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Linking Oceanographic Modeling and Benthic Mapping with Habitat Suitability Models for Pink Shrimp on the West Florida Shelf

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Abstract

Research was undertaken to model and map the spatial distributions and abundances of pink shrimp *Farfantepenaeus duorarum* on the West Florida Shelf (WFS) using habitat suitability modeling (HSM). Data loggers and electronic logbook systems on three shrimp boats were used to gather catch and effort data along with bottom temperature, salinity, and depth data at the fishing locations. Vessel monitoring system (VMS) data supplied by the fishing company helped delineate areas with high fishing activity. For the vessels participating in this study, significantly higher mean catch per unit effort (CPUE) of pink shrimp was realized on the WFS during June–September 2004 and October–December 2004 than during January–March 2005 and April–June 2005. Suitability functions were created to predict CPUE in relation to depth, aspect, bottom type, bottom temperature, current speed, current direction, and VMS zone. Oceanographic modeling was conducted monthly from March 2004 to June 2005. Bottom current speed and direction indicated marked upwelling onto the WFS during 2004 and

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downwelling during 2005. The HSM linked to GIS was used to predict the spatial distributions and abundances of pink shrimp monthly from March 2004 to June 2005. While seven factors contributed to the HSM, current speed and current direction appeared to be most important during June–December 2004. The areas with the most pronounced upwelling were also the areas that the HSM predicted would have the highest mean CPUEs. This relationship was verified by overlaying the observed CPUE from the fishing vessels onto the suitability zones predicted by the HSM.

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 (EFH) regulations for fishery management plans (NMFS 1996) and that the councils describe these habitats in text, tables, and maps in such plans (NMFS 1997b). Essential fish habitat 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 (e.g., coral reefs, marshes, and kelp beds) and water column characteristics (e.g., turbidity zones, thermoclines, and fronts separating water masses) that focus the species' distribution (NMFS 1997a). 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—areas judged particularly important for the long-term productivity of one or more managed species or that were vulnerable to degradation. The Magnuson–Stevens Reauthorization Act required the councils to create fishery ecosystem plans to better relate fishery species and fisheries to their supporting ecosystems (MSRA 2007).

The goals of this study were to determine the environmental conditions associated with high CPUE of pink shrimp *Farfantepenaeus duorarum* on the West Florida Shelf (WFS). Maps that depicted the spatial and temporal distributions of catch and fishing effort were needed. The shrimp industry and the scientific community would benefit from understanding what combination of habitat and environmental conditions contributed to high catch rates for shrimp. The time spent searching for areas with high shrimp concentrations might be reduced with better knowledge of the oceanographic and benthic-habitat conditions preferred by pink shrimp.

A coordinated program designed to gather oceanographic and atmospheric data is in place on the WFS. The Coastal Ocean Monitoring and Prediction System is managed by the University of South Florida (USF) (Weisberg et al. 2000, 2005, 2009a, 2009b). The USF data set for the WFS ranges from current profiles at some locations to full sets of air–sea interaction variables at others. Current velocity data from an array of acoustic Doppler current profilers show that the long-term mean flow of water, which upwells onto the WFS seasonally (Liu and Weisberg 2012), is oriented approximately along-isobath (lines of constant depth) and directed southeastward (Weisberg et al. 2009b).

The bottom types on the WFS feature a broad south–north transition from a very wide, low-energy, sediment-starved carbonate shelf to a mixed siliciclastic–carbonate shelf (Hine and Locker 2011). From south to north along the coast there are sectors dominated by mangrove, seagrass, or marshes and by barrier-beach chains.

At depths of 20–50 m, Minerals Management Service (MMS) and National Oceanographic and Atmospheric Administration (NOAA) regional maps show most of the bottom on the WFS as consisting of sand (MMS 1983; Sheridan and Caldwell 2002). However, when detailed surveys were made, the bottom was found to be much more heterogeneous. For example, using side-scan sonar, underwater television, and still photography, Woodward-Clyde Consultants (1979) showed variability on a scale of just meters between soft bottom, hard bottom, and scattered hard-bottom in six MMS lease blocks situated east of the Florida Middle Grounds (Figure 1).

A NOAA Data Atlas (Map 1.03, titled Coral Reefs and Hard-Bottom Areas) depicts a hard-bottom zone running up through the center of the WFS from east of the Dry Tortugas north to the area east of the Florida Middle Grounds (NOAA 1985). This zone is labeled "Supposed Areas of Scattered Coral Heads, Banks, or Hard Bottoms." The final amendment for addressing essential fish habitat requirements by the Gulf of Mexico Fisheries Management Council (GMFMC) assumed that this zone was not EFH for the shrimp fisheries, since shrimp vessels do not trawl over hard bottom (GMFMC 2005). But some areas within this zone on the WFS are in fact not hard bottom and are fished by the shrimp fishery (Rubec et al. 2006).

The GIS modeling and mapping conducted by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute have been used to relate pink shrimp abundance to environmental conditions. The first phase of the study included mapping benthic and water column habitats. Shrimp CPUEs were analyzed across environmental gradients to produce suitability functions. Then habitat suitability modeling (HSM) was conducted monthly for 16 months to produce HSM maps with low to optimum zones on the WFS.

METHODS

The West Florida Shelf, situated off the west coast of Florida, is the largest continental shelf area in the United

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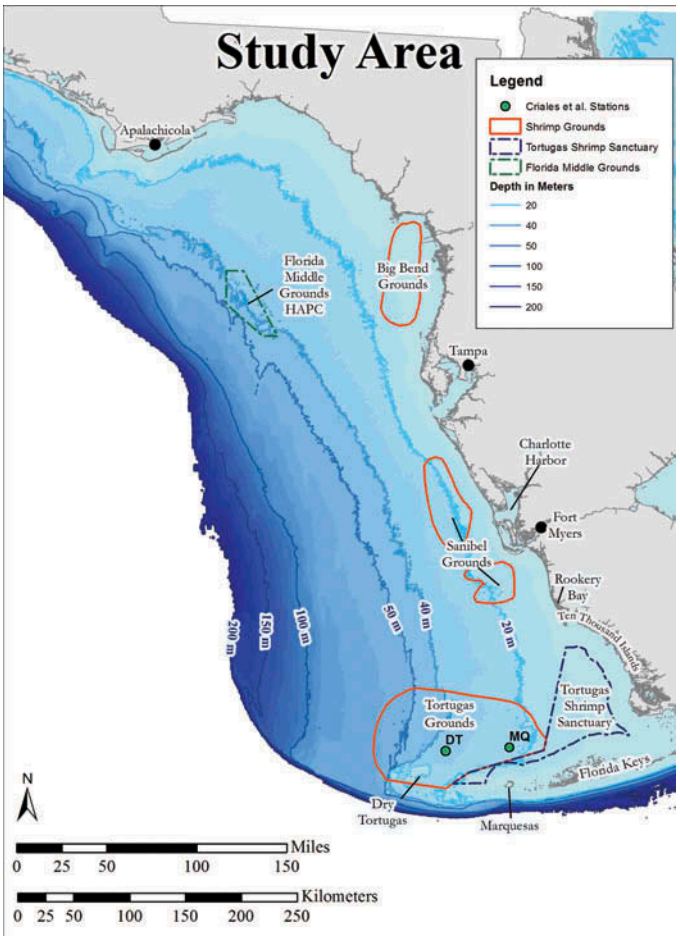


FIGURE 1. Map depicting locations on the West Florida Shelf mentioned in the article.

States. Figure 1 depicts the locations of various features (estuaries, seamounts, shrimp fishing grounds, areas closed to fishing, and cities) mentioned in this article.

We used an electronic logbook (ELB) to collect trawl catch, effort, and associated environmental data from three shrimping vessels operating on the WFS from July 1, 2004, to June 30, 2005 (Rubec et al. 2006, 2016). The beginning and ending times of each trawl haul recorded by each boat's GPS receiver were used to compute fishing effort in terms of hours fished by the main trawls. Catch (lb) and effort (h) were added to the database. Conductivity, temperature, and depth (CTDs) data obtained by data loggers deployed from the vessels were added to the catch and effort data in the main trawls data set.

Habitat modeling and mapping.—Circulation modeling was conducted monthly for 16 months using the Finite Volume Coastal Ocean Model (FVCOM; Chen et al. 2003). Daily predictions for surface, midwater, and bottom conditions (temperature, salinity, water current direction, and current velocity) were derived from March 1, 2004, to June 30, 2005. Since the present study focused on bottom conditions, data sets were created representing averaged monthly conditions (March 2004–June 2005) for bottom temperature, bottom salinity, bottom current direction (ranging from 0° to 359°), and bottom current speed (ranging from 0 to 12 cm/s) on the WFS. The oceanographic data points were unequally spaced because they were derived from nodes in the FVCOM triangular grid.

The Geostatistical Analyst extension within ArcGIS 9 was used to produce semivariograms (by varying the radius around the points in order to determine the optimal radius and number of adjoining points) associated with each of the water column data sets (Johnston et al. 2001). The Spatial Analyst extension was then used to conduct ordinary kriging using the optimal parameters to produce 16 monthly grid layers with 90-m × 90-m cells for bottom temperature and bottom current speed. Current directions were interpolated using inverse distance weighting (IDW) to produce 16 monthly bottom current direction grids (Williams 1999).

Sediment and hard-bottom data for the WFS obtained from the U.S. Geological Survey (Reid et al. 2005) and other sources were used to create benthic sediment maps using the methods and software associated with dbSEABED (Williams et al. 2003; Jenkins et al. 2006; Goff et al. 2008). The data contained values for the following factors: (1) gravel, sand, and mud contents, (2) rock exposure, and (3) average grain size.

Geographical information system–based sediment grids were created representing (1) mean grain sizes (phi values), (2) percentage mud, (3) percentage silt, (4) percentage sand, (5) percentage gravel, and (6) percentage rock exposure. A grid resolution of 0.02° latitude and longitude was used. The IDW interpolation method was modified (1) to vary the search radius by proximity to the coast and (2) to employ the root mean squares of the distances (km) and water depth differences (m) combined as weights. Cells with more than one data point were assigned the median value to create raster maps of mean grain size, percentage gravel, and percentage sand. A benthic sediment grid classified by phi size was reclassified into a bottom-type grid with the following zones: mud, fine sand, medium sand, coarse sand, and gravel. True hard-bottom areas (with large rocks, boulders, or bare bedrock) are not included since the data were insufficient for mapping these features.

An interpolated bathymetric grid of 90-m × 90-m cell size was obtained from the NOAA National Geophysical Data Center (Divins and Metzger 2004). An aspect grid was derived from this grid. Aspects were mapped as F (flat), NE (0–89°), SE (90–179°), SW (180–269°), and NW (270–359°).

The Fish and Wildlife Research Institute obtained 31,185 data points representing approximately 16,000 trawl hauls by six shrimping vessels that had fished on the WFS from 1995 to 2003. The data were recorded by a Sasco Vessel Fleet Tracker Vessel Monitoring System (VMS) installed on each boat. The VMS data were used to map the frequency of fishing using the

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point-density function in ArcGIS 9. Polygons were designated as low-, medium-, or high-intensity fishing zones.

The number of habitat grid layers created was as follows: 1 for bottom type, 1 for bathymetry, 1 for aspect, 1 for VMS zone, 16 (i.e., monthly) for bottom current speed, 16 for bottom current direction, and 16 for bottom temperature.

The ELB system was used to collect catch and effort data during 2004–2005 from the main trawl tows and associated bottom conductivity (salinity), temperature, and depth, as measured by the CTDs from July 2004 to June 2005. Latitude and longitude were automatically recorded at the beginning and end of each tow using the boat's global positioning system. Standardized CPUEs (lb/h) were derived from the catch and effort data.

Seasonal point-distribution maps were created with seasonal fishing locations (January–March 2005, April–June 2005) and CPUEs (July–September 2004, October–December 2004). The CPUEs were partitioned into quartiles and mapped as circles of different colors depicting the seasonal locations of low to high CPUEs.

Habitat suitability modeling.—Suitability functions were fit to bottom temperature and depth data by season using SAS JMP version 5.0 (SAS 2002). Splines (variable lambda) were fitted to the CPUE data by 1°C temperature intervals and by 1-m depth intervals for each season. There was little variation in the conductivity data, so no suitability functions were created across salinity gradients.

Suitability was also determined by overlaying fishing locations (by latitude and longitude) onto the habitat grids within seasons. Tables were created for (1) mean CPUE by sediment type (five types), (2) mean CPUE by aspect (F, NE, SE, SW, or NW), (3) mean CPUE by VMS zone (three zones), (4) mean CPUE by current speed, and (5) mean CPUE by current direction. For the oceanographic data with a directional component (current speed and current direction), the directional bearings were partitioned into four ranges: NE, SE, SW, and NW.

The CPUE data from the suitability functions were assigned to corresponding environmental intervals in the following habitat grids: (1) sediment type, (2) bathymetry, (3) aspect, (4) VMS zone, (5) monthly bottom current speed, (6) monthly bottom current direction, and (7) monthly bottom temperature.

Composite CPUE values within 90-m × 90-m cells were derived from the CPUEs associated with seven habitat layers using the geometric mean algorithm: $\text{HSM} = (\Pi\ \text{CPUE}_i)^{1/n}$. The Model Builder extension was used with the Spatial Analyst extension in ArcGIS 9 to support creation of monthly HSM maps for pink shrimp on the WFS. The continuous CPUE grid produced for each month was then partitioned into four HSM zones with approximately equal areas. Zones on the HSM map can be used to depict areas with low to optimum habitat suitability.

Model verification.—We verified the model results by overlaying the observed CPUE (lb/h) data by latitude and longitude onto the predicted HSM zones. The observed data were tagged with the codes for the HSM zones (low to optimum), and mean observed CPUEs were computed for each zone. The model can be considered to have successfully predicted the spatial distributions of the shrimp if the mean observed CPUEs exhibited an increasing relationship across the low to optimum predicted HSM zones.

RESULTS

Fishing Zones from VMS

Most of the fishing was found to occur within an area of 66,031 km^2 (19,251 square nautical miles). Hence, this area was chosen as the fishable area for HSM analyses (Figure 2A). Little difference was found in the relative frequencies for the low- and moderate-intensity VMS zones (Figure 2B). Most of the fishing activity (83%) was concentrated in the high-intensity zone. With respect to the relative percentages of the total area occupied by each VMS zone, the high-intensity zone occupied the smallest proportion of the total area, only 12.9% (Figure 2C).

Oceanography

Maps were produced monthly from March 2004 to June 2005 to display bottom current speeds and directions (Rubec et al. 2006). Especially noticeable in these maps is that bottom currents exhibited upwelling to the WFS during July–December 2004 and downwelling during January–June 2005. The 2004 period was one in which the monthly means for current speed and mean direction showed an upwelling-favorable circulation field, that is, one in which the near-bottom circulation tended to be directed onshore and downcoast (to the south); by contrast, in 2005 a downwelling-favorable field predominated in which the near-bottom circulation tended to be directed offshore and upcoast (northward) over most of the WFS.

Most bottom currents within the shrimp-fishing boundary on the WFS originated from the northwest in October 2004 (Figure 3A). In contrast, most of the bottom currents within the boundary originated from the southeast in March 2005 (Figure 3B).

Figure 4A depicts current speeds in October 2004 binned by 1 cm/s intervals. Currents mostly ranged from 0–0.9 to 3.0–3.9 cm/s. The higher current speeds in the southern part of the WFS were associated with strong upwelling. Bottom current speeds associated with current patterns directed offshore were not as strong in April 2005 (Figure 4B). Most currents were in the range of 0–1.9 cm/s. Currents ranging from 2.0 to 3.9 cm/s occurred along the western side of the shrimp fishing boundary. Bottom currents intensified and extended over the southern part of the WFS from September to December 2004.

The monthly bottom temperature maps produced during the study depict the cooling of shelf waters in fall and winter and their warming in spring and summer. During summer 2004, the surface

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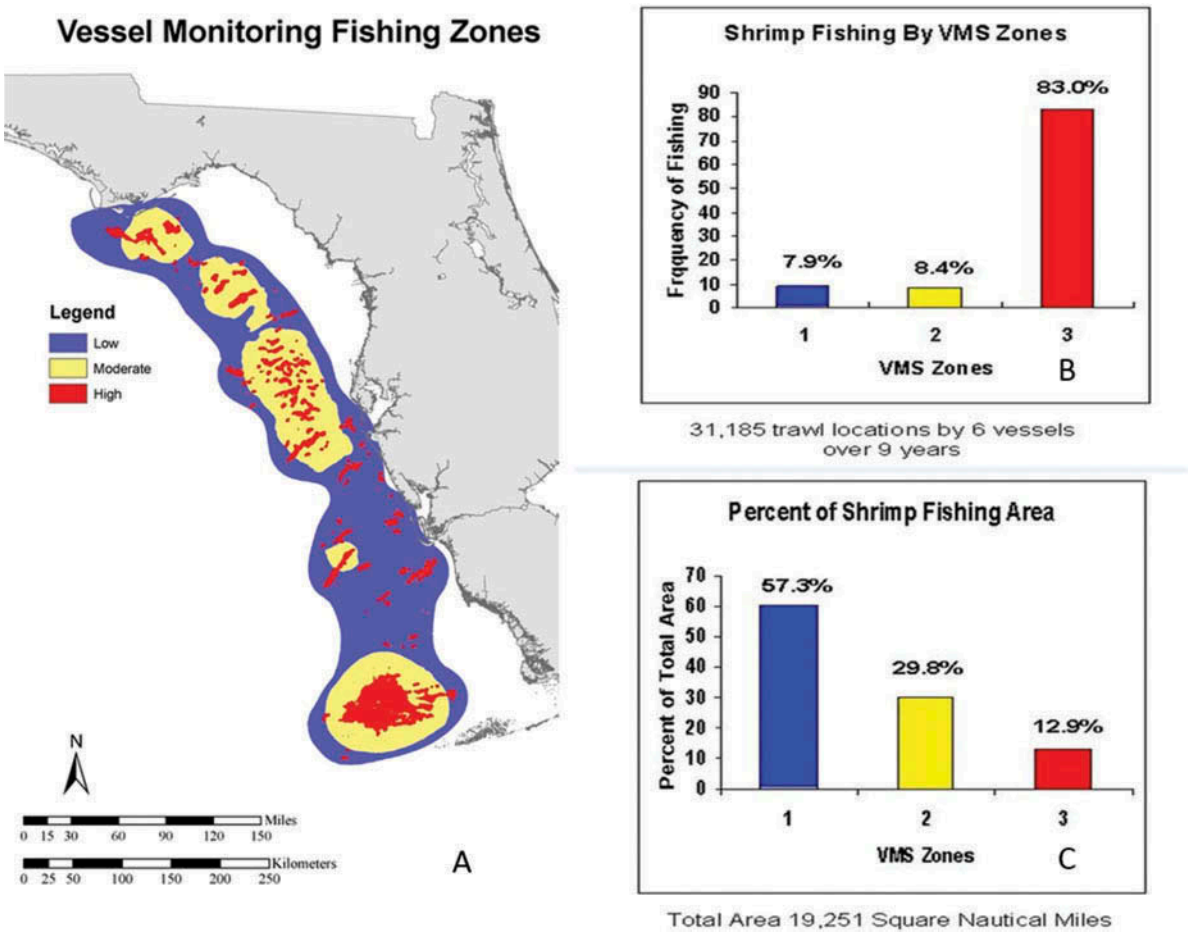


FIGURE 2. **(A)** Map of vessel monitoring zones (VMSs) derived from an analysis of fishing location data collected from 1995 to 2003 (blue = low-, yellow = moderate-, and red = high-intensity fishing activity); **(B)** relative frequencies of fishing activity within the VMS zones; and **(C)** relative proportions of the total area occupied by the VMS zones.

temperatures were 6–8°C higher than the bottom temperatures. Bottom temperatures appeared to be related to the upwelling of cooler water onto the WFS. During winter, little difference (<2°C) was found between the surface and bottom temperatures.

During 2004, the warmest water occurred close to shore from April to September. In September, cooler temperatures occurred in deeper areas offshore due to upwelling onto the shelf (Figure 5A). During 2005, warm bottom temperature zones in the south shifted northward from January through June. In April 2005, cooler bottom temperatures occurred northward, with the warmest water occurring near the Ten Thousand Islands and the Florida Keys (Figure 5B).

A sediment type map derived from the classification of sediments by phi values is presented in Figure 6A.

Fishing Patterns

Shrimp fishing locations were mapped to determine seasonal fishing activity in relation to mapped sediment types. Most of the shrimping in January–March 2005 was concentrated northeast of the Dry Tortugas (Figure 6A). The bottom types on the Tortugas Grounds are primarily fine sand and mud. In April–June 2005, most of the fishing was located farther north over medium sand, coarse sand, and gravel (Figure 6B). During 2004, fishing activity was distributed both north and south in July–September and October–December over a range of sediment types.

Figure 7A depicts the spatial distribution of CPUEs in July–September 2004. While fishing activity was greater north of Tampa, high CPUEs (red circles) were seen both north and south of Tampa. During this period upwelling occurred over most of the WFS, with bottom currents originating from the northwest (Figure 3A). In October–December 2004, fishing took place both north and south of Tampa, but high CPUEs were concentrated on the Tortugas Grounds (Figure 7B) in the area associated with strong onshore upwelling (Figure 3A).

Mean CPUEs across the WFS were computed for each season during 2004 and 2005 when shrimp fishing was

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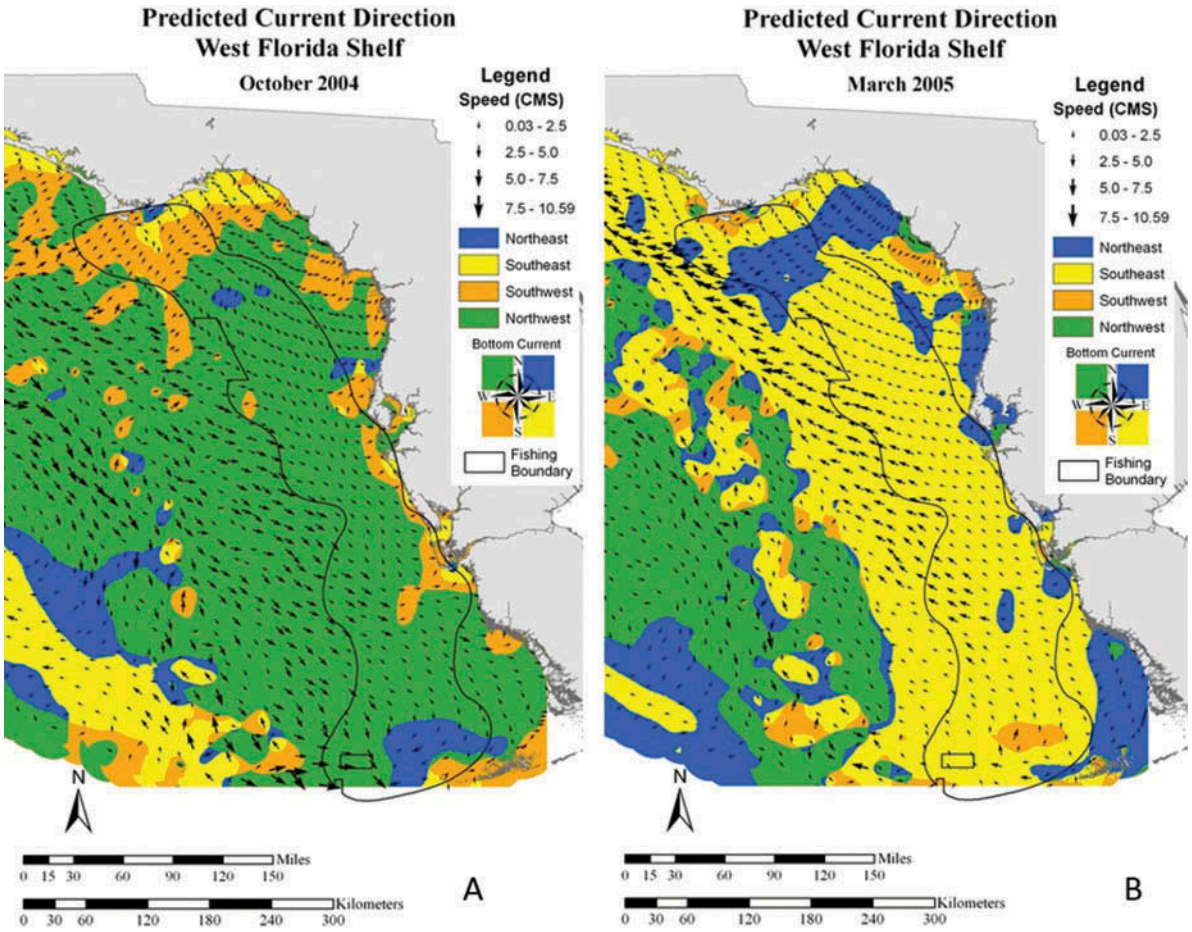


FIGURE 3. Maps depicting where bottom currents originated off the west coast of Florida. Panel **(A)** shows an upwelling pattern during October 2004, with most currents within the fishing boundary originating from the northwest. Panel **(B)** shows a downwelling pattern during March 2005, with most currents within the fishing boundary originating from the southeast.

monitored with the ELB (Figure 8). Based on one-way analysis of variance (ANOVA), there were significant difference in mean CPUE ($P \leq 0.0001$). Mean CPUEs were higher in October–December 2004 (67.46 lb/h) and July–September 2004 (46.89 lb/h) than in January–March 2005 (24.28 lb/h) and April–June 2005 (27.72 lb/h).

Suitability Functions

Suitability functions revealed that the vessels caught more shrimp at higher bottom temperatures during both seasons in 2005 (Figure 9A, B). In July–September 2004 (Figure 9C), CPUEs were greater at lower bottom temperatures (22–25°C). A small increase in the CPUE was also noted at the highest water temperature (31°C). During October–December 2004, higher CPUEs occurred at both low (19–21°C) and high bottom temperatures (26–28°C) (Figure 9D). Hence, higher catch rates occurred at both low and high bottom temperatures during 2004.

Figure 10 shows seasonal splines fitted to CPUEs versus depth. No fitted trend (increasing or decreasing) was apparent for CPUEs with respect to depth for January–March 2005 (Figure 10A) or April–June 2005 (Figure 10B). Higher CPUEs were noted in both shallow and deeper water during July–September 2004 (Figure 10C). An increasing relationship was found with fitted CPUEs in relation to increasing water depth for October–December 2004 (Figure 10D).

In April–June 2005, shrimp fishing did not occur deeper than 35 m (Figure 10B). During the other three seasons fishing extended to 50 m (Figure 10A, C, and D). During 2004, those fishermen who fished in deeper water (35–50 m) obtained higher catch rates.

Seasonal graphs (not presented) were created to examine the frequency of fishing activity within the VMS zones. The highest frequency of fishing activity occurred in the high-intensity VMS zone during each season (80% in July–September 2004, 80% in October–December 2004, 92% in January–March 2005, and 70% in April–June 2005). The

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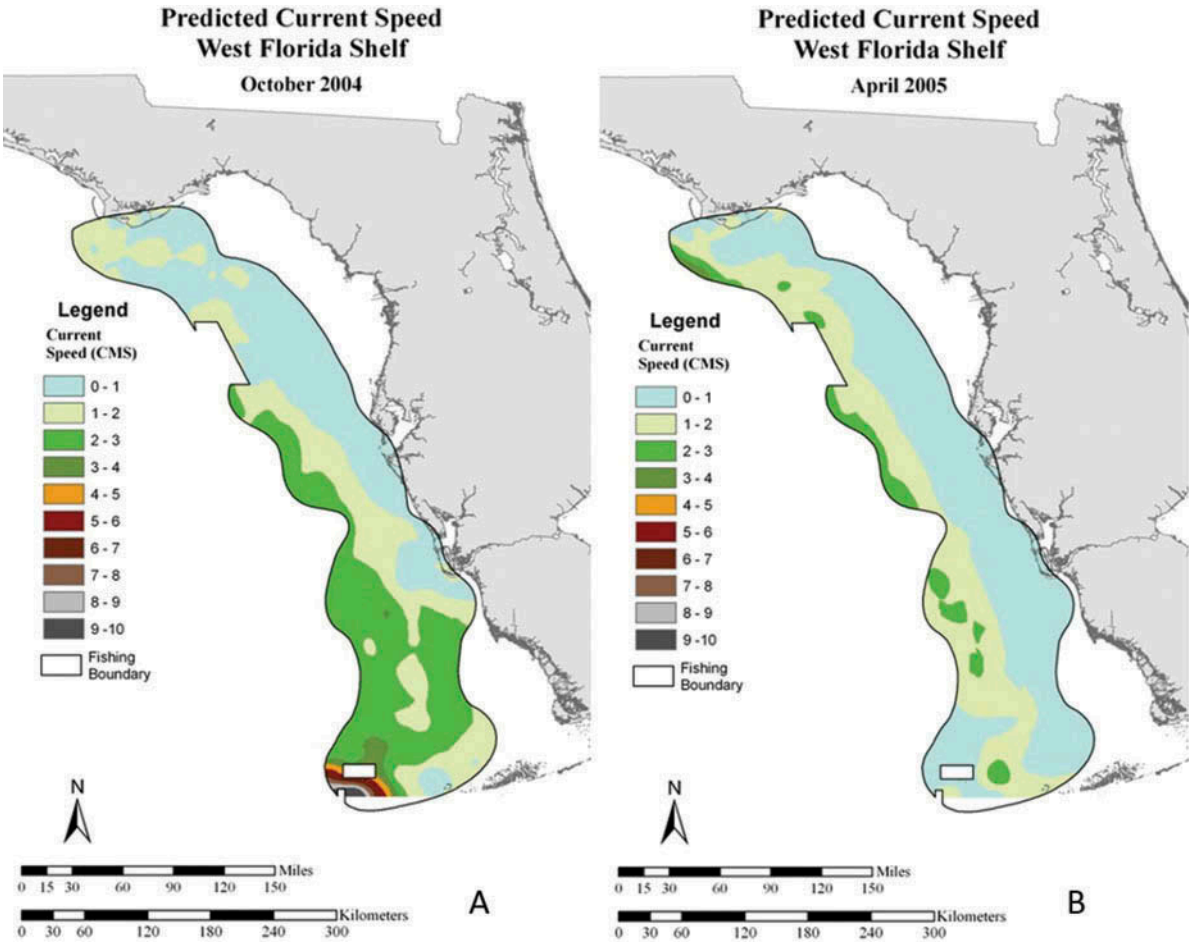


FIGURE 4. Maps of monthly predicted bottom current speeds (cm/s) within the shrimp fishing boundary in **(A)** October 2004 and **(B)** April 2005.

seasonal results were similar to that derived from the analysis of fishing activity from 1995 to 2003 (Figure 2B), with most shrimping being concentrated in the high-intensity fishing zone (Figure 2A). However, one-way ANOVAs found that mean CPUEs by VMS zone were not significantly different within each season (Table 1).

Highly significant differences in mean CPUEs by bottom sediment type were found for the first three seasons (Table 2). Higher mean CPUEs occurred over fine sand during July–September 2004, over both mud and fine sand in October–December 2004, and over mud in January–March 2005, indicating that the shrimp exhibited a strong habitat affinity for these substrate types. There was no significant difference in mean CPUEs by bottom sediment type in April–June 2005, when fishing occurred over fine sand, medium sand, coarse sand, and gravel.

Vessel positions were overlaid onto the monthly current direction grids to determine the frequency of bottom currents by fishing location. During July–September 2004, 83.0% of the bottom currents came from the northwest. In October–December 2004, 66.7% of the bottom currents came from this direction. During January–March 2005, 78.9% of the currents came from the southeast, and in April–June 2005 52.9% of the currents came from the northeast and 39.1% from the southeast.

One-way ANOVAs found that the mean CPUEs by current direction were significantly different during July–September 2004, when the predominant current was from the northwest (Table 3). No significant differences were found for mean CPUEs by bottom current direction within the other three seasons. However, there were seasonal changes in the greatest mean CPUEs for different current directions, which indicate that pink shrimp were responding to changes in current direction between seasons.

Mean CPUEs with respect to current speed were determined within each seasonal time period (Table 4). During July–September 2004 and October–December 2004, the differences in mean CPUEs were highly significant. The highest mean CPUEs were 3–3.9 cm/s in both seasons. While CPUEs were greatest at the highest available current speeds during January–March 2005 (3–3.9 cm/s) and April–June 2005 (2–2.9 cm/s), they were not significantly different from the CPUEs at lower current speeds.

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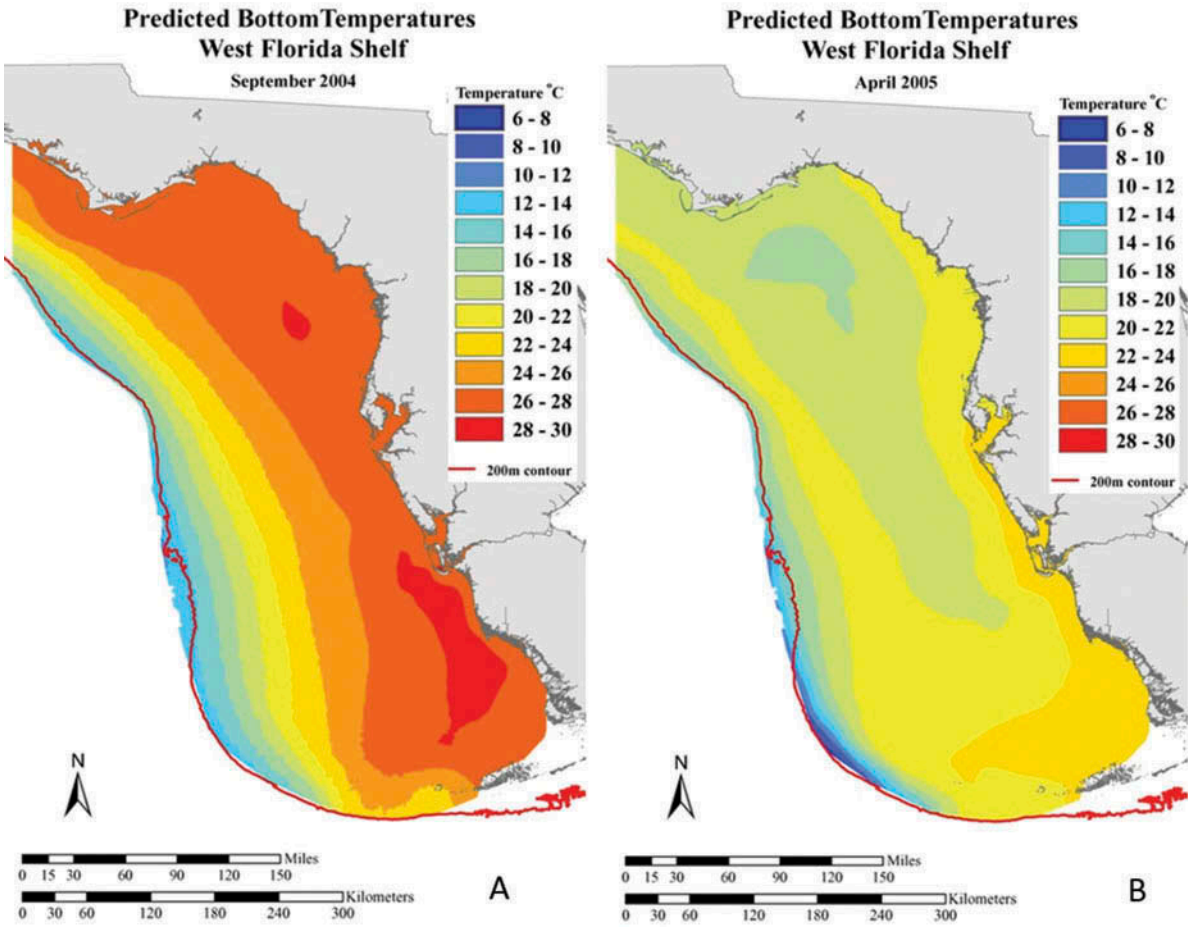


FIGURE 5. Maps of monthly bottom water temperatures on the West Florida Shelf in **(A)** September 2004 and **(B)** April 2005.

Mean CPUEs by aspect were not significantly different within each season (Table 5). During January–March 2005, the largest CPUEs were associated with aspects sloping to the southeast and southwest. The largest mean CPUE in April–June 2005 was associated with aspects facing southwest. The greatest mean CPUEs during July–September 2004 occurred with aspects facing to the northeast and northwest. The largest mean CPUEs in October–December 2004 occurred over flat bottom and with aspects sloping to the northwest and southwest.

Habitat Suitability Maps

Examples selected from the 16 monthly HSM maps are presented to show how habitat suitability changed between 2004 and 2005. The HSM map for July 2004 (Figure 11A) has the optimum zone (blue) distributed in deeper water along the western side of the fishable zone when the upwelling pattern was concentrated in deeper water. The HSM map for November 2004 (Figure 11B) shows that the optimum zone had extended farther onto the shelf, particularly in the southern area near the Dry Tortugas. This is appears to be related to the upwelling that expanded onto the shelf during the fall. On the HSM map for March 2005 (Figure 12A), the optimum zone is distributed mostly in the southern part of the WFS. By contrast, on the HSM map for June 2005 (Figure 12B), the optimum zone is mostly distributed in the northern part of the WFS.

Verification Tests

Table 6 presents mean observed CPUEs by HSM zone monthly from March 2004 to June 2005. Mean CPUEs increased across the predicted HSM zones for all 16 months analyzed. Hence, it is believed that the HSM analyses were successful in predicting the spatial distributions and relative mean abundances of pink shrimp by HSM zone for every month.

Monthly one-way ANOVAs found significant differences between the mean CPUEs for April, June, July, August, September, October, November, and December 2004 and May 2005 (Table 6). The months with significant differences in mean CPUEs mostly coincide with the months in which

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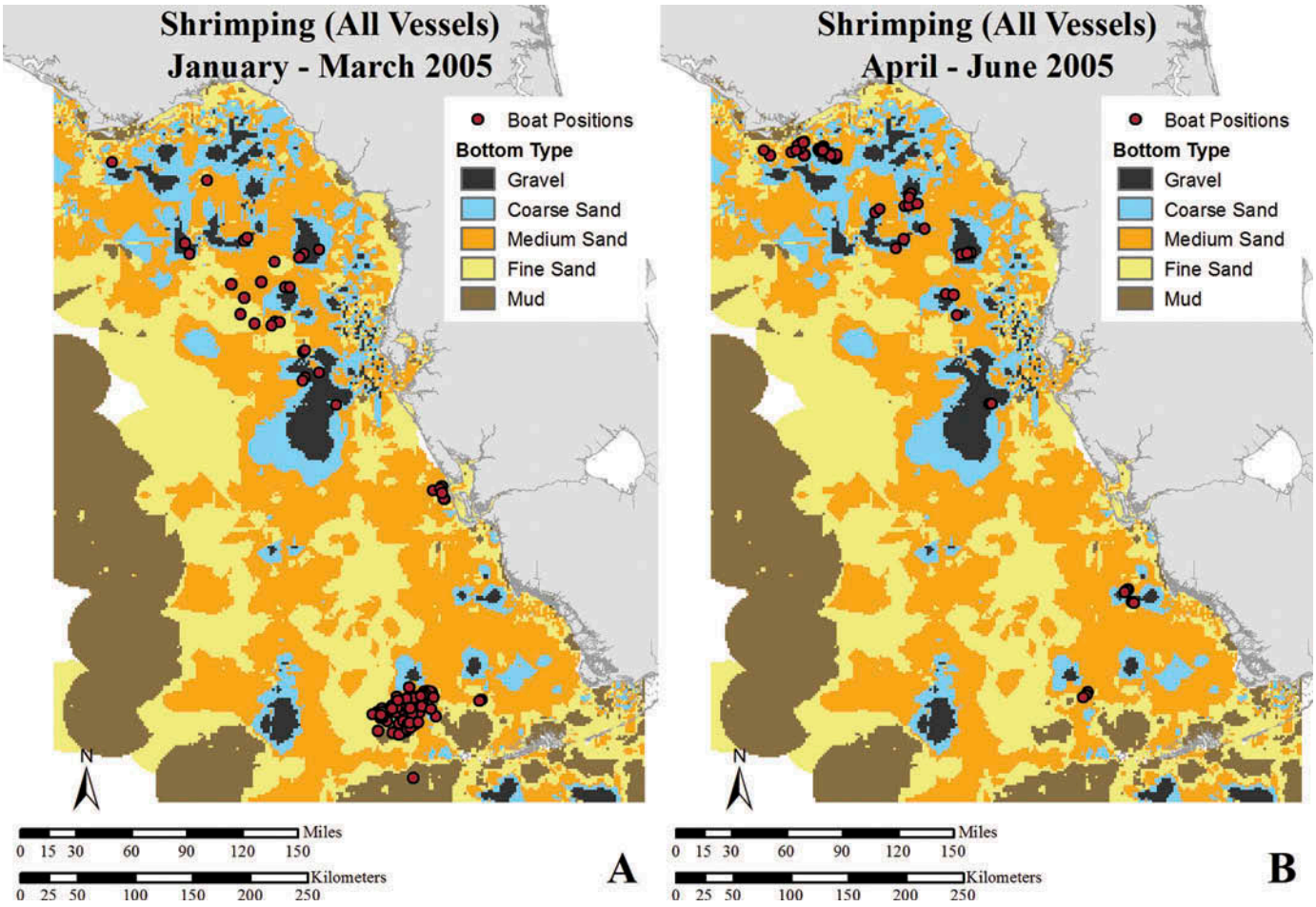


FIGURE 6. Seasonal maps depicting fishing locations with red dots plotted over different sediment types in **(A)** January–March 2005 and **(B)** April–June 2005.

there were onshore current speeds of 3 cm/s associated with upwelling onto the WFS. The mean CPUEs in the optimum zone were markedly higher than those for the other HSM zones for each month from June to December 2004. The verification test for September 2004 is presented in Figure 13.

DISCUSSION

The present study created monthly HSM maps that depict changes in zones of abundance based on CPUE relationships with both benthic and water column habitats. The HSM analyses were successful in predicting the spatial distributions and relative abundances of adult pink shrimp monthly from March 2004 through June 2005.

According to earlier research, adult pink shrimp prefer rather firm bottoms of mud and silt with coral sand containing a mixture of shell (Springer and Bullis 1954; Hildebrand 1955; Williams 1958; Kennedy and Barber 1981; Drexler and Ainesworth 2013; Grüss et al. 2014). Our study tends to agree with this research. There were significantly higher mean CPUEs over mud and/or fine sand during January–March 2005, June–August 2004, and October–December 2004 (Table 2). But these sediment types were not associated with significantly greater mean CPUEs during April–March 2005, when pink shrimp were most abundant over medium sand, coarse sand, and gravel. Mud is only found near the Dry Tortugas. The absence of mean CPUEs over mud from April to June 2005 is probably related to the shift of shrimp fishing activity farther north (Figure 6B).

The optimum HSM zone was found in the southern part of the WFS during January–March 2005 (Figure 12A) and farther north in April–June 2005 (Figure 12B). The most important habitat condition influencing the mean CPUEs of shrimp during 2005 appears to be bottom temperature (Figure 5B). Changes in bottom temperature can explain the northward shift in fishing activity during 2005. The shrimp vessel captains explained (personal communications) that they fish further south on the Tortugas Grounds during January–March, where bottom temperatures are warmer. Later in the year (April–June), after bottom temperatures have increased due to seasonal warming,

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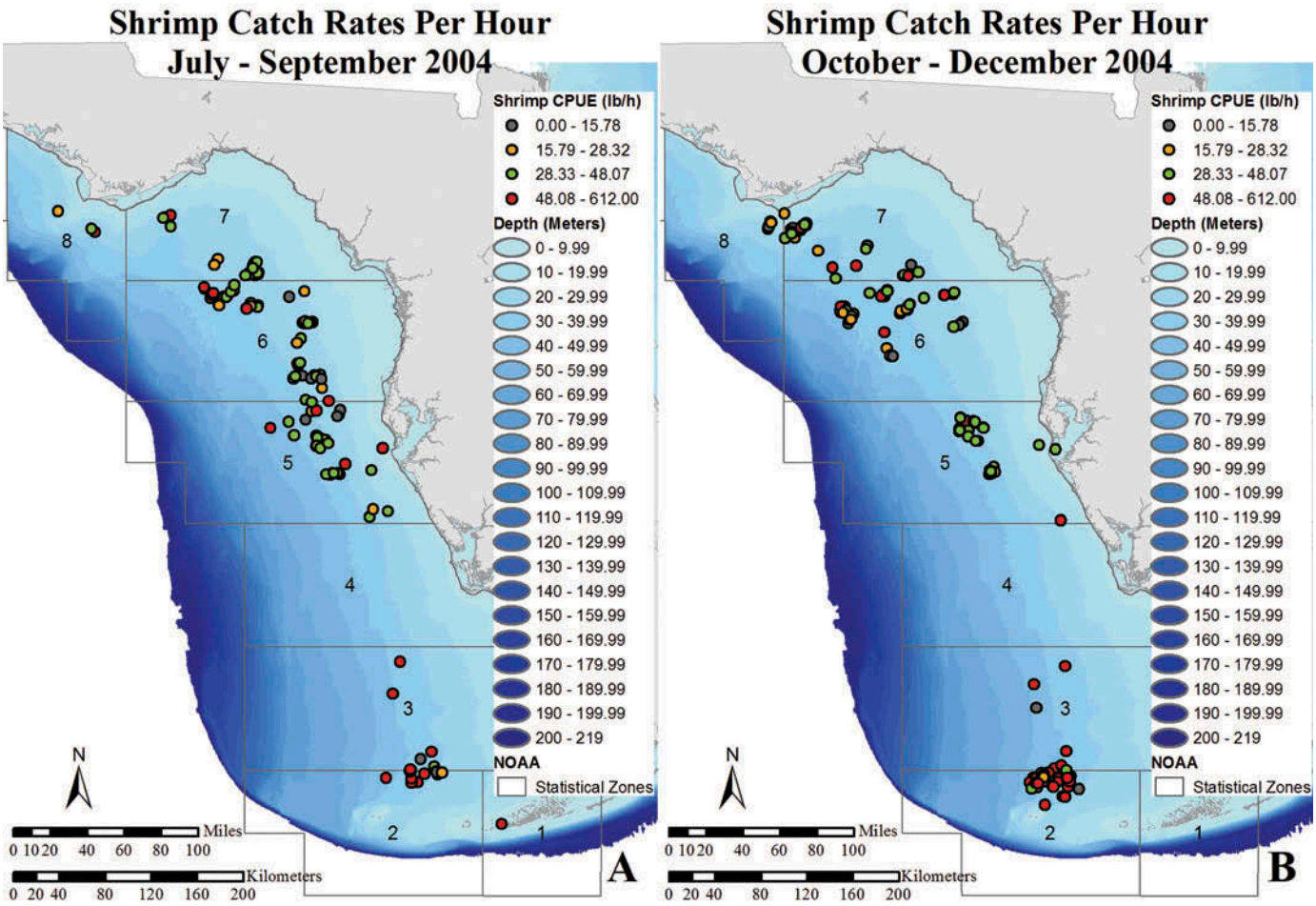


FIGURE 7. Seasonal maps depicting fishing locations with low to high CPUEs (lb/h) of pink shrimp represented by different colored dots in **(A)** July–September 2004 and **(B)** October–December 2004.

they usually fish northeast of the Florida Middle Grounds and on the Big Bend Grounds.

It is unlikely, however, that the pink shrimp found near the Dry Tortugas during January–March 2005 moved northward to areas north of the Florida Middle Grounds during April–June 2005. Several studies have demonstrated that there are different populations of pink shrimp on the WFS, including those on the Tortugas Grounds, the Romano and Sanibel Grounds off Charlotte Harbor, and the Big Bend Grounds (Beilsa et al. 1983). Tagging studies have documented movements of shrimp from Florida Bay and other smaller estuaries in southwest Florida to the Tortugas Grounds (Costello and Allen 1966; Gitschlag 1986). Pink shrimp were found to migrate to the Sanibel Grounds from Charlotte Harbor. Hence, it is believed that there are distinct populations of pink shrimp in southwest Florida. It also seems likely that there are different pink shrimp populations in estuaries farther north that move offshore to the Big Bend Grounds to spawn later in the season. This assumes that the species has the same temperature requirements for spawning on the Big Bend Grounds as that documented on the Tortugas Grounds (Munro et al. 1968).

While pink shrimp spawning has been documented on the Tortugas Grounds over most months of the year between 19.6°C and 30.6°C (Jones et al. 1970), spawning activity was greatest during the months with the highest bottom temperatures (Munro et al. 1968). It is of interest to note (Figure 3 in Munro et al. 1968) that the peak months when pink shrimp protozoea were most abundant on the Tortugas Grounds changed from year to year. The percentage of the annual catch of protozoea was highest in September 1959, August 1960, March 1961, October 1962, August 1963, and June 1964. The average bottom temperature on the Tortugas Grounds during peak months generally ranged from 28°C to 30°C. March 1961 was an exception not only because spawning peaked earlier but also because the mean bottom temperature was about 15°C.

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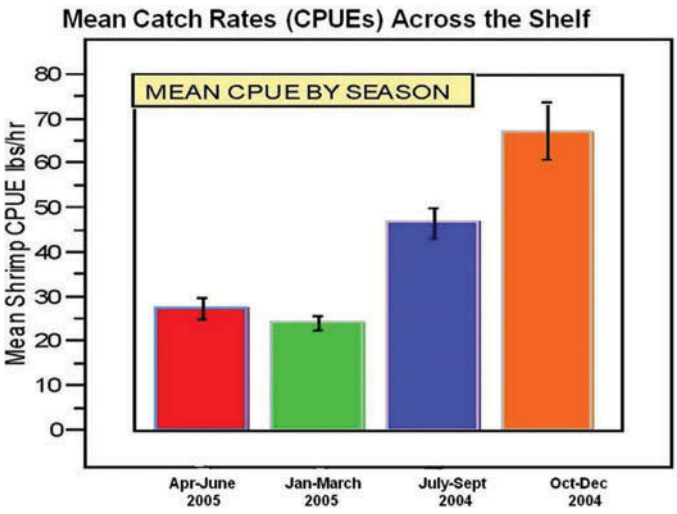


FIGURE 8. Mean CPUEs of pink shrimp on the West Florida Shelf for four seasons during 2004 and 2005; error bars = SEs.

The CPUE × depth functions (Figure 10C, D) during 2004 indicate that the shrimp were more abundant in deeper water (35–50 m). The species spawns throughout the year on the Tortugas Shelf at depths of 15–48 m (Beilsa et al. 1983). Based on the relative abundance of first protozoea, Munro et al. (1968) found that pink shrimp spawning activity reaches a maximum when bottom temperatures are highest and that it shifts from shallow water to deeper water as the spawning season progresses. This tends to agree with our findings that during October–December 2004 larger CPUEs occurred in warmer (27–28°C), deeper (35–50-m) water (Figures 9D, 10D). But it does not explain why pink shrimp were more abundant in cooler (22–25°C), deeper (35–50-m) water during July–September 2004 (Figures 9C, 10C).

The WFS circulation has a robust seasonal cycle and exhibits synoptic variations, primarily in response to local forcing (Liu and Weisberg 2005, 2007, 2012). Circulation on the inner shelf predominately favors upwelling from fall to spring (October–April) and downwelling in summer (June–

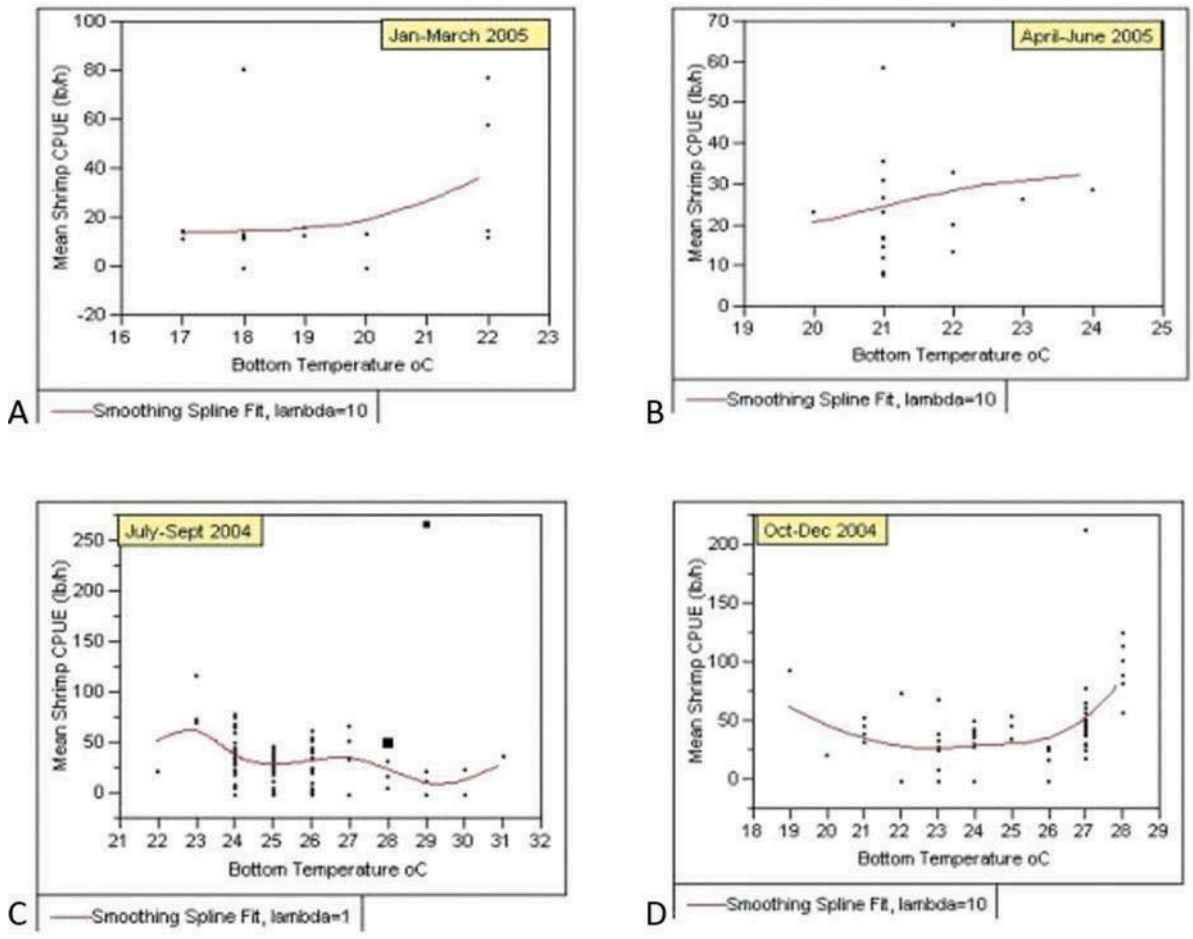


FIGURE 9. Seasonal splines fit to CPUE (lb/h) of pink shrimp by bottom temperature (°C) in **(A)** January–March 2005, **(B)** April–June 2005, **(C)** July–September 2004, and **(D)** October–December 2004.

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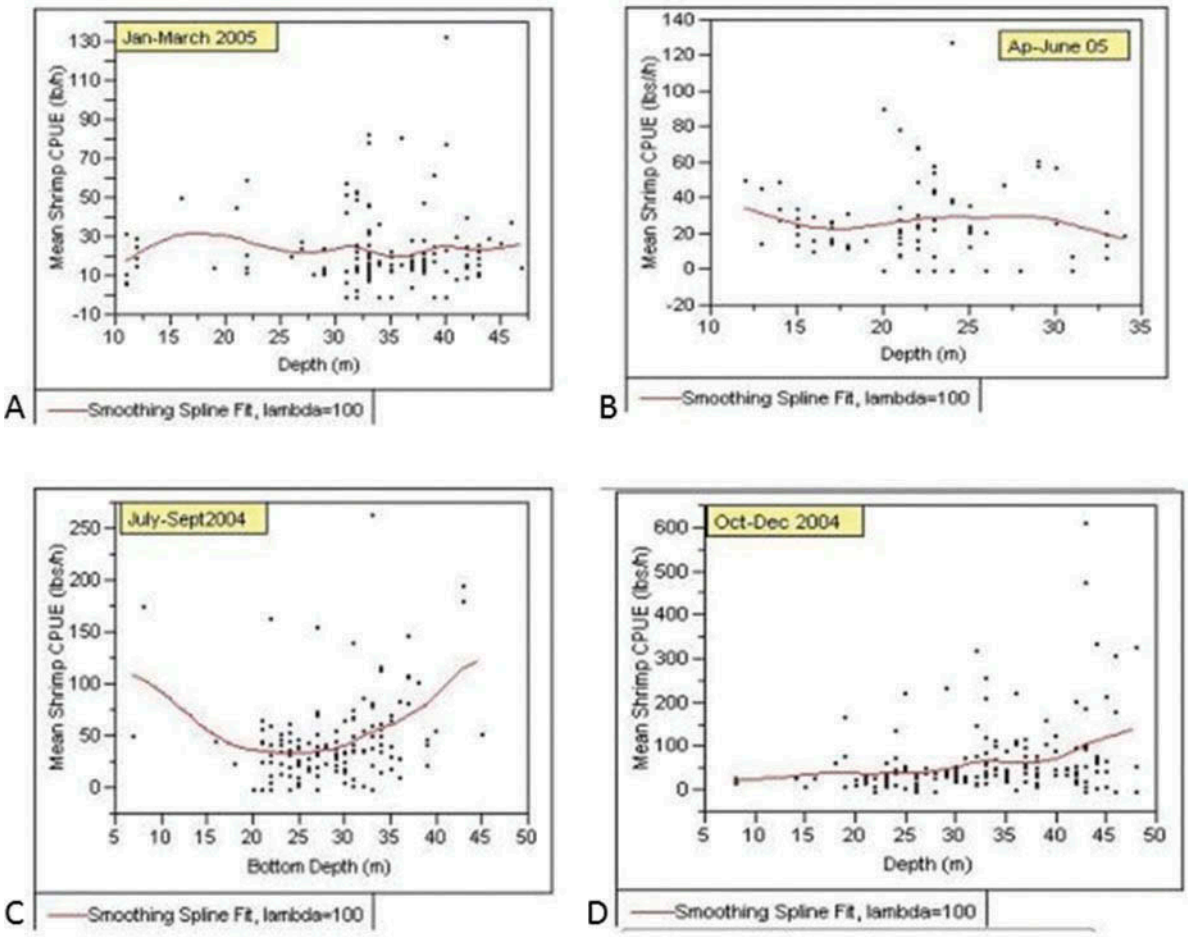


FIGURE 10. Seasonal splines fit to CPUE (lb/h) of pink shrimp by depth (m) in **(A)** January–March 2005, **(B)** April–June 2005, **(C)** July–September 2004, and **(D)** October–December 2004.

September). Seaward from the 50-m isobath, the seasonal variation is less pronounced due to the increasing importance of baroclinicity and the influence of the Gulf of Mexico Loop Current and eddies (Liu and Weisberg 2012). However, the strength and duration of upwelling varies between years. Our study found that upwelling occurred from July to December 2004.

Current speeds of 3 cm/s appear to have contributed to significantly greater mean CPUEs of pink shrimp in the optimum zones predicted by the HSM from July to December 2004 (Table 6). Verification tests using statistical differences between mean observed CPUEs across HSM zones showed that CPUEs tended to be higher during the months with upwelling in 2004. Significantly greater catch rates occurred

TABLE 1. One-way ANOVA of seasonal mean CPUE (lb/h) of pink shrimp by vessel monitoring zone (VMS) on the West Florida Shelf.

	VMS zone			
Season and year	Low	Moderate	High	*P*
Jul–Sep 2004	58.13	41.57	49.33	0.5969
Oct–Dec 2004	59.40	87.34	64.21	0.3828
Jan–Mar 2005	19.38	13.59	24.93	0.4045
Apr–Jun 2005	19.89	28.98	28.51	0.5202

TABLE 2. One-way ANOVA of seasonal mean CPUE (lb/h) of pink shrimp by bottom type on the West Florida Shelf (MD = mud, FS = fine sand, MS = medium sand, CS = coarse sand, and G = gravel).

	Bottom type					
Season and year	MD	FS	MS	CS	G	*P*
Jul–Sep 2004		101.77	41.80	32.03	43.54	<0.0001
Oct–Dec 2004	101.70	116.69	55.36	52.61	52.93	0.0016
Jan–Mar 2005	30.59	21.90	22.12	17.75	17.74	0.0084
Apr–Jun 2005		20.55	24.17	26.60	28.77	0.9312

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TABLE 3. One-way ANOVA of mean CPUE (lb/h) of pink shrimp by bottom current direction (direction from which the current comes) on the West Florida Shelf.

Season and year	Current direction				
	NE	SE	SW	NW	*P*
Jul–Sep 2004	80.75	23.59	65.47	43.51	0.0157
Oct–Dec 2004	67.56	48.51	44.31	71.03	0.5424
Jan–Mar 2005	21.15	25.38	13.41	21.85	0.4580
Apr–Jun 2005	24.26	34.16	14.41	19.98	0.1468

TABLE 5. One-way ANOVA of mean CPUE (lb/h) of pink shrimp by bottom aspect direction on the West Florida Shelf.

Season and year	Bottom aspect direction					
	F	NE	SE	SW	NW	*P*
Jul–Sep 2004	44.24	59.34	44.52	43.84	52.53	0.7687
Oct–Dec 2004	72.35	53.02	52.04	69.44	73.13	0.7445
Jan–Mar 2005	19.75	23.11	30.56	28.57	24.95	0.3052
Apr–Jun 2005	25.73	25.71	23.69	34.74	22.22	0.2853

in the optimum zones associated with upwelling onto the WFS. This intensified on the Tortugas Grounds from September to December.

The migration patterns and geographical distribution of pink shrimp may be controlled to a large extent by ocean currents (Beilsa et al. 1983). In experimental tank studies, juvenile pink shrimp showed positive rheotaxis, which gave way to active downstream swimming when salinity decreased (Hughes 1969a). Juveniles were reported to move offshore on ebbing currents (Burkenroad 1949; Hughes 1969b). Adult pink shrimp are also positively rheotactic (Fuss and Ogren 1966).

The seasonal mean CPUE × aspect data indicate that adult pink shrimp were more abundant on the sides of offshore sand banks with slopes facing oncoming bottom water currents (Table 5). If we assume that the shrimp are responding to bottom currents, the aspect data indicate that they occur over bottom sedimentary waves (sand ridges) on slopes facing the oncoming bottom currents. During 2005, when most of the currents came from the southeast and southwest, the shrimp were most abundant on the slopes facing those directions. Likewise, during 2004, when the current came onshore primarily from the northwest, the shrimp were most abundant on slopes facing the northwest and southwest. The fishermen confirmed that they often fished on the sides of sand banks and that their choice of sides changed seasonally depending on where they obtained the highest catches.

TABLE 4. One-way ANOVA of mean CPUE (lb/h) of pink shrimp by bottom current speed (cm/s) on the West Florida Shelf.

Season and year	Current speed					
	0–0.9	1–1.9	2–2.9	3–3.9	4–4.9	*P*
Jul–Sep 2004	40.05	34.19	66.26	153.60		<0.0001
Oct–Dec 2004	70.79	38.04	63.07	121.14	72.39	<0.0001
Jan–Mar 2005	18.54	23.85	23.46	29.02		0.4900
Apr–Jun 2005	17.93	29.32	30.52			0.2076

The significantly greater CPUEs in the optimum zones from July to December 2004 (Table 6) indicate that pink shrimp were most abundant in deeper water (Figure 10C, D) in areas associated with upwelling having current speeds of 3 cm/s. It is possible that pink shrimp moved into deeper water (35–50 m) to spawn. Little is known about whether they aggregate and spawn in areas associated with upwelling.

Criales et al. (2007) conducted a survey during July 2004 to study the cross-shelf transport of pink shrimp larvae on the southwest portion of the WFS. Sampling was conducted at two stations (DT and MQ) previously identified as important spawning sites on the Tortugas Grounds: (1) northeast of the Dry Tortugas and (2) north of the Marquesas (Figure 1). The water column near the Dry Tortugas station was found to be vertically stratified with a thermocline between 15 and 22 m deep. Below the thermocline the water temperature was 25°C. Criales et al. (2007) suggested that the low abundance of pink shrimp larvae caught in Tucker trawls at the DT station might be related to the low bottom temperature. They also stated that spawning may have shifted farther east, since high concentrations of protozoea were found near the MQ station at a depth of 20 m. Protozoea were found deeper than later larval life stages. Further studies were conducted using circulation modeling to simulate the transport and settlement of larval pink shrimp in this region (Criales et al. 2015). Lagrangian trajectories indicated that the migration paths of shrimp larvae changed radically between summer and winter during model years 1995–1997. The winter trajectories showed different patterns of larval dispersal from those in summer (their Figure 10). During the summer the majority of larvae recruited to coastal areas from the MQ station, while recruitment originating near the DT station occurred more in the winter months. Trajectories for July 1995 and August 1996 simulated the movements of shrimp larvae from the MQ station using currents originating from the southeast near the Marquesas.

The thermocline mentioned by Criales et al. (2007), which was also found in our study, most likely explains why adult pink shrimp were most abundant at temperatures from 22°C to 25°C during July–September 2004 (Figure 9C). Low bottom temperatures probably inhibited spawning northeast of the Dry Tortugas near the DT station during the summer. Spawning

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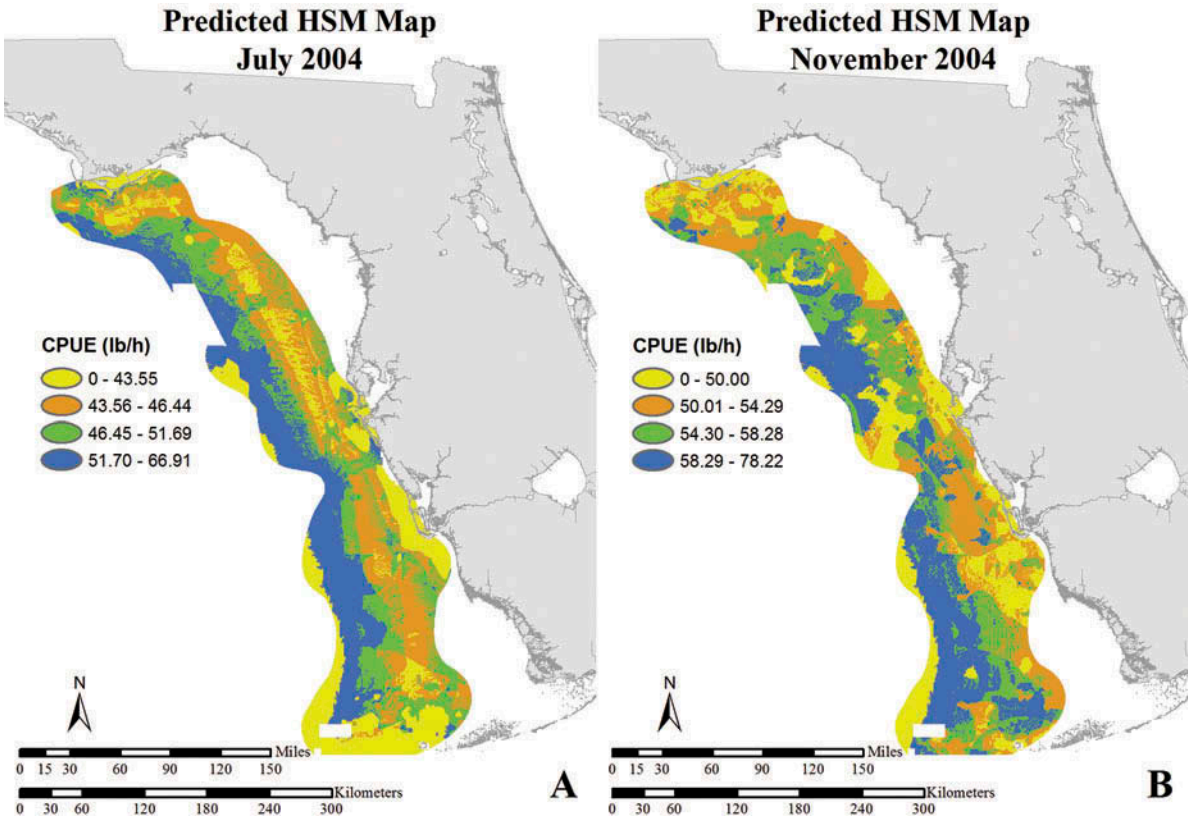


FIGURE 11. Habitat suitability modeling maps for pink shrimp for **(A)** July 2004 and **(B)** November 2004.

may have occurred from October to December at this location when bottom temperature conditions were favorable (Figure 9D). Research should be conducted to determine whether spawning locations and timing depend on upwelling bottom currents (i.e., whether spawning occurs near the DT station when there is upwelling from the northwest and near the MQ station when there is upwelling from the southeast).

By linking oceanography and benthic mapping with HSM, we improved our understanding of the factors influencing the spatial distributions and abundances of adult pink shrimp on the WFS. The study demonstrates that they were more abundant in areas associated with upwelling originating predominantly from the northwest during 2004 (Table 6). Using the Coastal Ocean Monitoring and Prediction System, USF has recently created daily predictions of bottom current patterns that are viewable on the Internet. Shrimp fishing vessels can use the predicted bottom current patterns to locate pink shrimp in upwelling zones, facilitating higher catch rates. This can help boost the profitability of shrimp fishing companies in Florida beset by competition from cheap imported shrimp and fluctuating fuel prices.

Shrimp fishing mostly occurred on the WFS on offshore sand ridges (the high-intensity zone) because these areas are trawlable (Figure 2A). The most likely reason that there was less fishing activity in the low- and moderate-intensity VMS zones is that many locations in these zones are not trawlable, consisting as they do of hard bottom or mixed hard bottom habitats. This was confirmed by interviewing the vessel captains who viewed the bottom with depth sounders.

GIS staff associated with the GMFMC requested a copy of the VMS grid depicting the low- to high-intensity VMS zones (Figure 2A). The GMFMC will review this information as they consider changes and updates to fishery management plans. The high-intensity zones may be used to amend the EFH map for shrimp associated with the shrimp fisheries management plan (GMFMC 2005). Likewise, the low- to moderate-intensity VMS zones (indicating spatial distributions of hard bottom or mixed hard bottom on the WFS) may be used to amend the composite EFH map for snapper and grouper species associated with the reef fish fisheries management plan (GMFMC 2005). The optimum zones in 16 monthly HSM maps could be used to support the designation of habitat areas of particular concern.

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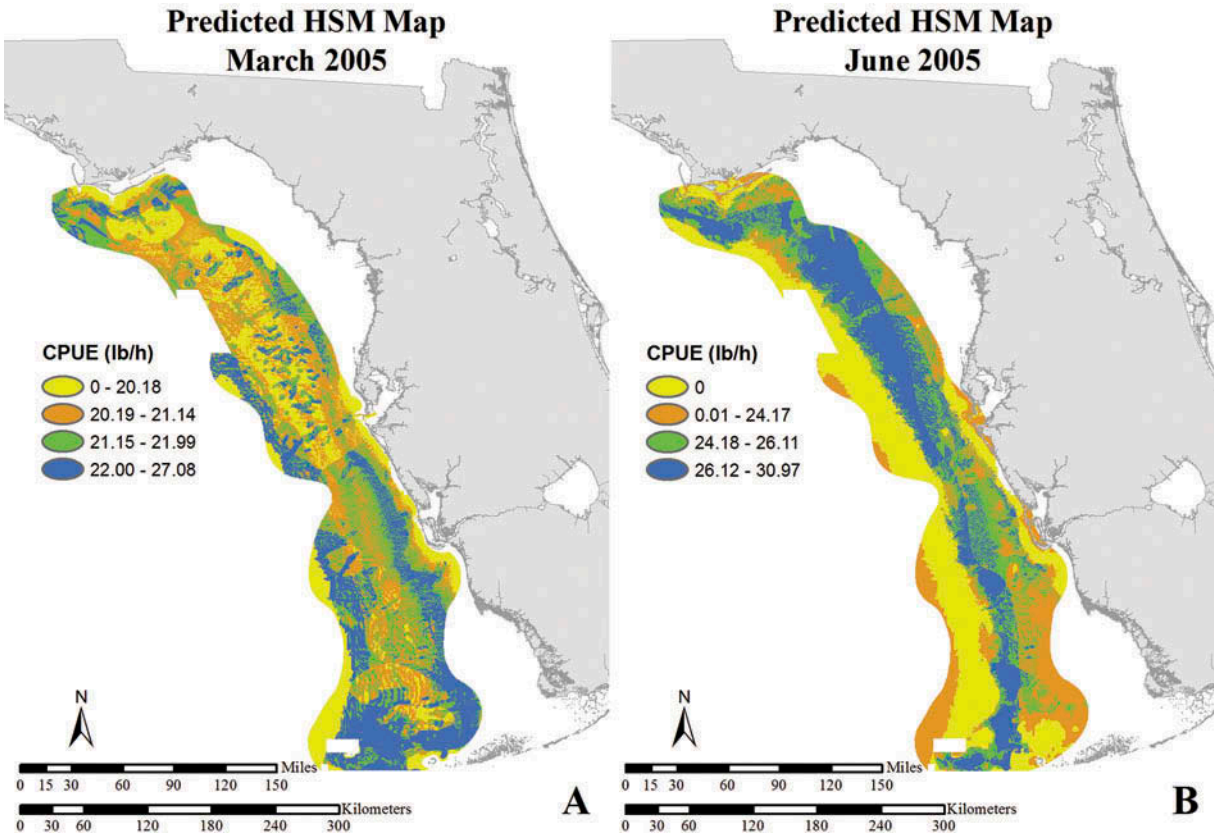


FIGURE 12. Habitat suitability modeling maps for pink shrimp for **(A)** March 2005 and **(B)** June 2005.

TABLE 6. One-way ANOVA of mean CPUE (lb/h) of pink shrimp by HSM zone on the West Florida Shelf.

	HSM zone				
Month	Low	Moderate	High	Optimum	*P*
			2004		
Mar	14.92	17.72	20.15	25.60	0.4584
Apr	0.00	21.43	28.56	45.00	0.0033
May	0.00	24.79	25.99	29.67	0.6658
Jun	0.00	20.91	21.89	35.36	0.0102
Jul	33.38	41.53	51.21	83.81	0.0142
Aug	32.04	43.87	49.19	91.04	0.0022
Sep	37.58	40.97	54.06	95.52	0.0004
Oct	55.63	55.05	57.39	102.99	0.0176
Nov	57.34	48.58	50.45	102.29	0.0065
Dec	53.67	72.24	50.20	102.82	0.0064
			2005		
Jan	16.29	17.87	23.76	25.17	0.5907
Feb	13.87	17.88	27.53	25.09	0.4654
Mar	14.53	21.36	16.85	26.55	0.1034
Apr	0.00	20.23	25.16	30.52	0.3743
May	0.00	21.08	27.36	37.28	0.0181
Jun	0.00	22.96	26.42	36.39	0.0859

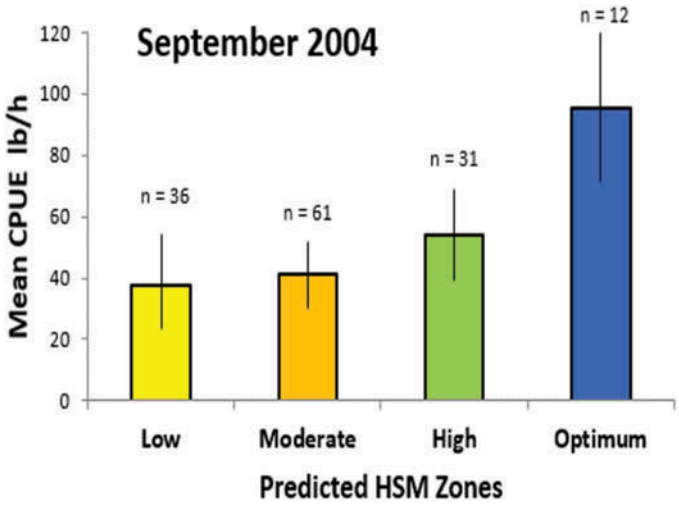


FIGURE 13. Verification test for habitat suitability modeling conducted in September 2004. The increasing mean observed CPUEs across the predicted HSM zones indicate that the data used in the model agree with the predicted spatial distributions and relative abundances of pink shrimp in the HSM map.

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