in depth ranges between the estuaries and/or because the GAMs did not account for the high frequency of zero catch values in the FIM datasets.

FWRI contracted Jerald Ault at the University of Miami to develop SAS software for the standardization of gear-types (Ault & Smith 1998, 2000). This involved the computation of gear-correction factors to adjust CPUEs for various gears to the gear-type with the highest mean CPUE. CPUEs for 10 fish species and for pink shrimp were gear-corrected within the HSM to produce seasonal splines with fitted GC-CPUEs across environmental gradients.

FWRI also contracted Jerald Ault to develop methods for analyses of station-specific data using statistical procedures capable of dealing with the non-normality of FIM datasets (Ault & Smith 2001; Ault et al., 2002). Single regression models were first developed using SAS for each habitat variable. To satisfy error distribution assumptions of the GLIM procedure, estimation was carried out in two stages. Dual-regressions were necessary due to the high frequency of zero catches in the FIM datasets. One stage utilized presence–absence data to fit logistic regression models, and the other stage used non-zero CPUEs to fit generalized linear regression models. Multiplying the probability of occurrence, p, predicted by logistic regression with u, the predicted non-zero CPUE from GLIM yielded the predicted CPUE. The single regression p and u models were then combined into multiple regression habitat suitability models. Backward selection was employed to eliminate non-significant regression coefficients to derive a final multiple regression model for both p and u.

Seasonal HSMs built by adding terms using SAS created suitability functions with smooth wide curves (Ault & Smith 1998, 2000). But this was very time consuming (Rubec et al., 2003). Seasonal splines fitted to mean CPUEs across environmental gradients (Figure 3) using SAS JMP required less programming and provided better fits to the data (Rubec et al., 2005, 2016d). The function peaks were narrower, providing better predictions of the environmental ranges that have the highest fitted CPUEs. So, we adopted this method with subsequent studies using CPUEs. The disadvantage of fitting splines to mean CPUEs across environmental gradients is that the variability associated with the original CPUEs is lost making it impossible to create confidence intervals for the fitted splines and bottom type histograms.

2.5 | Report to U.S. Fish and Wildlife Service

Spatial models and methods were developed to conduct habitat suitability modelling in TB and CH (Rubec et al., 2003). The models predicted seasonal distributions of estuarine species from data collected by FIM and other sources. Several methods were developed to fit suitability functions across environmental gradients. Scaled SIs were used as input to HSI models. Mean CPUEs derived from polynomial regressions were used as input to HSM models. Both models calculated the geometric mean of abundance indices (either SIs or CPUEs) associated with grid-based habitat layers within the ArcView GIS Spatial Analyst to produce predicted seasonal habitat suitability maps. The models were verified by overlaying CPUEs onto the predicted maps to determine whether observed mean CPUEs increased across predicted suitability zones.

2.6 | Reciprocal transfer between Tampa Bay and Charlotte Harbor

The main goal of the study by Rubec et al. (2005) was to conduct HSM analyses using seasonal suitability functions reciprocally transferred between the two estuaries (Figure 4). The full models used five factors in the HSM for temperature, salinity, dissolved oxygen, depth, and bottom type. Then, we varied the number of factors to evaluate whether fewer factors improved performance of the HSMs for predicting the relative abundance of species life-stages. GC-CPUEs, derived from the splines and a histogram for bottom type output from the HSM, were assigned to the habitat grid layers using the ArcView Spatial Analyst module within ArcGIS 8.3. Computations were conducted across the raster-based grids within the GIS to produce predicted seasonal HSM maps for pink shrimp, Bay Anchovy, Spotted Seatrout, and pinfish, depicting four suitability zones for each species' life-stage. The HSM output included tabulated mean GC-CPUEs (No. of fish/m^2) within each suitability zone and the areas of each zone in hectares. Maps created from abundance indices within each estuary and transferred from the other estuary were used to test transferability of the models between TB and CH. In 2009, the number of species life-stages was increased from 4 to 11 (Rubec et al., 2009). With large sample sizes, the suitability functions for the two estuaries were similar and most of the seasonal within and transfer HSM maps derived for each estuary were similar.

The life-stages analyzed during 2006 in CH and TB included size ranges for spotted seatrout, pinfish, bay anchovy, pink shrimp, red drum, southern kingfish, sand seatrout, common snook, hardhead catfish, spot, and sheepshead (Table 1). Due to the complexity of running HSMs by varying the number of factors, the analyses were conducted outside the GIS (Figure 5). Optimum zones associated with seasonal HSM map pairs (within and transfer) were similar 78% of the time in CH and 91% of the time in TB.

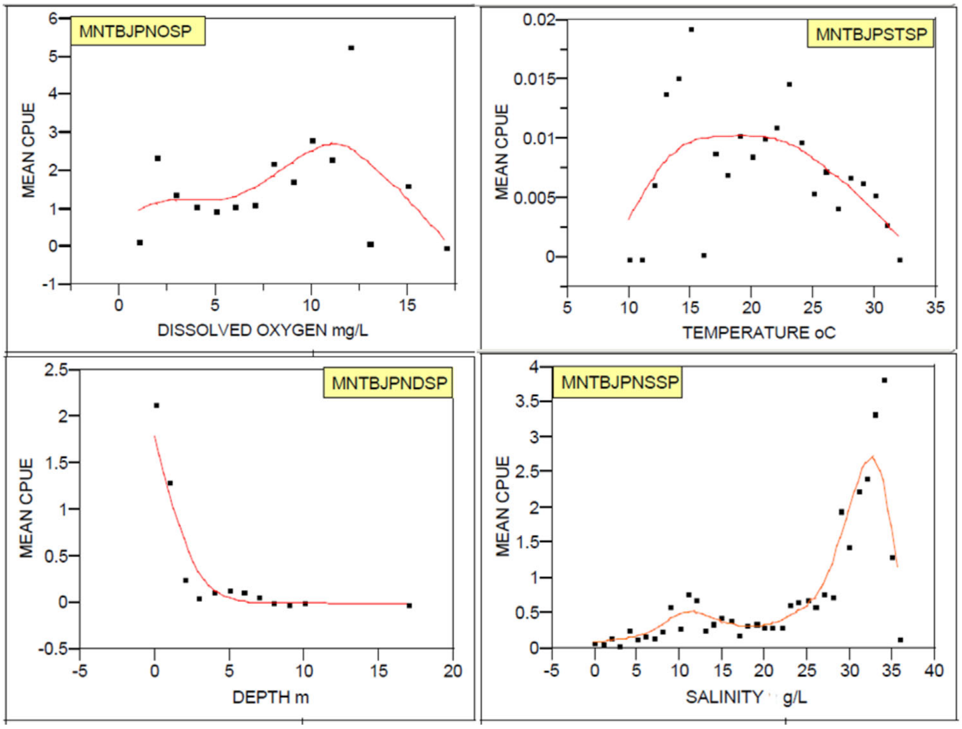


FIGURE 3 Suitability functions consisting of splines fitted to mean catch-per-unit-effort across temperature (T), salinity (S), dissolved oxygen (O), and depth (D) gradients for juvenile Pinfish during spring in Tampa Bay. The bottom type (B) histogram was not used with this HSM analysis.

2.7 | Verification tests

The seasonal HSM analyses were extended in 2009 to include 22 life-stages (early-juvenile, juvenile, and/or adult) of 11 species (Rubec et al., 2016d). The HSMs run in CH and in TB were verified by graphing increasing mean observed GC-CPUEs (within and transfer) across predicted HSM zones using SAS JMP. The criteria used to assess the efficacy of the maps were (1) that mean GC-CPUEs increase across HSM zones, and (2) the zones in HSM maps associated with transfer (independent) suitability functions appear similar to the HSM maps with functions from within each estuary. The optimum zones usually were the most similar (Figure 6). Suitability functions TSOD are for temperature, salinity, dissolved oxygen, and depth.

Seasonal HSM maps created in each estuary during 2009 exhibited verification scores of 1, which indicated that mean GC-CPUEs increased across HSM zones (Rubec et al., 2016d). The within and transfer HSMs that were run with five factors did not work as well as models built by varying the number (<5) of factors.

Seasonal HSMs produced a relatively high proportion of increasing verification scores for within maps, respectively, in CH (62.5%) and in TB (79.6%), but exhibited a low proportion of increasing transfer scores (51%–52%) in each estuary. Increasing mean GC-CPUEs across HSM zones were found with several seasonal HSM maps produced with fewer than five factors, making it difficult to determine which one was the best HSM map. Differences in the depth functions for TB and CH primarily account for the differences in verification scores between the within and transfer HSM maps.

Since we did not have a statistical model to select the best combination of factors, it was necessary to run HSMs to determine which factor combinations worked best. The study (and all previous studies) was based on a time-consuming trial and error. Over 4000 HSM maps were created during 2009 associated with varying the number of factors used in the HSM (Rubec et al., 2016d). While we did HSM analyses with fewer than five factors, we did not evaluate all factor combinations because there are 31 possible combinations of one to five factors.

2.7.1 | Transfer of suitability functions to Rookery Bay and Fakahatchee Bay

The transfer of suitability functions between estuaries were used to predict species distributions and abundance in estuaries lacking long-term FIM (Rubec et al., 2006). The study was conducted to assess the influence of changes in freshwater inflow on distributions and relative abundance of estuarine species in Henderson Creek and Rookery Bay. Originally, freshwater entered the bay via storm-generated runoff. The creation of a canal system in the 1960s, which funnels water through a weir situated on Henderson Creek, altered the pattern of freshwater inflow. To assess the effect of these changes, monitoring was initiated in Rookery Bay and Fakahatchee Bay. The latter estuary served as a control because it still had largely natural freshwater inflows.

When the study was initiated in 2003, no long-term FIM data had been collected in Rookery Bay (Rubec et al., 2006). Consequently, FIM data collected in CH were analyzed to create suitability functions for

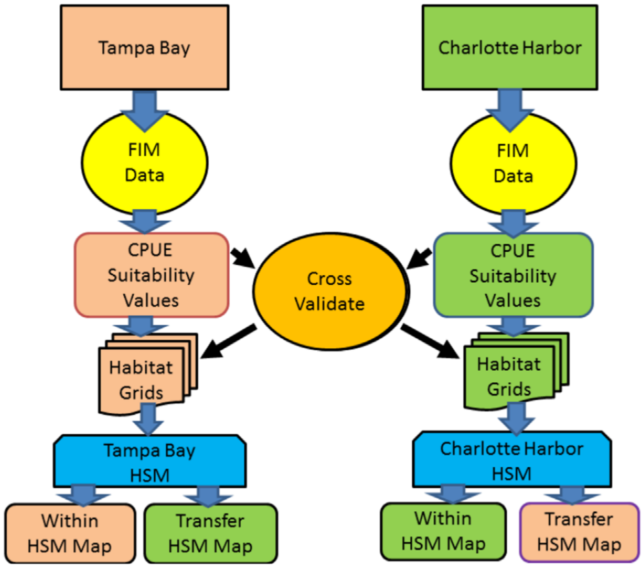


FIGURE 4 Flow diagram showing the process for producing seasonal within and transfer habitat suitability model (HSM) maps in Tampa Bay and in Charlotte Harbor with suitability values (gear-corrected catch-per-unit-efforts [GC-CPUEs]) assigned to corresponding intervals in the habitat grids. The suitability values were obtained either from within the same estuary or transferred from the other estuary to facilitate reciprocal cross-validation of the HSM maps.

22 life-stages of 10 species of fish and for pink shrimp. Abundance indices transferred from CH were applied to Rookery Bay and Fakahatchee Bay habitat layers, so we could conduct raster-based HSM for a dry season (spring) and two wet seasons (during summer) in Rookery Bay with differing freshwater inflows. The length ranges for the species life-stages are presented in Table 1.

The modelling in Rookery Bay and in Fakahatchee Bay found that most of the 22 life-stages of 11 species modelled responded to changes in salinity, related to changes in freshwater inflow (Rubec et al., 2006). Salinities were similar in both estuaries (30–33 psu) during May 2003 (the dry season). Marked differences in salinity within optimum zones were found between Fakahatchee Bay (8–16 psu) and Rookery Bay (30–33 psu) during August 2002. Inflow data obtained from SWFWMD indicated that the higher salinities in Rookery Bay during August 2002 were related to the fact that the weir situated at the head of Henderson Creek reduced the inflow of freshwater entering Rookery Bay.

2.8 | Dual regression modelling

With advances in statistics, it became possible in 2012 to fit splines using delta-gamma GAMs associated with generalized additive models for location, scale, and shape (GAMLSS) with programs written in R (Rigby & Stasinopoulos 2005; Stasinopoulos & Rigby 2007). FWRI's statistician, Richard Kiltie, modified the delta-gamma GAM software to support analyses of zero-inflated FIM data (Rubec et al., 2016c). He adapted the software to support HSM analyses in Florida estuaries. Version 54 of the Kiltie software used raw CPUE data from TB as input, gear-corrected the CPUE data within the HSM, fitted splines to GC-CPUEs across environmental gradients for temperature, salinity, dissolved oxygen, and depth, and created a mean GC-CPUE histogram for bottom type. To deal with zero-inflation of the FIM data, the program separately fitted splines to positive GC-CPUEs and frequency of zero occurrence data across environmental gradients, and then combined the functions and output predicted GC-CPUE functions for each environmental gradient. The main advantage of the delta-gamma GAM program in R was that it developed 31 models for combinations of one to five factors and selected the best model with the lowest Akaike information criterion (AIC).

2.9 | Tampa Bay studies

Most of our previous verifications used suitability functions created from the same CPUE data that were used to create the HSM maps. We compared observed mean GC-CPUEs with predicted mean GC-CPUEs associated with the zones in the HSM maps for 1989–1998. This is an internal verification. When an independent dataset is used to create suitability functions, it becomes an external validation. Hence, the reciprocal transfer of suitability functions from the other estuary between TB and CH was associated with external validations (Rubec et al., 2005, 2009).

An early-recent approach was taken in 2012 with GC-CPUE functions derived from HSM analyses using v58 of the Kiltie software in R. The species analyzed in TB were adult southern kingfish, adult sheepshead, adult hardhead catfish, and juvenile pink shrimp collected during the summer. Figure 7 depicts the internal verification for adult southern kingfish during summer in which observed mean GC-CPUEs, created from 1998 to 2009 data, were plotted against predicted mean GC-CPUEs associated with the zones in an HSM map created using CPUE data collected from 1998 to 2009 (recent time period). Internal verifications were also done for the other species life-stages. We did external (independent) validations for TB by plotting mean GC-CPUEs derived from 1989–1997 FIM data (early time period) against mean GC-CPUEs in HSM maps derived from data collected from 1998 to 2009 (recent time period) with adult southern kingfish (Figure 8). External validations were also done with the other species life-stages previously listed. The early (external) and recent (internal) summer maps were almost identical across the HSM zones for the life-stages of the four species. The suitability functions used to create external HSM maps for the early time period were very similar to those used to create internal HSM maps for the recent time period. Mean GC-CPUEs by HSM zones were presented associated with the internal verification and external validation analyses of juvenile pink shrimp during summer in TB (Rubec et al., 2016c). However, there was concern that sample sizes were too low for the early and recent analyses of the four species life-stages. Hence, we decided not to use the early-recent approach in subsequent studies.

Using v70 of the Kiltie software in R, FIM data from TB were analyzed seasonally in 2013–2014 for early-juvenile, juvenile, and/or adult life-stages of pink shrimp, common snook, bay anchovy, hardhead catfish, southern kingfish, pinfish, sand seatrout, sheepshead, spotted

TABLE 1 Length ranges used by Rubec et al. (2006) and in other studies of Rubec.

Life-stage	Species	Scientific name	Length range
Juvenile+adult	Hogchoker	*Trinectes maculatus*	10–100 mm SL
Juvenile+adult	Blue crab	*Callinectes sapidus*	10–150 mm CW
Juvenile	Bay anchovy	*Anchoa mitchilli*	15–29 mm SL
Adult	Bay anchovy	*Anchoa mitchilli*	≥30 mm SL
Juvenile	Pinfish	*Lagodon rhomboides*	10–99 mm SL
Adult	Pinfish	*Lagodon rhomboides*	≥100 mm SL
Juvenile	Sand seatrout	*Cynoscion arenarius*	10–149 mm SL
Adult	Sand seatrout	*Cynoscion arenarius*	≥150 mm SL
Early-juvenile	Southern kingfish	*Menticirrhus americanus*	10-119 mm SL
Adult	Southern kingfish	*Menticirrhus americanus*	≥180 mm SL
Early-juvenile	Spotted seatrout	*Cynoscion nebulosus*	10–119 mm SL
Juvenile	Spotted seatrout	*Cynoscion nebulosus*	120–199 mm SL
Adult	Spotted seatrout	*Cynoscion nebulosus*	≥200 mm SL
Juvenile	Common snook	*Centropomus undecimalis*	150–279 mm SL
Adult	Common snook	*Centropomus undecimalis*	≥280 mm SL
Adult	Hardhead catfish	*Ariopsis felis*	≥110 mm SL
Early-juvenile	Sheepshead	*Archosargus probatocephalus*	10–139 mm SL
Juvenile	Sheepshead	*Archosargus probatocephalus*	140-239 mm SL
Adult	Sheepshead	*Archosargus probatocephalus*	≥240 mm SL
Juvenile	Pink shrimp	*Farfantepenaeus duorarum*	5–17 mm CL
Adult	Pink shrimp	*Farfantepenaeus duorarum*	≥18 mm CL
Early-juvenile	Red drum	*Sciaenops ocellatus*	10–299 mm SL
Early-juvenile	Spot	*Leiostomus xanthurus*	10–149 mm SL
Juvenile	Spot	*Leiostomus xanthurus*	150–199 mm SL

Abbreviations: CL, carapace length; CW, carapace width; SL, standard length.

seatrout, and red drum (Rubec unpublished). HSMs were run by varying the number of factors included in the models from 1 to 5 to account for 31 possible combinations. The delta-gamma GAM program selected the best TB model with the lowest AIC. The software created better graphical outputs including confidence intervals around the fitted splines and graphs for bottom type and gear type. Confidence intervals were computed by bootstrapping the results 500 times. The predicted GC-CPUE grids (created by transferring GC-CPUEs from the fitted splines and bottom type histogram to the habitat grids and then averaging the habitat grids) were partitioned using equal areas in the GIS to create seasonal HSM maps.

2.10 | Charlotte Harbor

A contract was obtained from the SWFWMD in 2015 to assess the impact of potential freshwater withdrawals from the tidally influenced lower Peace River and CH. Delta gamma GAMs were applied with seasonal modelling of eight species life-stages in the CH study area with highest abundances in low to moderate salinities (Rubec et al., 2019, 2021). The species life-stages analyzed in 2015–2016 are presented in Table 2. The v73 delta-gamma GAMs in R associated with GAMLSS varied the number of factors in models for 31 combinations of one to five factors. The best seasonal model for each species life-stage was chosen based on it having the lowest AIC.

Fitted splines were created using delta-gamma GAMs for both positive CPUE (+CPUE) data (Mu) and probability of zero occurrence data (Nu) across environmental gradients for each species life-stage analyzed by season in CH (Rubec et al., 2019, 2021). The CPUEs for each gear type were gear-corrected and combined (Mu X Nu) within the HSM to create GC-CPUE splines for each environmental factor and histograms for bottom type, season, and year. The v73 software also created confidence intervals associated with the suitability functions and histograms. An example is depicted for juvenile+adult Hogchoker in the fall (Figure 9). Then, GC-CPUEs from the fitted splines for salinity, temperature, dissolved oxygen, and depth, and mean GC-CPUEs from the histogram for bottom type were assigned to corresponding intervals in the habitat grids. A key improvement in v73 was the addition of a year term in the delta-gamma GAMs that allowed the computation of seasonal GC-CPUEs by year from 1996 to 2013.

The HSM studies prior to 2018 partitioned the predicted GC-CPUE grids to determine the spatial extent of HSM zones using equal areas or equal intervals. When equal intervals were used, they were found to produce very small optimum zones for some species life-stages that

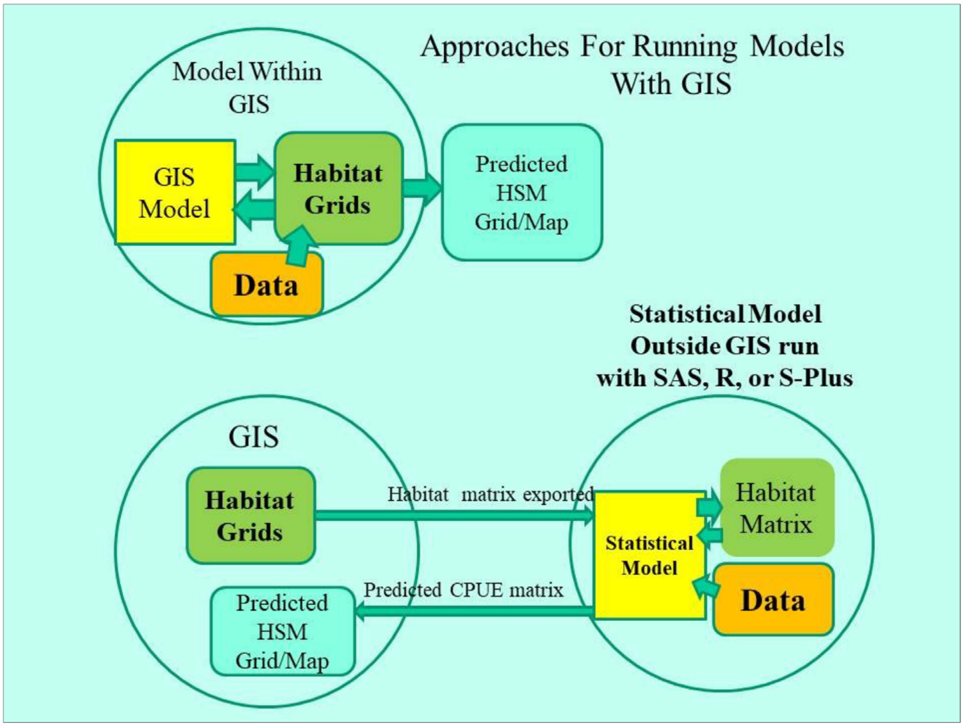


FIGURE 5 Comparison of habitat suitability model (HSM) analyses within geographic information system (GIS) and outside GIS

were not visible in the HSM maps (Rubec et al., 2019). Equal areas produced visible optimum zones in the HSM maps. However, in most cases, the optimum zones filled the rivers.

The natural breaks is an objective method was used with recent HSM studies (Rubec et al., 2019, 2021). The natural breaks method is an option included in the ArcGIS Spatial Analyst. The method specifies that the classes will be based on natural groupings inherent in the data (Jenks, 1967). Break points are identified by choosing class breaks that group similar values to maximize the differences between classes. The natural breaks is an objective quantitative method, which used the GC-CPUE data in the predicted grids to determine the spatial extent of brackish zones in seasonal HSM maps for each species life-stage. The optimum zones for resident species were visible in HSM maps in parts of the rivers adjoining CH.

To simulate the effects of flow reductions on salinity distributions in tributary rivers for CH, a coupled three-dimensional (3D)–two dimensional vertical (2DV) hydrodynamic model was developed by SWFWMD (Chen, 2020). Non-conventional seasonal temperature and seasonal salinity grid data averaged across years (2007–2014) were used with HSM analyses of species life-stages in CH for Baseline and Minimum Flows conditions associated with projected freshwater withdrawals (Rubec et al., 2021).

Salinity was significant during most seasons for the species life-stages listed for both studies in CH (Rubec et al., 2019, 2021). The optimum zones in seasonal HSM maps for the first six species life-stages, classified as estuarine residents, indicate that they were most abundant in either low or moderate salinities in the lower Peace River during most of the year (Rubec et al., 2019). The 2019 study found that each estuarine resident species life-stage occupied a different salinity range. The first six species in Table 2 list species life-stages that occupy low to moderate salinity ranges. It is of interest that the salinity range occupied by each resident species life-stage stayed about the same between seasons, although the areas occupied expanded associated with increases in freshwater inflow during the summer. Red drum and spot were classified as estuarine transients because they spawn in the Gulf of Mexico. But both species life-stages moved into low salinity (0.05–5 psu) in the Upper P segment of the lower Peace River during part of the year (early-juvenile red drum in winter, early-juvenile spot in spring).

Delta-gamma GAMs associated with GAMLSS were used, with FIM data collected from 1996 to 2013, to estimate seasonal population numbers in the CH study area for eight species by life-stages (Rubec et al., 2019). In our most recent study (Rubec et al., 2021), seasonal habitat grids for temperature and salinity were created using data derived from hydrodynamic modelling conducted from 2007 to 2014 by SWFWMD (Chen, 2020).

The seasonal population number estimates (Table 2) in the Baseline and Minimum Flows study (Rubec et al., 2021) for species life-stages in CH averaged across years (2007–2014) were lower than those averaged across years (1996–2013) during the previous study (Rubec et al., 2019). Since the same FIM data were used to create seasonal HSM maps for species life-stages in both studies, the differences in population number estimates appear to be related to the habitat grids. The depth, bottom type, and dissolved oxygen grids used were the same in both studies. Hence, the lower population estimates in the 2021 study appear to be related to the seasonal

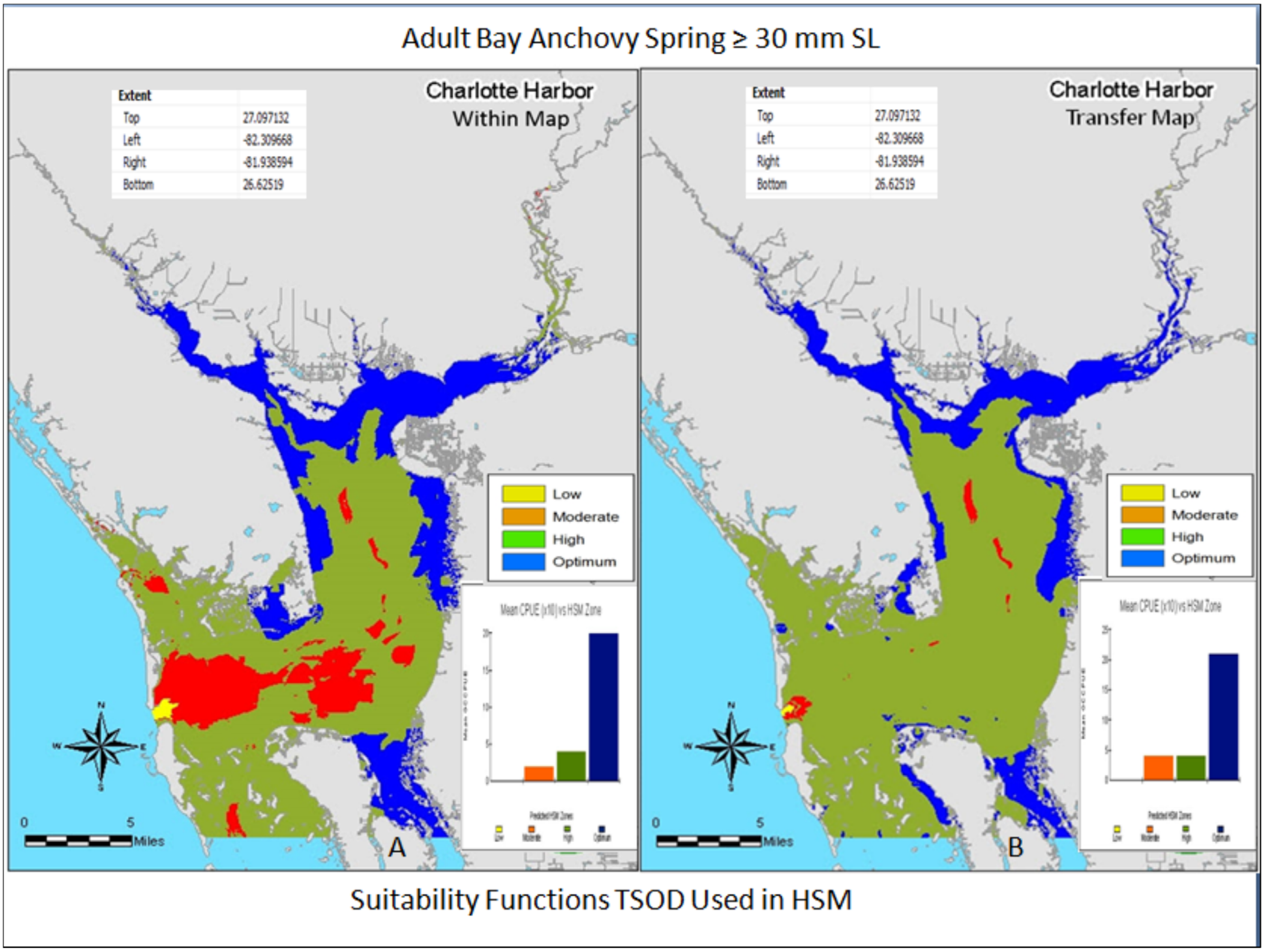


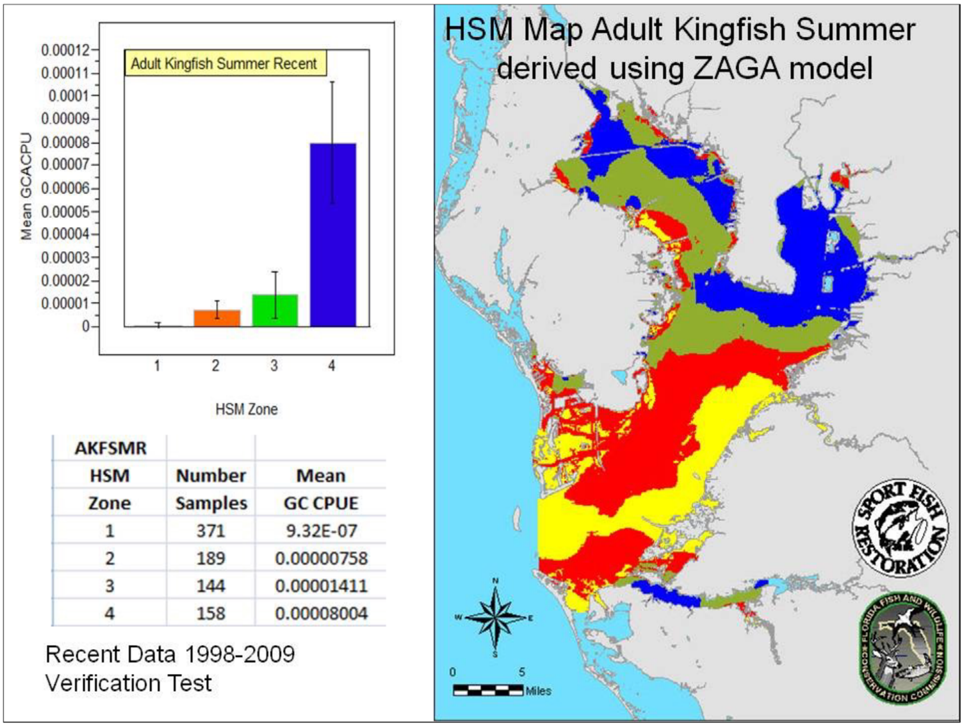
FIGURE 6 Habitat suitability model (HSM) maps (within and transfer) in Charlotte Harbor for adult Bay Anchovy in spring produced using: A-habitat layers and suitability functions 'within' Charlotte Harbor and B-habitat layers from Charlotte Harbor and suitability functions 'transferred' from Tampa Bay. Suitability functions TSOD

temperature grids and seasonal salinity grids derived from data produced by hydrodynamic modelling and used for the Baseline and Minimum Flows analyses (Rubec et al., 2021). The most likely explanation is that the higher population number estimates in the 2019 study were related to generally higher rainfall and freshwater inflows that occurred prior to 2007, which influenced seasonal salinity grids (Rubec et al., 2019).

2.11 | Coastal studies

Electronic Logbooks West Florida Shelf Two electronic logbook (ELB) systems were developed in 2001 and 2005 by FWRI in cooperation with Versaggi Shrimp Corporation and Sasco Inc. (Rubec et al., 2016a, 2016b). The shrimp species fished were primarily pink shrimp (*Farfantepenaeus duorarum*) on the West Florida Shelf (WFS) and primarily brown shrimp (*Farfantepenaeus aztecus*) along the coast of Texas. ELB software was used to record catch, effort, and environmental data on computers situated in the wheelhouse of three shrimp fishing vessels fishing on the WFS (both ELB studies) and along the coast of Texas (first study). A specific conductance, temperature, depth (CTD) data logger associated with each boat's trynet recorded vertical and horizontal profiles with both ELB studies. Counts of shrimp numbers from the trynet and weights of size grades of shrimp species obtained from the main trawls were recorded on the computer by each shrimp boat captain. Positions (latitude and longitude) automatically recorded by each boat's Global Positioning System allowed determination of fishing effort (hours fished). Data collected by the CTD were displayed on the computer in the wheelhouse of each vessel to depict changes in temperature, salinity, and depth over the path taken by the trynet. The ELBs for both studies maintained a database of use by each boat captain and provided catch, effort, and location data to FWRI to support modelling and mapping using GIS (Rubec et al., 2016b).

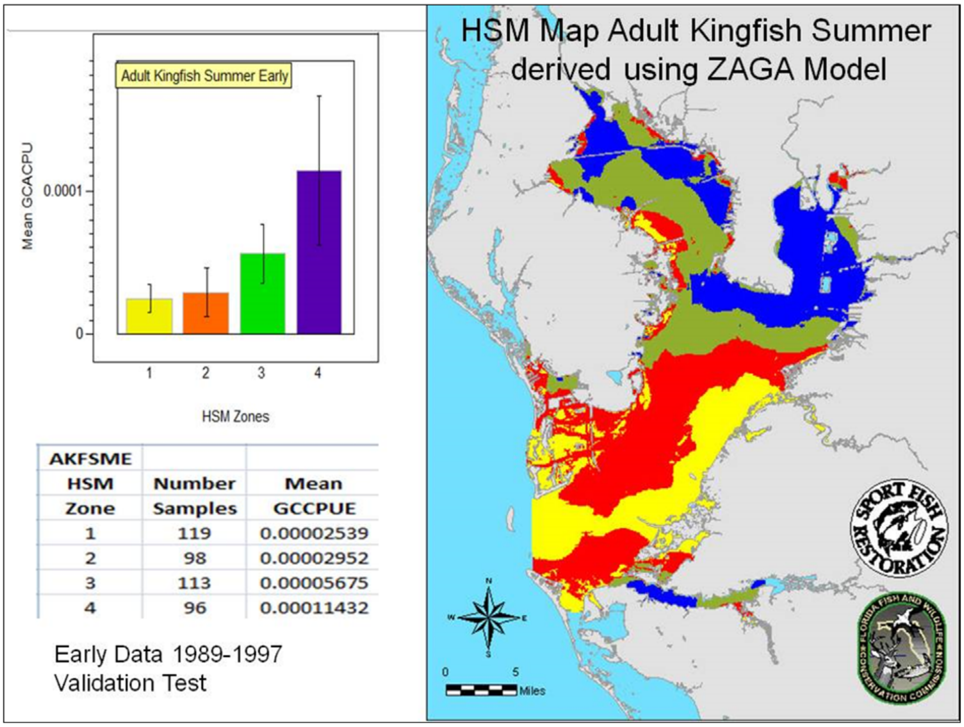
The University of South Florida (USF) maintains a network of data loggers on the WFS. Circulation modelling was conducted monthly for 16 months using the Finite Volume Coastal Ocean Model. The



AKFSMR HSM Zone	Number Samples	Mean GC CPUE
1	371	9.32E-07
2	189	0.00000758
3	144	0.00001411
4	158	0.00008004

Recent Data 1998-2009
Verification Test

FIGURE 7 Habitat suitability map for adult southern kingfish in Tampa Bay during summer derived from fisheries-independent monitoring (FIM) data collected during the recent time period (1998–2009). Mean gear-corrected catch-per-unit-efforts (GC-CPUEs) used to create the internal verification histogram are included in the associated table. ZAGA is an abbreviation used by Rigby and Stasinopoulos which stands for Zero Adjusted Gamma. It is associated with GAMLSS. ZAGA is similar to the gamma distribution but uses zeros adjusted by adding a small coefficient. HSM zone: 1 = low, 2 = moderate, 3 = high, and 4 = optimum. Suitability functions TSODB



AKFSME HSM Zone	Number Samples	Mean GCCPUE
1	119	0.00002539
2	98	0.00002952
3	113	0.00005675
4	96	0.00011432

Early Data 1989-1997
Validation Test

FIGURE 8 Habitat suitability map for adult Southern Kingfish in Tampa Bay during summer derived from fisheries-independent monitoring (FIM) data collected during the early time period (1989–1997). Mean GC-CPUEs used to create the external validation histogram are included in the associated table. Suitability functions TSODB

TABLE 2 Changes in population numbers of species life-stages by season between Baseline and Minimum Flows in lower Peace River/lower Shell Creek and Charlotte Harbor

Life-stage	Season	Population number	Population number	Percent change
Species		**Baseline**	**Minimum Flows**	**Population No.**
juvenile+adult	Fall	701,377	620,900	11.5
Hogchoker	Winter	553,351	482,250	12.8
	Spring	126,269	102,233	19.0
	Summer	124,983	109,281	12.6
juvenile+adult	Fall	337,046	315,665	6.3
Blue crab	Winter	5,577,933	5,338,615	4.3
	Spring	204,920	189,248	7.6
	Summer	93,881	89,385	4.8
juvenile	Fall	983,889	863,283	12.3
Sand seatrout	Winter	16,827	14,446	14.1
	Spring	4,527,044	4,388,843	3.1
	Summer	2,999,378	2,369,853	21.0
early-juvenile	Fall	480,831	414,399	13.8
Southern kingfish	Winter	289,190	267,599	7.5
	Spring	289,894	255,701	11.8
	Summer	177,108	146,191	17.5
Juvenile	Fall	411,688,848	386,446,156	6.1
Bay anchovy	Winter	1,278,661,747	1,213,423,074	5.1
	Spring	2,098,586,359	1,996,069,439	4.9
	Summer	301,026,145	278,322,254	7.5
Adult	Fall	409,669,579	386,497,346	5.7
Bay anchovy	Winter	1,114,145,755	1,069,235,403	4.0
	Spring	2,098,463,644	1,995,985,434	4.9
	Summer	275,313,382	278,372,737	**1.1**
Early-juvenile	Fall	12,599,998	12,357,379	1.9
Red drum	Winter	2,771,344	2,762,907	0.3
	Spring	363,119	363,129	**0.0**
	Summer	265,019	250,736	5.4
Early-juvenile	Fall	6153	6635	**7.8**
Spot	Winter	107,931	106,339	1.5
	Spring	783,736	770,237	1.7
	Summer	58,781	6,1605	**4.8**

Note: Percent changes in population numbers between flow conditions: decreasing (regular font) and increasing (bold font) (Rubec et al., 2021).

oceanographers at the USF modelled and mapped circulation patterns on the WFS from March 2004 to June 2005 to predict monthly bottom temperature, bottom salinity, and bottom current patterns (speed and direction). Geologists at the University of Colorado aggregated available grab sampling data from the U.S. Geological Survey and other sources and produced maps depicting bottom sediment types at sampling locations on the WFS. GIS staff at FWRI interpolated the data collected by the shrimp boat captains, oceanographers, and geologists to produce habitat grids and maps for the WFS (Rubec et al., 2016b).

Monthly HSM maps (from March 2004 to June 2005) for pink shrimp on the WFS were created using the catch, effort, and environmental data collected on shrimp fishing vessels and the habitat data provided by oceanographers and geologists (examples in Figure 10). CPUEs in pounds per hour were graphed across environmental gradients using SAS or SAS JMP to produce suitability functions for depth and bottom type, and seasonal functions for fitted CPUEs by temperature, salinity, current speed, current direction from origin, aspect, and shrimp fishing zones. Fitted CPUEs from the suitability functions were applied to the habitat grids and monthly HSM maps created

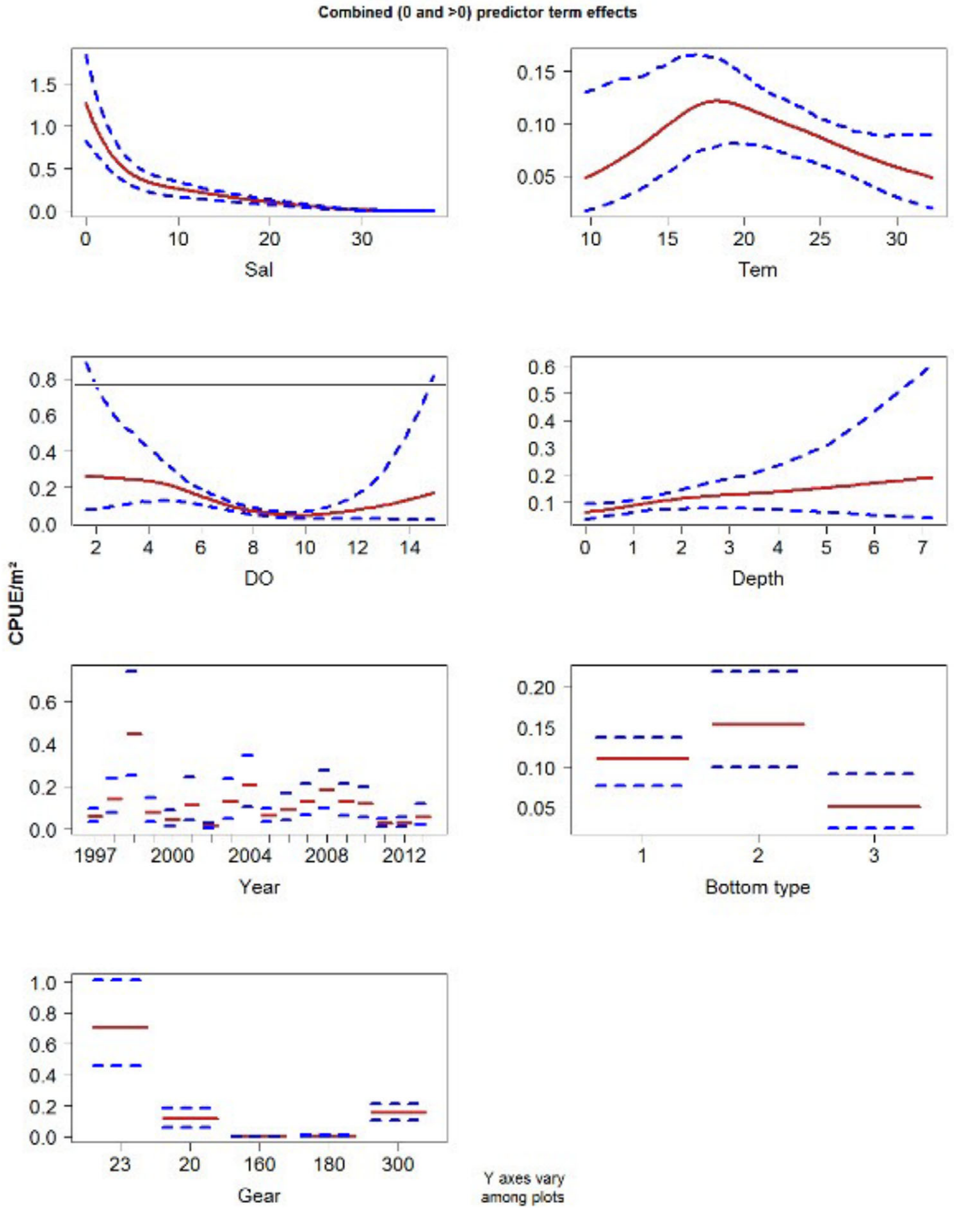


FIGURE 9 Back-transformed suitability functions for juvenile+adult Hogchoker in Charlotte Harbor during the fall, across environmental gradients for salinity (Sal), temperature (Tem), dissolved oxygen (DO), depth, and histograms for bottom type, gear type, and year output from the delta-gamma generalized additive model (GAM) analysis. The dashed lines are upper and lower confidence intervals. Bottom type: 1 = sand, 2 = mud, 3 = submerged aquatic vegetation. Gear types: gear 20 = 21.3 m circular bag seine, 23 = 21.3 m boat bag seine, 160 = 183 m haul seine, 180 = 61 m haul seine, 300 = 6.1 m otter trawl

within the shrimp fishing boundary (Rubec et al., 2016b). The analyses demonstrated that shrimp were significantly more abundant on the WFS associated with onshore currents during 2004 than during 2005 when offshore currents prevailed. This can also account for increasing mean CPUEs associated with higher current speeds, and higher CPUEs were found associated with currents coming from the northwest during 2004. The cooperative research approach sponsored by the Gulf and South Atlantic Fisheries Foundation supported sustainable fisheries, better fisheries management, and the delineation and management of essential fish habitat.

The areas analyzed in the estuaries and coastal zones of Florida used either HSI or HSM modelling and mapping (Table 3). The table progresses from the estuaries to coastal zones. The collection of pink shrimp data on the WFS and brown shrimp data along the coast of Texas in 2001 and pink shrimp data on the WFS in 2005 was conducted in collaboration with Versaggi Shrimp Corporation (Rubec et al., 2016a, 2016b). The second study on the WFS, using catch, effort, and environmental data collected on shrimp fishing vessels along with circulation modelling data provided by Robert Weisberg (University of South Florida) and sediment grain size

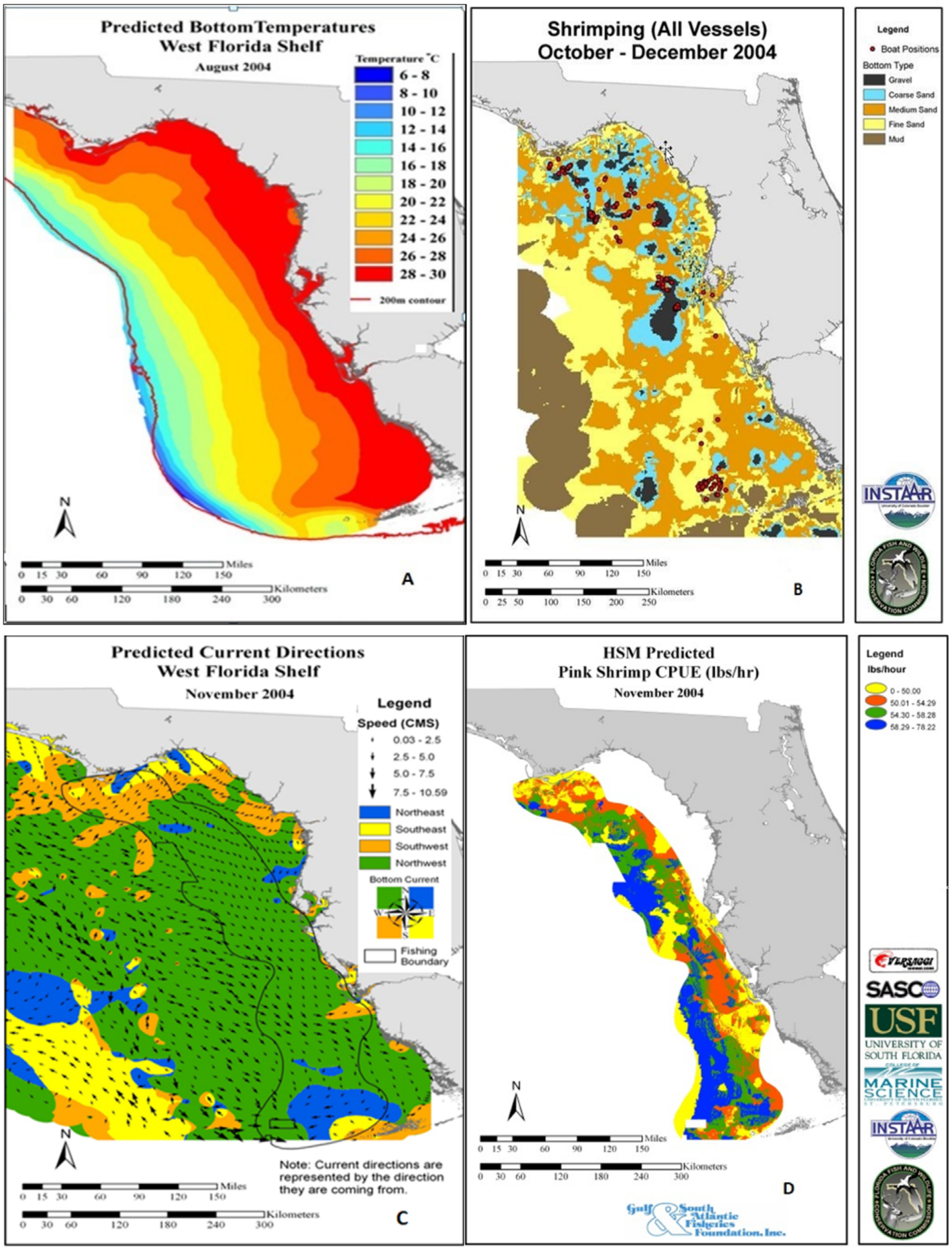


FIGURE 10 The maps depicted include bottom temperature (°C) in August 2004, bottom types and shrimp fishing locations (red dots) from October to December 2004, current speed and current directions from origin for November 2004, and a habitat suitability modelling map for pink shrimp abundance (low to optimum gear-corrected catch-per-unit-efforts [CPUEs]) in November 2004 on the West Florida Shelf.

data from Chris Jenkins (University of Colorado), represents cost-effective collaborations with the fishing industry, oceanographers, and geologists.

HSM analyses were conducted during 2004–2005 using pink shrimp data collected monthly on fishing vessels on the WFS (Rubec et al., 2016b). Suitability functions were used with habitat grids derived from benthic sampling that did not change (depth and bottom type) and grids derived from circulation modelling that changed between months and years (salinity, current speed, and current direction) to create CPUE grids, which were averaged to derive predicted CPUE grids.

HSM maps depicting distribution-abundance of pink shrimp for the WFS were created monthly for 16 months by using delta-gamma GAMs and transferring CPUEs from the fitted functions to habitat grids for water current patterns and other environmental variables (Rubec et al., 2016b). Spatial distributions and highest seasonal abundance of pink shrimp were associated with onshore currents and upwelling onto the WFS during October to December 2004. The study demonstrated that bottom currents during the fall were primarily from the northwest. The upwelling of nutrients onto the WFS probably supported production of food for pink shrimp such as benthic algae and planktonic organisms.

TABLE 3 Evolution of habitat mapping and habitat suitability modelling in Florida estuaries and coastal zones

Papers and reports	Area mapped	Model type	Model validation
Christensen et al. (1997)	Pensacola Bay	HSI-3 species	Expert opinion
Rubec et al. (1998a)	Southeast Florida coast	Pink shrimp and stone	Species life histories and HSIs
	Big Bend NW Florida coast	Crab closure zones	being developed
Rubec et al. (1998b)	Tampa Bay Charlotte Harbor	HSI model	Reciprocal SI transfer developed
			between estuaries
Rubec et al. (1999)	Charlotte Harbor fall season	HSI-fall	SIs transfer from TB to CH
Rubec et al. (2001)	Charlotte Harbor four seasons	Seasonal HSIs	SIs within and transfer
			in both estuaries
Clark et al. (2002)	Pensacola Bay-Galveston Bay	Seasonal HSIs	Mean SIs Pensacola Bay
			vs. mean CPUEs Galveston Bay
Rubec et al. (2005)	Tampa Bay-Charlotte Harbor	Seasonal HSMs	Reciprocal CPUE transfer between
			estuaries four species life-stages
Rubec et al. (2009)	Tampa Bay-Charlotte Harbor	Seasonal HSMs	Reciprocal CPUE transfer between
			estuaries 11 species life-stages
Rubec et al. (2006)	Rookery Bay-Fakahatchee Bay	Seasonal HSMs	Seasonal CPUES transferred from
			CH linked to habitat grids
Rubec et al. (2016a)	West Florida Shelf in 2001	Monthly HSMs	CPUES from ELBs and habitat grids
Rubec et al. (2016b)	West Florida Shelf in 2005	Monthly HSMs	CPUEs from ELBs and habitat grids
			from oceanographers and geologists
Rubec et al. (2016c)	Tampa Bay	Seasonal HSMs	CPUEs and habitat grids estimate
			population numbers for pink shrimp
Rubec et al. (2019)	Charlotte Harbor	Seasonal HSMs	CPUEs linked to habitat grids
		Population estimates	to create seasonal HSM maps
Rubec et al. (2021)	Charlotte Harbor	Seasonal HSMs	CPUEs associated with habitat grids
		population estimates	for withdrawal conditions based on
			Baseline and Minimum Flows

Abbreviations: CH, Charlotte Harbor; CPUEs, catch-per-unit-efforts; ELBs, electronic logbooks; HIS, habitat suitability index; HSMs, habitat suitability models; SIs, suitability indices; TB, Tampa Bay.

3 | DISCUSSION

The creation of HSI maps provides useful information on spatial distributions of species life-stages based on frequency of occurrence data. In many cases, this is the only data available for management of habitats and species in estuaries and coastal zones. There are a variety of spatial ecological methods for analyses of presence/absence data including species distribution modelling (Hunsaker et al., 1993; Skidmore et al., 2011).

Browder and Moore (1981) reviewed literature concerning the effects of freshwater inflow on fish and invertebrate species in bays and estuaries situated in the Gulf of Mexico. Freshwater inputs to estuaries appear to enhance the production of marine organisms because the highest marine standing stocks along shorelines are found in or near estuaries. With respect to habitat areas, they noted that there are at least three reasons why the production of fishery species may correlate with area of favourable habitat: (1) growth may be related to the total quality of available food, and total quantity of available food is the product of food concentration and area; (2) survival and growth rates probably are negatively density dependent; therefore, the larger the favourable HUA, the higher the survival and growth rates within it; and (3) the smaller the area of favourable habitat, the greater the percentage of juvenile animals found in poor habitat, where lower survival and growth rates would be expected. They proposed an input–output model of freshwater inflow tied to fisheries production with the production area being based on a combination of dynamic and stationary habitats. Since no analyses were presented to support these assertions, they should be considered to be hypotheses.

Browder (1991) noted that estuaries serve as nursery habitat for many fishery species, including those caught offshore. Many species of fish and shrimp spawn offshore, then newly hatched larvae or early juveniles move into the estuary. Relative densities of juveniles in estuaries suggest that shallow seagrass beds, tidal creeks, emergent marsh vegetation, and mangrove prop roots are optimal juvenile habitat. Postlarvae first settle out of the plankton into a demersal life in the freshest part of the estuary. They then gradually move to more saline areas as they grow. Freshwater is the basis of estuarine production, establishing the salinity gradients, circulation patterns, and nutrient concentrations that distinguish estuaries from the rest of the coastline.

The main goal of the studies in 2009 within TB and CH was to conduct analyses using suitability functions reciprocally transferred between the estuaries to produce seasonal HSM maps for various species life-stages (Rubec et al., 2009, 2016d). The transfer of suitability functions between estuaries produced similar HSM maps in each estuary, provided the suitability functions (within and transfer) were similar.

The early-recent analyses in 2012 (Figures 7 and 8) demonstrated that similar suitability functions (internal and external) from the same estuary produced almost identical HSM maps (Rubec et al., 2016c). But it is not safe to assume that the statistical analyses associated with the HSMs using fewer than five factors always predicted the same significant factors. The factors can be significant in HSMs without the suitability functions (fitted splines) being very similar. Different depth ranges in each estuary resulted in differing suitability functions for depth (within and transfer) being produced by the TB and CH HSMs. Different within and transfer HSM maps were produced when the functions were applied to the habitat grids in each estuary. If the suitability functions associated with significant factors were different, it was not possible to derive similar HSM maps from the fitted splines.

HSM analyses were conducted in TB during 2013–2014 using v70 of the HSM software (Rubec unpublished) and in CH during 2015–2016 using v73 of the software in R (Rubec et al., 2019, 2021). SWFWMD provided predicted seasonal grid data for temperature and salinity in CH for each year from 2007 to 2014 derived from hydrodynamic modelling (Chen, 2020). We intended to test transferability of the models between TB and CH. But this did not happen due to time constraints and because the months associated with the non-conventional seasons used for the CH freshwater inflow studies in 2019 and 2021 were different from the months comprising conventional seasons used with the HSM analyses for TB.

The salinity ranges in optimum zones occupied by each resident species life-stage in the lower Peace River remained about the same across seasons, while the spatial distribution of salinity zones in the river expanded associated with changes in freshwater inflow (Rubec et al., 2019). The spatial distributions and abundance of six resident species life-stages of fish and blue crab were highest in different salinity segments of the river for most seasons. The Upper P segment had low salinity (0.5–5.0 psu). The abundance of juvenile+adult Hogchoker was highest in this salinity segment for all four seasons. The abundance of early-juvenile Red Drum was highest in this segment during winter (January–March), and highest for early-juvenile Spot during spring (April–June). The question becomes did the species life-stages studied have preferences for low or moderate salinity ranges or were their spatial distributions related to the abundance of prey organisms sustained by nutrients entering the lower Peace River associated with freshwater inflows?

Rubec et al. (2019) noted that SWFWMD had sponsored short-term monitoring and research studies to relate the species composition and abundance of phytoplankton, zooplankton, larval fish, and larval invertebrates to changes in salinity and temperature as well as other water quality and benthic habitat variables in the lower Peace River. The short-term studies and the research by Rubec et al. (2016c, 2019, 2021) with early-juvenile to adult life-stages of fish species, pink shrimp, and blue crab did not discuss the effects of nutrient loading on the production of species life-stages or fisheries production in estuaries situated in southwest Florida.

Peebles et al. (1991) conducted a fish nursery study in the tidal portion of Little Manatee River entering TB to determine relationships with physicochemical gradients and the distribution of food resources. Ichthyoplankton, juvenile fishes, zooplankton, phytoplankton, water chemistry, and freshwater inflows were monitored over 2 years. Salinity zone volumes in the tidal river were found to have a curvilinear relationship with freshwater flow. The tidal portion was heavily utilized by young estuarine-dependent fish species. Migrations into the tidal river were evident in relationships between fish length and salinity at capture and also in age-specific plots of fine-scale spatial distribution. Most fish species migrated to and concentrated within the lower 16 km of the Little Manatee River during the post-larval or early-juvenile life-stages, with spatial peaks in mean fish concentration coinciding with peaks in mean mysid, amphipod, and harpacticoid copepod abundance. Calanoid and cyclopoid copepods, which invaded the lower river from TB at times of low discharge, appeared to be more susceptible to discharge-induced displacement downstream than did mysids, amphipods, and harpacticoid copepods. Various nutrients and dissolved organic carbon were positively correlated with freshwater discharge, while chlorophyll-a levels in the water column of the upper tidal river were negatively correlated with discharge. A trophic study indicated that detritus deposition and benthic diatom production were important contributors to the base of the tidal river's food web, with mysids, amphipods, harpacticoid copepods, and juvenile anchovies functioning as trophic intermediates for young estuarine-dependent fishes.

Peebles et al. (1996) monitored spatial distributions and abundances of copepod nauplii, copepodite/adult copepods, and the larvae of Bay Anchovy in TB at 2-week intervals for 2 years. All possible pairings of the three time-series variables yielded significant positive correlations. Nearly all of the collected anchovy larvae occurred with prey (nauplius) densities higher than those reported to affect larval starvation. The larval association with abundant prey could be explained as (1) the remnants of earlier larval starvation or (2) spawning being concentrated in zooplankton-rich waters. To evaluate these hypotheses, the diet of adult Bay Anchovy was analyzed, and egg/adult prey surveys were conducted across a 290 km^2 area of TB. In five of the six spatial surveys, Bay Anchovy egg abundance was correlated with the abundance of calanoid copepods (primarily adult *Acartia tonsa*). Calanoids were aggregated near sites of stable freshwater discharge during a dry season but became dispersed as discharge increased during a rainy season. Among spatial surveys, egg abundance exhibited a strong non-linear relationship with calanoid aggregation. These findings suggest that the size-specific fecundity of Bay Anchovy is related to adult prey availability, with adult prey availability being represented by a combination of abundance and patchiness.

Bay Anchovy egg abundance in the tidal portion of the Manatee River in TB was compared with conditions in the spawning ground before and after spawning to distinguish prey-supply-based spawning responses from post-spawning advective effects (Peebles, 2002). Plume fronts were a prominent feature of the spawning ground. Egg distribution, copepod distribution, and front development were surveyed 25 times across a wide range of freshwater inflow conditions. Surface-front strength (maximum interpolated salinity slope) was strongly correlated with the size of the frontal zone. Eggs were most abundant landward of the frontal zone at a location with consistently high abundance of the copepod *A. tonsa*, which is consumed by adult and larval Bay Anchovy. Large, significant changes in egg abundance were observed over both long (seasons) and short (<3 days) periods. An El Niño-associated flood event caused the rapid evolution of a large, seaward-moving frontal system that initially had a negative effect on egg abundance. Spawning resumed in reduced salinity following passage of the front, demonstrating a level of plasticity in spawning response to salinity change. A stepwise regression model explained 92% of the variation in egg abundance. Egg abundance appeared to be determined initially by pre-spawning prey supply and temperature, and subsequently by variable retention behind the frontal zone.

Since salinity covaries with the amount of freshwater inflow, it may be serving as a marker of the low salinity water mass containing nutrients rather than a direct driver of fish and macroinvertebrate species distributions (Rubec et al., 2019). The role of salinity in patterning species distributions and determining overall abundance is especially important given that salinity is a major characteristic of estuarine habitat that will be affected by changes in water management. Relationships with salinity are key to predicting species distributions, species abundances, and their changes in relation to freshwater inflow in Florida estuaries. Research should be conducted in Florida estuaries to determine nutrient inputs associated with freshwater inflows and used to develop associated food web models. However, this is not a practical method for water managers to presently use in setting Minimum Flows and Levels. A percent-of-flow approach to support water withdrawals and maintenance of salinity ranges that are not detrimental to fish and macroinvertebrate species has been adopted by SWFWMD (Flannery et al., 2002; SWFWMD 2010). It appears likely that both salinity and the availability of prey influence spatial distributions and population abundance of early life-stages of fish and macroinvertebrate species in estuaries. In many cases, it is not possible to separate the effects of salinity from the availability of prey.

The finding that each species life-stage studied occupied a different salinity range in CH that stayed about the same between seasons (Rubec et al., 2019) is not explained by the existing literature. Research should determine prey items consumed by each species life-stage and whether their prey items are similar within each species' salinity range between seasons.

Analyses using models and GIS, summarized in the present paper, provide information concerning the seasonal habitat requirements of estuarine and coastal species of fish and macroinvertebrates. They can be used to help determine EFH and habitat areas of particular concern to support ecosystem-based fishery management, to support inclusion of fish habitat information in fisheries ecosystem plans by U.S. fishery management councils, to determine critical habitats for threatened and endangered species, to support oil spill response and natural resource damage assessments of areas impacted by chemical spills, to support the placement and management of artificial reef fisheries, and to support coastal zone planning and management (Rubec, 1999; Rubec et al., 2019).

The studies by Rubec et al. (2016c, 2019, 2021) have mapped habitat types in TB and CH and modelled and mapped the seasonal abundance of species life-stages. Mean CPUEs multiplied by the areal extent of suitability zones (HUAs) were used to derive estimates of population numbers. While FWRI collects extensive data in Florida estuaries, there is limited use of the FIM data. The creation of seasonal HSM maps for fish and macroinvertebrate species life-stages in estuaries is an important use of the data. The prediction of population numbers from the HSM maps makes this spatial modelling-mapping approach a stock assessment method. This fills an important gap, since no one has been estimating population numbers of fish and macroinvertebrate species life-stages in estuaries situated in Florida and elsewhere.

Stock assessments generally need time series of abundance over a period of 6 or more years. One advantage of HSM analyses using FIM data and salinity and temperature patterns derived from hydrodynamic modelling (Chen, 2020) is it can facilitate the assessment of impacts on population numbers from short-term climatic events such as droughts or flooding. The data could be used to create interannual CPUE time series and seasonal HSM maps by year.

HSM maps, derived from delta-gamma GAMs linked to habitat grids, can be used to support management due to changes in environmental conditions and changes in freshwater inflows to estuaries. They provide useful information concerning the seasonal habitat requirements of estuarine species for various life-stages. The main products are predicted grids with GC-CPUEs computed in numbers per square meter, HSM maps created using GIS, and seasonal estimates of population numbers derived from the maps. Salinity was statistically significant for most species' life-stages that were analyzed. Therefore, analyses such as those reported here can be used to inform management actions associated with water withdrawals or climatic effects. Given appropriate actual or simulated environmental data, HSM maps and associated analyses of species life-stages can be prepared to support various management scenarios.

AUTHOR CONTRIBUTIONS

Peter Rubec was a fisheries research scientist associated with the FWC Center for Spatial Analysis (CFSA) in St. Petersburg, Florida. He was involved in conceptualization, spatial modelling, and collaboration with others involved in the studies conducted from 1997 to present. Christine Santi presently with CFSA provided advice concerning the methods used for mapping by GIS staff at CFSA and co-authored three papers. Jerald Ault and Mark Monaco were members of the committee created to develop modelling and mapping methods. Ault developed

SAS programs to support habitat suitability modelling by analyses of HSI-data and HSM-data in five reports and was a co-author for two papers. Monaco supervised NOAA staff involved in GIS-based mapping and was a co-author for six papers.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This study is a review of previous work. Therefore, no ethics statement was obtained by the authors.

ORCID

Peter J. Rubec https://orcid.org/0000-0002-9378-0776

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