# Discontinuities concentrate mobile predators: quantifying organism–environment interactions at a seascape scale

Cristina G. Kennedy,[1,2,6,†] Martha E. Mather,[1,2,3] Joseph M. Smith,[2,4]
John T. Finn,[1] and Linda A. Deegan[5]

[1]Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts 01003 USA
[2]University of Massachusetts Graduate Program in Marine Sciences, Amherst, Massachusetts 01003 USA
[3]United States Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit,
Kansas State University, Manhattan, Kansas 66506 USA
[4]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195 USA
[5]Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA

**Abstract.** Understanding environmental drivers of spatial patterns is an enduring ecological problem that is critical for effective biological conservation. Discontinuities (ecologically meaningful habitat breaks), both naturally occurring (e.g., river confluence, forest edge, drop-off) and anthropogenic (e.g., dams, roads), can influence the distribution of highly mobile organisms that have land- or seascape scale ranges. A geomorphic discontinuity framework, expanded to include ecological patterns, provides a way to incorporate important but irregularly distributed physical features into organism–environment relationships. Here, we test if migratory striped bass (*Morone saxatilis*) are consistently concentrated by spatial discontinuities and why. We quantified the distribution of 50 acoustically tagged striped bass at 40 sites within Plum Island Estuary, Massachusetts during four-monthly surveys relative to four physical discontinuities (sandbar, confluence, channel network, drop-off), one continuous physical feature (depth variation), and a geographic location variable (region). Despite moving throughout the estuary, striped bass were consistently clustered in the middle geographic region at sites with high sandbar area, close to channel networks, adjacent to complex confluences, with intermediate levels of bottom unevenness, and medium sized drop-offs. In addition, the highest striped bass concentrations occurred at sites with the greatest additive physical heterogeneity (i.e., where multiple discontinuities co-occurred). The need to incorporate irregularly distributed features in organism–environment relationships will increase as high-quality telemetry and GIS data accumulate for mobile organisms. The spatially explicit approach we used to address this challenge can aid both researchers who seek to understand the impact of predators on ecosystems and resource managers who require new approaches for biological conservation.

[6] Present address: Massachusetts Office of Coastal Zone Management, Boston, Massachusetts 02114 USA.
† E-mail: cristina.kennedy@state.ma.us

## INTRODUCTION

Understanding drivers of spatial patterns across all scales is an important and persistent problem in ecology (Chave 2013). Effective conservation planning needs to incorporate these patterns into organism–environment relationships (Jones-Farrand et al. 2011). Spatial discontinuities are irregularly distributed, environmental conditions (such as drop-offs, confluences, dams, forest edges, pipelines, roads) that can influence the distribution of highly

mobile organisms with land- or seascape scale ranges (e.g., turtles, gazelles, Atlantic salmon, caribou; Aresco 2005, Ito et al. 2005, Wilcove and Wikelski 2008, Marschall et al. 2011, Beauchesne et al. 2013). In aquatic ecosystems, spatial discontinuities can alter bathymetry, modify hydrodynamics, and increase habitat heterogeneity in a way that juxtaposes metabolically conservative resting areas with energetically profitable feeding areas. Here we test if an expanded geomorphic discontinuity framework can predict how these unusual, irregular, and potentially influential physical features alter distribution of migratory striped bass (*Morone saxatilis*) predators within an estuary.

Spatial discontinuities can change ecological structure and function. Alternating geomorphic structures (Poole 2002), distinct habitats within a mosaic (Pringle et al. 1988), and abrupt transitions between adjacent segments (i.e., discontinuities; Ward and Stanford 1995) can reset ecological patterns by creating functionally important, ecological hotspots with higher complexity, productivity, and diversity. In aquatic systems, a confluence, the intersection of a tributary with a larger body of water, is an example of a discontinuity that can create heterogeneous hotspots and positively influence ecological function (Benda et al. 2004, Kiffney et al. 2006). Dams are examples of discontinuities that result in ecological dysfunction (Stanford and Ward 2001), often at great distances from the dam spillway (Marschall et al. 2011). Discontinuities such as roads, pipelines, and forest edges can also alter mobile organism distribution in terrestrial ecosystems (e.g., Wilcove and Wikelski 2008). The discontinuity concept has roots in geomorphology and ecosystem ecology (e.g., Poole 2002) and is one of several approaches [e.g., network dynamics (Benda et al. 2004), boundaries or ecotones (Naiman et al. 1988), and patch dynamics (Winemiller et al. 2010)] that have been developed to organize patterns of physical heterogeneity at larger spatial scales (e.g., river network, watershed, estuary). The discontinuity concept has been less used in population and community ecology, but has great potential to provide transdisciplinary insights.

Coastal migratory striped bass are model organisms to test if the discontinuity concept can provide new insights into how these abundant predators on a feeding migration are distributed within an estuary. Coastal striped bass spawn primarily in the Chesapeake, Delaware, and Hudson estuaries in the spring and make a northward migration to New England in late spring and early summer (Waldman et al. 1997, Mather et al. 2009, 2013). In fall, these migrants return south to overwinter (Mather et al. 2013). Migratory striped bass can remain within a single target estuary for several months in the summer (Pautzke et al. 2010), where they feed intensively (>85% of 799 striped bass sampled had food in their stomachs; Ferry and Mather 2012). Although striped bass distribution has been associated with depth (e.g., Ng et al. 2007), temperature (e.g., Nelson et al. 2010), salinity (Able et al. 2012), and dissolved oxygen (e.g., Coutant 1985), models including only these regularly occurring fish habitat variables have limited predictive capabilities. Larger scale anthropogenic features [e.g., docks, landings, artificial reefs, oyster reefs (Harding and Mann 2003); sandbars and submerged woody debris, shorelines, dropoffs, channels (Ng et al. 2007); and confluences (Tupper and Able 2000)] have only been anecdotally linked to striped bass distribution. Migratory striped bass offer an opportunity to examine the influence of both regularly distributed physical variables and irregularly distributed spatial discontinuities in the seascape.

Understanding the spatial distribution of mobile predators in the seascape and the processes underlying those patterns are critical for predicting the consequences of trophic-mediated energy routing. The seascape, a "wholly or partially submerged marine landscape" (Pittman et al. 2011), is a "spatially heterogeneous area of coastal environment …that can be perceived as a mosaic of patches, a spatial gradient, or some other geometric patterning" (Boström et al. 2011). Seascape ecology is the marine and coastal extension of landscape ecology, a now established discipline that takes an integrated, interdisciplinary approach to the examination of causes and consequences of spatial patterns across a range of scales (Boström et al. 2011, Pittman et al. 2011). The appropriate spatial scale or size of a seascape varies with the question, study system, and organism (Pittman 2013, e.g., 100 m$^2$ to 2000 km$^2$, Boström et al. 2011). Here, we use "seascape scale" to frame our investigation of

spatial patterns of mobile predators associated with physical features that may define patches within a heterogeneous 20 km² estuary.

We expand the geomorphic discontinuity framework to test three ecological questions about the relationship between the spatial distribution of migratory striped bass and physical habitat features that may act as spatial discontinuities within the estuarine seascape. We first asked whether striped bass were consistently aggregated in space and time. Even though dispersal of predators and consumer-driven interactions can alter the outcome of predator–prey interactions, specific patterns of movement are rarely quantified. Second, we combined multiple linear regression (MLR) and regression trees to test which discontinuities were influential drivers of the distributional patterns of these acoustically tagged predators. Finally, we asked if individual discontinuities function independently or interact to create additive physical heterogeneity, because physical habitat variables do not occur in isolation. We predict that the discontinuity-related bathymetric heterogeneity will concentrate striped bass, especially where physical features co-occur.

## METHODS

### Study system

Plum Island Estuary (PIE) is a shallow, vertically well-mixed estuary on the north shore of Massachusetts, USA (Fig. 1A) that has four coastal river inputs (Parker, Rowley, Ipswich, Plum Island Rivers) (Fig. 1B). PIE has a mean tidal range of 2.9 m, which results in a spatially variable and temporally dynamic bathymetric structure (Deegan and Garritt 1997). Surface area of the estuary varies from 12.8 km² at low tide to 20.0 km² at high tide (Pautzke et al. 2010). We divided the estuary into three geographic regions [(upper (U), middle (M), and lower (L)] to reflect riverine, mixing, and oceanic influences (Fig. 1C). The upper region is dominated by the large Parker River, includes several small creek confluences, has variable bathymetry with a few very shallow and very deep sites, and contains several small, salt marsh islands. The middle region mixes riverine and oceanic influences and includes the consistently shallow habitat within the Rowley River, the deeper Rowley River confluence, a large salt marsh island (Middle Ground), many small tidally influenced
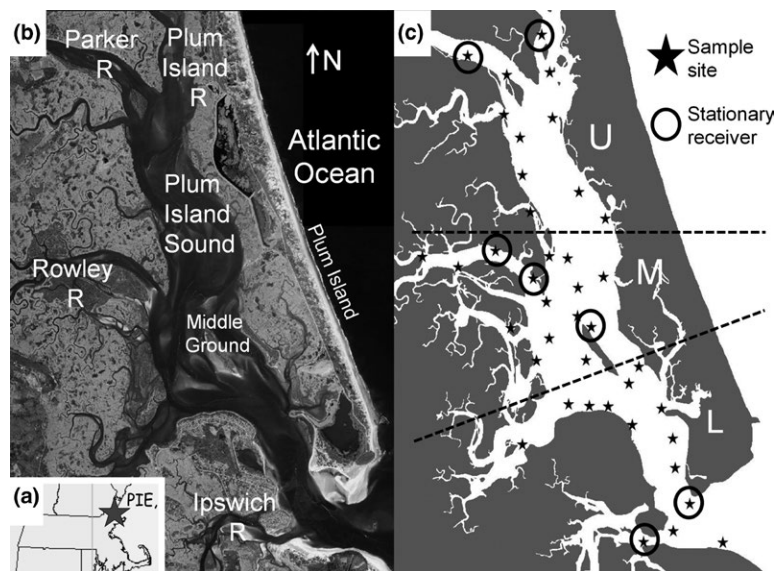


Fig. 1. (a) Location of Plum Island Estuary (PIE) in northeastern Massachusetts, USA. (b) Aerial ortho image of PIE (USGS) depicting Plum Island River, Parker River, Rowley River, Ipswich River, and Middle Ground, a large island. (c) In this study, PIE was divided into three regions: upper (U), middle (M), and lower (L). Stars represent the 40 sites that were sampled monthly for tagged fish using a tracking receiver. Circles represent continuously recording stationary receiver sites.

confluences, numerous sandbars, and a large number of underwater channel confluences. The lower region has a strong oceanic influence, includes the mouths of both the entire estuary and the large Ipswich River, is generally very deep, has the strongest current, has the most variable bathymetry in the estuary, and contains few sandbars or tidal creeks. The estuary supports resident and seasonally abundant fish and invertebrate prey (Ferry and Mather 2012).

## Tagging

Striped bass ($N = 50$; mean total length = 510 mm, SE = 7 mm, range = 403–597 mm TL) from the coastal migratory stock were tagged with VEMCO V13-R64k-coded acoustic transmitters (frequency of 69 kHz, ping rate of 60–180 s, estimated tag life of 1 yr). The weight of the acoustic tags (11 g in air) was less than 2% of the mass of the lightest tagged striped bass (652 g; Winter 1983). Striped bass were caught via hook-and-line on June 17–18 ($N = 30$) and 29 June 2009 ($N = 20$). Fishing effort covered all areas of the estuary, but catch rates were highest in the middle region of PIE. After capture, fish were held in a large, continually aerated holding tank until tagging (time held pretagging < 1 h). Using clove oil as an anesthetic (1.5 µL of clove oil/L of water; mean application time = 8.9 min, SE = 1.1 min; Pautzke et al. 2010), fish were first weighed (g) and measured (TL, mm). Tags were then surgically implanted using a sterile scalpel to make a 2.5-cm incision 2 cm above the ventral midline and approximately 1.5 cm behind the rear insertion of the pelvic fin. Through this opening, a transmitter was inserted into the peritoneal cavity and the incision was closed with three sterile dissolvable sutures (Ethicon Monocryl with 3/8″ curved cutting needle). All equipment was sterilized prior to surgery. To reduce stress during surgery, the gills, external body surface, and operating table were irrigated at all times with estuary water. Fish were not sexed in order to minimize stress and time out of water. The entire tagging process took an average of 5.4 min (SE = 0.2 min). After tagging, each striped bass was injected with oxytetracycline (0.1 mg/kg of fish; Liquamycin; Pfizer, New York, USA) and placed in a recovery tank until the fish swam upright (mean recovery time = 21.3 min; SE = 1.2 min). Then tagged fish were released at the approximate location of capture. Detections of tagged fish were analyzed in five ways to verify that striped bass survived tagging (Appendix A).

## Detections of tagged fish

We quantified fish distributions monthly from July–October 2009, with a tracking receiver (VEMCO VR100, VH-165 omni-directional hydrophone) at 40 sites (Fig. 1C, stars). Our experimental units were the survey sites, not the individual fish, because our research goal was to quantify the relationship between striped bass and physical features within the estuary. Sites contained a range of physical features. At each site, fish detections were recorded for 15 min (i.e., time required to definitively detect individual fish tags at a transmitter ping rate of 60–180 s). All 40 sites were visited on both ebbing and flooding tides within six consecutive days each month. Five groups of adjacent sites were visited in a random order for each monthly survey. To reduce spatial overlap of receiver ranges, we separated sites by 600 m, the average detection range of the tracking receiver (Appendix B).

At seven of the 40 sites, we also deployed a stationary receiver (VEMCO VR2W) to gate physical features (e.g., exits, river confluences, major land features such as islands; Fig. 1C, circles) and identify when tagged fish migrated out of the estuary. Stationary receivers, moored to the bottom of the estuary using paving stones and an anchor, were deployed before fish were tagged in June 2009, and removed in early November 2009, after no fish was detected >2 week.

## Striped bass response

To look at the spatial distribution, we calculated striped bass density, a measure of the range-specific concentration of tagged fish at each of the 40 sites. This striped bass response was defined as the mean number of tagged striped bass detected at each site (across all tides and months) divided by site-specific detection (or range) areas. We used July, August and September to calculate striped bass responses because non-metric multidimensional scaling examination of the similarity in mean number of fish across months showed that these three months were similar to each other but different from October (Kennedy 2013).

*Distribution*

To look at the spatial distribution of striped bass, *density* was mapped on a coastal outline of PIE (Office of Geographical Information, Commonwealth of Massachusetts, Information Technology Division) and analyzed in two ways. First, we used a chi-square goodness of fit test to examine whether striped bass were distributed evenly. For this, we calculated expected values by dividing the total fish response in PIE by 40 (number of possible survey sites). *P*-values were determined from 2000 Monte–Carlo simulations ("chisq. test" function; R Development Core Team 2010). As a second way to identify data lumps and gaps, we calculated the kernel density distribution (Nash et al. 2014) for striped bass along a latitudinal gradient ("density" function in R; Havlicek and Carpenter 2001).

*Physical features that act as discontinuities*

We tested how four physical discontinuities (*percent sandbar*, *confluence diversity*, *channel proximity*, *median drop-off size*), one continuous physical feature (*median depth variation*), and a geographic location variable (*region*) affected striped bass *density* (Table 1). In exploratory data analyses, we examined variables in a variety of ways (e.g., mean, maximum, standard deviation, absolute deviation; Kennedy 2013) and chose the expression of each variable based on our ecological knowledge, literature insights, and statistical judgment. For *percent sandbar*, *confluence diversity*, and *channel proximity*, we used ArcGIS on aerial color ortho layers of PIE (Office of Geographical Information, Commonwealth of Massachusetts, Information Technology Division). For *percent sandbar*

Table 1.  Response and explanatory variables used to quantify the spatial distribution of striped bass on a feeding migration in Plum Island Estuary.

| Variable | Calculation | Ecological predictions | β |
|---|---|---|---|
| **Response** | | | |
| Density | Mean count (across months) of tagged striped bass detected at each site divided by site-specific range area | | |
| **Explanatory** | | | |
| Percent sandbar | Area of sandbar within a receiver site divided by range area | Sandbar area increases bathymetric/hydrodynamic heterogeneity. Sites with more sandbar area will concentrate striped bass | + |
| Confluence diversity | Coefficient of variation in confluence mouth width | Varied confluences provide diverse bathymetric and hydrodynamic conditions across tides. An increased variety in confluence size will concentrate striped bass | + |
| Channel proximity | Distance to nearest underwater channel confluence (km) | The channel networks can increase heterogeneity and connectivity. Sites closer to the channel confluence will concentrate striped bass. | - |
| Median drop-off size | Absolute deviation from median of maximum drop-off size (m) | Small drop-offs provide little heterogeneity and very large drop-offs create excessive flow. Striped bass will concentrate at intermediate size drop-offs | – |
| Median depth variation | Absolute deviation from median of depth standard deviation (m) | Some heterogeneity in depth can be advantageous for feeding and resting. Striped bass will concentrate in areas with intermediate depth variation | – |
| Region | Upper, middle, and lower regions were created based on location, physical distribution, and an even distribution of area and receivers | Geographic region quantifies riverine (upper) and oceanic (lower) influence. Striped bass will concentrate in the middle region which mixes riverine and oceanic conditions | C |
| Index | Mean of additive rank for 13 physical variables at each site | A higher heterogeneity index (more co-occurring physical features) will aggregate striped bass | + |
| Cluster | Cluster analysis of the 13 heterogeneity index variables | Striped bass will concentrate at sites with greater multivariate complexity | C |

*Note:* β = predicted slope between the explanatory variable and striped bass response. C = categorical.
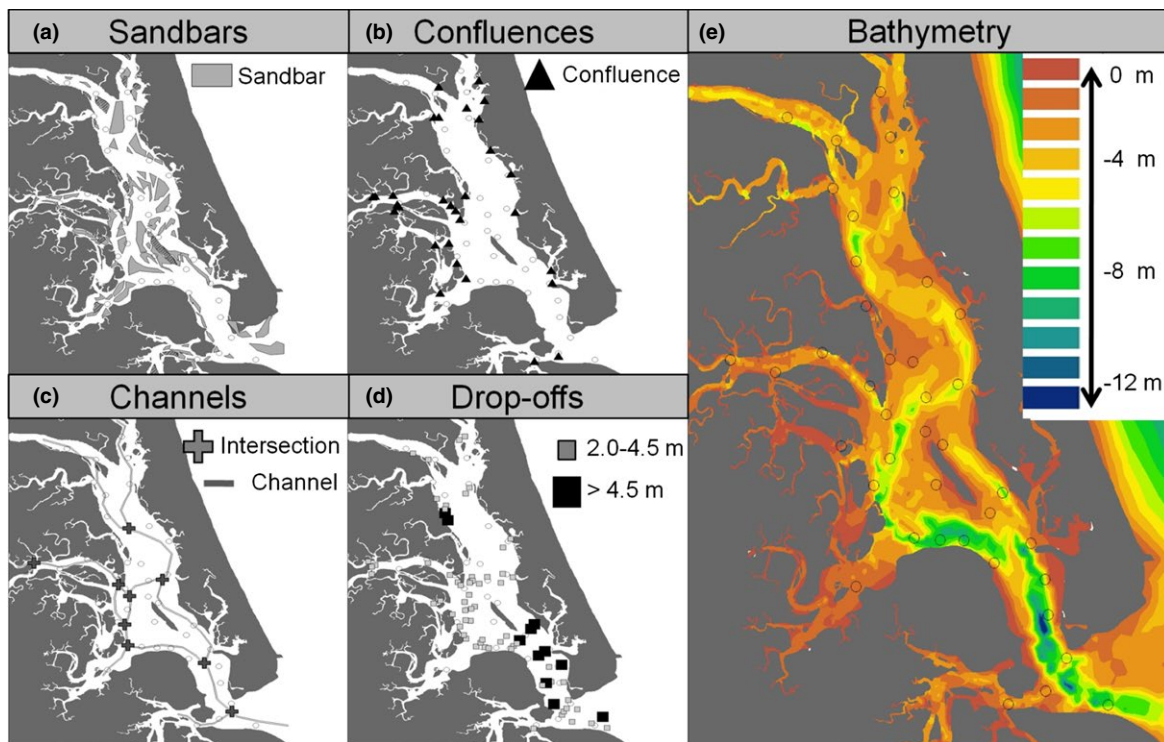
Fig. 2. Distribution of physical features that were used to calculate the discontinuity variables *percent sandbar*, *confluence diversity*, *channel proximity*, *median drop-off size*, and *median depth variation*. (a) sandbars, (b) confluence mouths, (c) channels and channel intersections, (d) drop-offs, and (e) bathymetry. Sample sites are indicated with hollow circles. Specific methods are described in detail in the text.

(Table 1), the area of sandbar at each site was divided by the site-specific receiver range (Fig. 2A). For *confluence diversity* (Table 1), the coefficient of variation of confluence mouth width within each site was calculated (Fig. 2B). To create *channel proximity* (Table 1), the distance from the receiver location to the nearest underwater channel intersection was calculated (Fig. 2C).

To calculate *median drop-off size* (Table 1), we used field measurements of depth taken every 100 m along four 500-m perpendicular transects at each of the 40 sample sites. A drop-off was defined as a >2 m change in depth between adjacent measurements (Fig. 2D). We used the maximum drop-off size at each site to calculate the variable. To quantify *median depth variation* (Table 1), we used an existing bathymetry data set (FVCOM hydrodynamic model; C. Chen, J. Vallino and L. Zhao, personal communication; Fig. 2E) and calculated the standard deviation of all depth measurements taken at each site. Because we

predicted that more striped bass would concentrate at intermediate values of *median drop-off size* and *median depth variation*, we calculated the absolute deviation from the median ($D_i = |x_i - \text{median}(X)|$; Pham-Gia and Hung 2001), a measure of whether organisms concentrated. Finally, a categorical geographic variable, *region* (Table 1) was created for which upper (U), middle (M), and lower (L) had similar numbers of sites (L = 14, M = 15, U = 11). In the statistical analyses, the lower region (L) was used as the baseline to quantify differences in the middle (M vs. L) and upper (U vs. L) regions. Categorical (*region*) and continuous (*latitude*, data not shown) measures of location revealed similar trends; we chose *region* for our analyses.

### Multiple regression and CART analyses

Multiple linear regression and an information-theoretic model selection approach were used to test relationships between striped bass *density* and the six explanatory variables that quantified

physical features in the estuary (*percent sandbar*, *confluence diversity*, *median drop-off size*, *median depth variation*, *channel proximity*), and *region*. Striped bass *density* was log transformed to satisfy the assumption of normality (Quinn and Keough 2002). The resulting models were calculated using $AIC_c$, a model selection tool for small sample sizes (Burnham and Anderson 2011). Models that varied in the number of regressors ($K$) were ranked in ascending order by $\Delta AIC_c$. Because both 2 and 4 $AIC_c$ units have been used to identify top models, here, we retained models within 4 $\Delta AIC_c$ units to ensure that all relevant models were included. The model weight ($\omega$) was calculated to measure importance for each model (Burnham and Anderson 2011). Top models ($\Delta AIC_c < 4$) were averaged using the "glmulti" and "glmulti.coef" functions in the "glmulti package" (Symonds and Moussalli 2011, Calcagno 2013) to calculate $\beta_j$, SE, and variable importance ($w + j$). We also report adjusted $R^2$. Homogeneity of variance and independence met MLR assumptions. Cook's $D$ (<1) and condition number (<25) did not identify influential observations or multicollinearity (Quinn and Keough 2002, Graham 2003).

As a second statistical approach, we tested relationships between striped bass *density* and all six physical explanatory variables with CART. Regression trees were created and plotted with the "tree" package (R Development Core Team 2010). The "randomForest" package in R was used to identify a measure of percent variance explained (Liaw and Wiener 2002).

### Role of additive physical heterogeneity

To quantify the additive heterogeneity of multiple physical features in the estuary, we created three multimetric indices by combining 13 metrics that described a range of regularly and irregularly distributed physical characteristics (Appendix C). Our goal in creating these additive indices was to combine multiple metrics within and across physical features. The three heterogeneity indices included: (1) a continuous additive index in which all metrics had equal importance, (2) a continuous additive index in which variables included were weighted based on the results of the multiple regression, and (3) a categorical index created with a cluster analysis on the same variables.

We tested the relationship between striped bass *density* and additive physical heterogeneity within the estuary using two approaches. First, we regressed striped bass *density* against the original and weighted heterogeneity indices. Second, we tested the difference in striped bass *density* across the heterogeneity clusters using a non-parametric Kruskal–Wallis test. Finally, we related the results of the additive index and heterogeneity cluster to a spatially explicit hydrodynamic model (FVCOM hydrodynamic model; Chen, Vallino, and Zhao, personal communication) for one high and one low fish density site to illustrate how variation in bathymetry might alter fish distribution.

### Unique individuals

In addition to striped bass density, we calculated a second striped bass response variable, unique individuals, which quantified how many different individual striped bass visited each of the 40 sites over the study duration (Appendix D). For this second predator response, we ran identical statistical analyses as described above (MLR, CART, additive indices).

## Results

### Within-estuary striped bass distribution

All striped bass survived tagging (Appendix A) and 40 fish (80%) were detected within PIE throughout most of the summer (mean = 51 d, range = 2; Fig. 3A). Tagged striped bass that remained in PIE moved between estuarine receivers on a regular basis (Fig. 3B). Despite their frequent within-estuary movement, tagged striped bass were not evenly distributed ($X^2 = 1557$, $P < 0.001$), but instead were clustered in the middle region of the estuary ($P < 0.01$; Fig. 4A). At most sites in the upper estuary and all but one site in the lower estuary, fewer fish were detected than expected. At >50% of sites in the middle region (9 of 16), more fish were detected than were expected (Fig. 4A). Kernel densities confirmed that striped bass were aggregated in the middle region of the estuary (Fig. 4B).

### Spatial discontinuities as drivers of striped bass distribution

The spatial discontinuities that acted as major drivers of striped bass distribution were similar
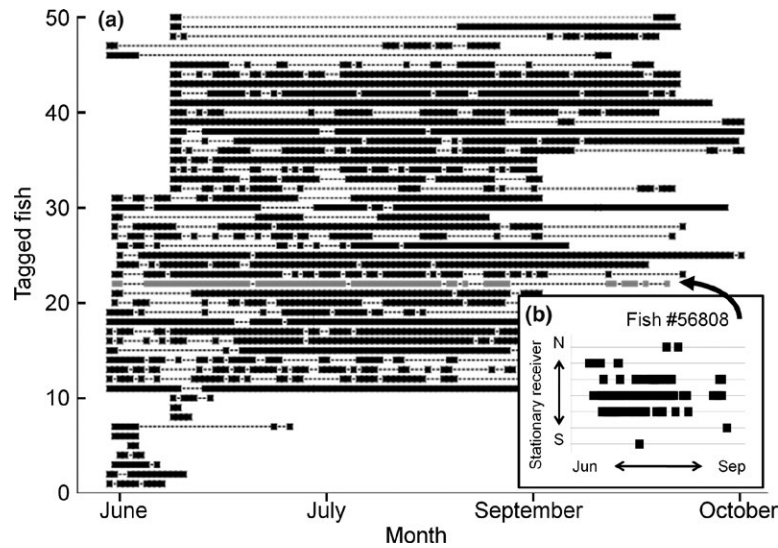
Fig. 3. (a) Dates in June through October, 2009, when 50 striped bass were tagged and detected by stationary receivers in PIE. Each individual horizontal line begins at the individual's date of tagging. Filled cells represent days when fish were detected in PIE. (b) An example of frequent and extensive within-estuary movement from June through September, 2009 is shown for one fish (#56808). The *X*-axis shows the date of detection and the *Y*-axis shows the location of detection. Fish #56808 is shown in gray in panel A. This movement pattern was typical of tagged fish and shows that seasonal resident striped bass move around PIE.
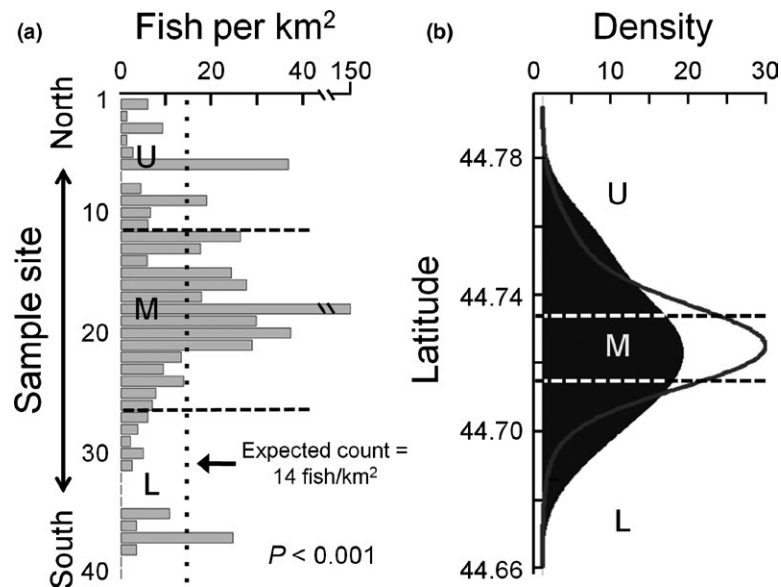


Fig. 4. Distribution of striped bass (mean fish/km$^2$) in PIE. (a) Striped bass *density* from north to south with the dotted line indicating the expected density of 14 fish/km$^2$ if fish were distributed evenly throughout the estuary. The *P*-value was derived from a chi-square goodness of fit test. (b) Kernel density plot of striped bass detected at survey sites. The black area indicates the distribution of manual survey sites by latitude. The line indicates the distribution weighted by striped bass density. Regions of the estuary are U (upper), M (middle), and L (lower), delineated by horizontal dashed lines.

Table 2. Top multiple regression models for striped bass *density*.

| Model | Percent sandbar | Median depth variation (m) | Median drop-off size (m) | Confluence diversity | Channel proximity (km) | M vs. L | U vs. L | ΔAICc | $\omega_i$ |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.37 ± 0.14 | | | 0.72 ± 0.40 | | 1.53 ± 0.32 | 0.57 ± 0.35 | 0.00 | 0.24 |
| 2 | 0.42 ± 0.14 | | | | | 1.59 ± 0.33 | 0.74 ± 0.35 | 0.67 | 0.17 |
| 3 | 0.35 ± 0.14 | | | 0.73 ± 0.41 | −0.27 ± 0.30 | 1.50 ± 0.32 | 0.78 ± 0.42 | 2.01 | 0.09 |
| 4 | 0.41 ± 0.14 | | | | −0.25 ± 0.31 | 1.56 ± 0.33 | 0.93 ± 0.42 | 2.69 | 0.06 |
| 5 | 0.37 ± 0.14 | −0.15 ± 0.32 | | 0.70 ± 0.41 | | 1.45 ± 0.37 | 0.50 ± 0.39 | 2.7 | 0.06 |
| 6 | 0.37 ± 0.14 | | −0.03 ± 0.11 | 0.70 ± 0.42 | | 1.50 ± 0.34 | 0.56 ± 0.36 | 2.86 | 0.06 |
| 7 | 0.42 ± 0.14 | −0.21 ± 0.32 | | | | 1.48 ± 0.38 | 0.63 ± 0.39 | 2.98 | 0.05 |
| 8 | 0.43 ± 0.14 | | −0.07 ± 0.11 | | | 1.53 ± 0.35 | 0.71 ± 0.35 | 3.04 | 0.05 |
| $\beta_j$ | 0.39 ± 0.05 | −0.03 ± 0.03 | −0.01 ± 0.01 | 0.41 ± 0.16 | −0.05 ± 0.04 | 1.53 ± 0.12 | 0.67 ± 0.14 | | |

*Notes:* The response was log transformed. Explanatory variables include *sandbar percent* (no units), *depth variation* (m), *drop-off size* (m), *confluence diversity* (no units), *channel proximity* (km) and *region* [Middle (M) vs. Lower (L), Upper (U) vs. Lower (L)]. Calculations for all variables are shown in Table 1. Evaluation criteria shown include $\Delta AIC_c$ and Akaike weights ($\omega_i$). $N = 40$. Also shown are the coefficients with standard errors for the averaged model $\beta_j$.

for MLR and CART, and both striped bass responses (*density, unique individuals*). For the MLR on striped bass *density*, eight "top" models were <4AIC$_c$ units and had an adjusted $R^2$ values of 0.50–0.54 (Table 2). *Percent sandbar* and geographic *region* were the most important variables in determining striped bass distribution [$(w + j) = 1.0$; Table 2]. More striped bass were detected at sites with a higher *percent sandbar* and at sites in the middle region, especially compared to the lower region (M vs. L; Table 2). *Confluence diversity* was of intermediate importance [$(w + j) = 0.57$; Table 2] with higher numbers of striped bass detected at sites with higher variation in confluence size. Relative to *channel proximity*, more striped bass spent time close to channel intersections [$(w + j) = 0.27$; Table 2]. More striped bass were detected at intermediate drop-offs and depth but m*edian depth variation* and *median drop-off size* were less influential [$(w + j) = 0.14$–$0.15$; Table 2]. For *unique individuals*, five MLR models were <4 AIC$_c$ units, identified the same influential regressors (*percent sandbar, region*, Appendix Table D1) as striped bass *density*, and had adjusted $R^2$ values of 0.67–0.68.

CART models explained 33% and 58% of the total variation for striped bass *density* (Fig. 5) and *unique individuals* (Appendix Fig. D1A), respectively. The highest striped bass *density* (mean = 32 fish/km$^2$) occurred at sites in the middle region with intermediate depth variation (*median depth variation* < 0.3 m; Fig. 5). In the
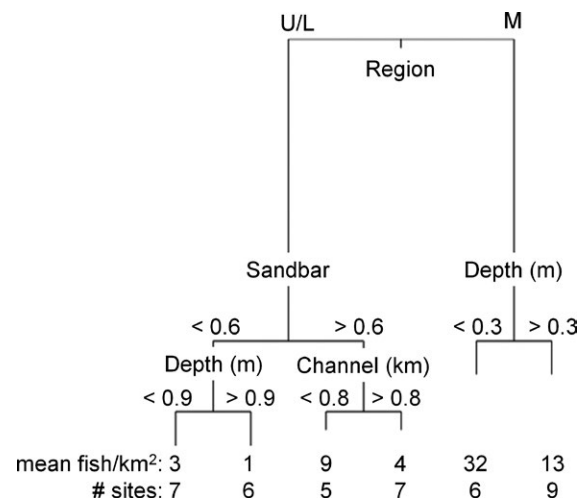


Fig. 5. Regression tree analysis of striped bass *density* (fish/km$^2$) showing the influence of the explanatory variables *region* (U, M, L), *percent sandbar* (no units), *median depth variation* (m), and *channel proximity* (km). Each split is labeled with the relevant values. Mean fish and number of sites in each terminal node are indicated.

lower and upper *regions*, the highest striped bass *density* (mean = 9 fish/km$^2$) occurred at sites with greater sandbar area (*percent sandbar* > 0.6 units) that were close to a channel intersection (*channel proximity* < 0.8 km). The lowest striped bass *densities* in PIE (mean = 1 fish/km$^2$) occurred at sites in the lower region with limited sandbars (*percent sandbar* < 0.6 units) and extreme depth variation

(*median depth variation* > 0.9 m). CART analysis of *unique individuals* confirmed the importance of *sandbar*, *region*, *channel proximity*, and *median drop-offs* (Appendix Fig. D1A).

### Striped bass and additive heterogeneity

Sites at which many discontinuities co-occurred attracted more striped bass (Fig. 6A–C). The heterogeneity index was positively related to both density ($R^2$ = 0.11, $P$ = 0.02; Fig. 6A) and unique individuals ($R^2$ = 0.30, $P$ < 0.001; Appendix Fig. D1B). Of the three indices, striped bass distribution had a stronger relationship with the weighted heterogeneity index, which incorporated the multiple regression results ($R^2$ = 0.14, $P$ = 0.01; Fig. 6B; $R^2$ = 0.37, $P$ < 0.0001; Appendix Fig. D1C). In addition, more striped bass occurred in heterogeneity cluster 2 ($P$ < 0.01, Fig. 6C; $P$ < 0.001, Appendix Fig. D1D) which had the highest mean heterogeneity index (Mean: 208-cluster 2 vs. 164-overall).

Spatially, sites with high additive heterogeneity (Fig. 7A, within outline) that occurred in heterogeneity cluster 2 (Fig. 7B, within outline) were the same as those sites with high striped bass densities (Fig. 7C, within outline). At one example of a high density site (Fig 7C, red sphere), large numbers of tagged striped bass aggregated near moderate variation in bathymetry and current (Fig. 7D, red sphere), but were dispersed at the low density site which had limited bathymetric and hydrodynamic heterogeneity (Fig. 7C, D, blue cube).

## DISCUSSION

Our use of the discontinuity framework provided novel insights about drivers of organismal distribution at the seascape scale. In PIE, a consistent aggregation of mobile predators persisted from spring to fall and was associated with four physical discontinuities (*percent sandbar*, *confluence diversity*, *channel proximity*, *median drop-off size*), one continuous physical feature (*median depth variation*), and a geographic variable (*region*). Elsewhere, discontinuities drive patterns and processes when physical features have a large spatial extent of influence. For example, anthropogenic structures (dams, roads, pipelines) that act as discontinuities alter the distribution of aquatic (Aresco 2005, Marschall et al. 2011) and terrestrial organisms (Cameron et al. 2005, Ito et al. 2005, Wilcove and Wikelski 2008, Beauchesne et al. 2013). The need to incorporate unusual, irregularly distributed features in ecology and biological conservation will only grow as both organismal movement data and spatial mapping data increase in quality and quantity.

Hydrodynamics associated with discontinuities in estuaries such as PIE can enhance habitat
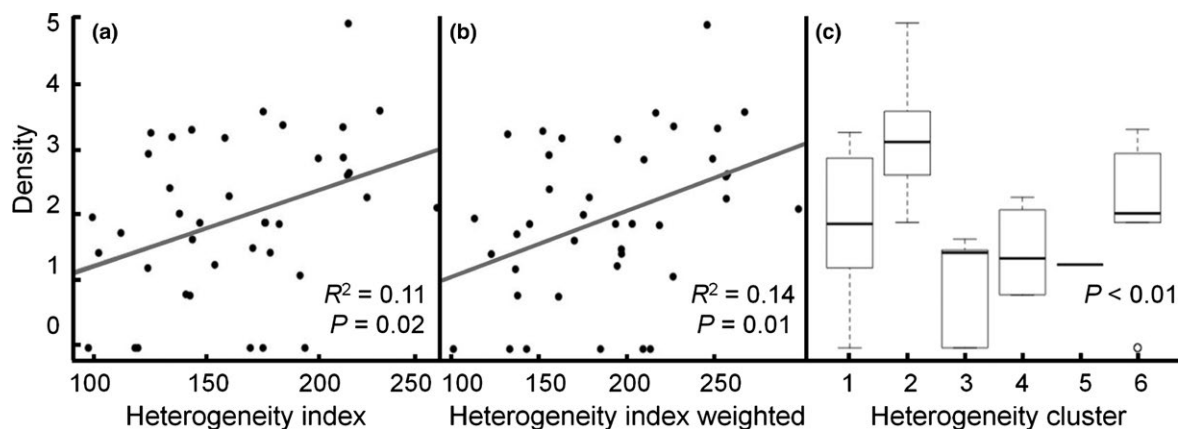


Fig. 6. Relationship between striped bass *density* (log-transformed fish/km$^2$) and three measures of multivariable heterogeneity: (a) heterogeneity index (no units), (b) heterogeneity index weighted by multiple linear regression results (no units) and (c) heterogeneity cluster group. For A and B, *P*-values and $R^2$ values result from linear regressions. For C, results of a Kruskal–Wallis test ($N$ = 40) are shown.
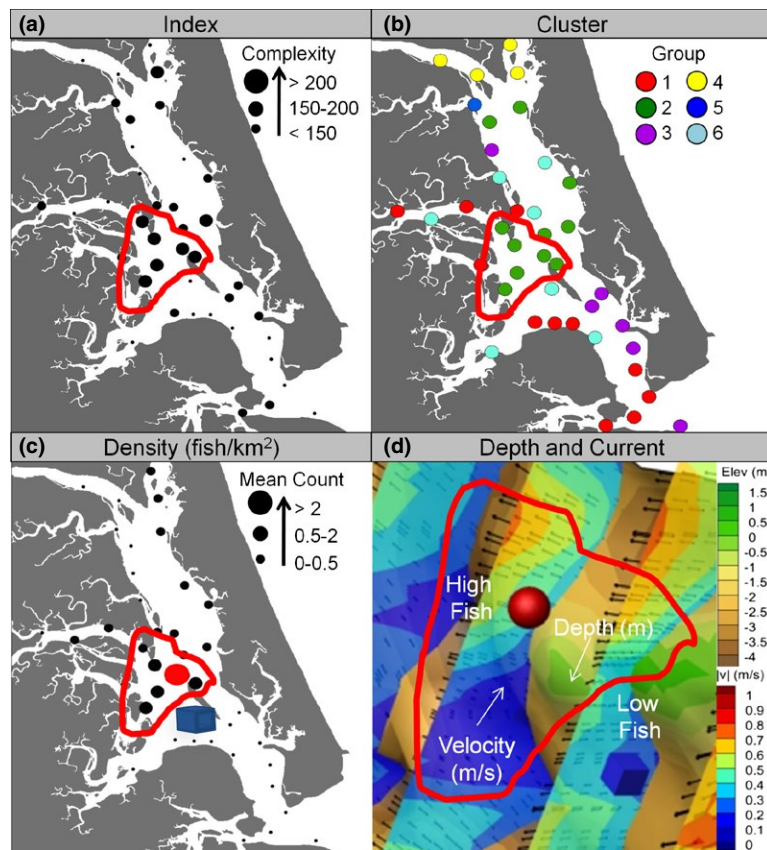
Fig. 7. Spatial depictions are shown of (a) heterogeneity index, (b) heterogeneity clusters, (c) fish counts, and (d) depth and current velocity variation at two receiver sites in PIE. In a–d, the red outline encloses an area of high striped bass density. In c, d, we show one example of a high fish density site (red sphere) and an adjacent low fish density site (blue square). In d, depth and current velocity were created by a hydrodynamic model (FVCOM hydrodynamic model; C. Chen, J. Vallino and L. Zhao personal communication). The hydrodynamic map is shown in slices of alternating bottom depth (m) and current velocity (m/s).

diversity, increase productivity, and aggregate prey in a way that provides foraging options across all tides. As a result, feeding predators may concentrate at the juxtaposition of energetically profitable feeding sites with metabolically conservative resting sites. The conceptual basis for energetics as a potential driver of ecological patterns, via optimal foraging, bioenergetics, ecological energetics, and other processes, is well established (e.g., Stephens and Krebs 1986, Hanson et al. 1997, Tomlinson et al. 2014). For fish in lotic systems, the increased profitability of food delivery provided by higher current velocity (e.g., Fausch 1984, Hill and Grossman 1993) may coincide with the increased metabolic cost of high flow and associated turbulence (e.g., Facey

and Grossman 1990, Enders et al. 2005). The need for organisms to alter distribution and behavior to balance conflicting demands has been demonstrated for a variety of ecological processes (e.g., habitat selection, foraging, predator avoidance; Sih 1980, Lima and Dill 1990, Hansen and Beauchamp 2015). However, whether mobile predators balance the velocity-based conflicting demands of foraging and position-holding has not been well documented in tidally dominated estuaries and requires testing.

Quantifying the influence of unusual or irregularly distributed physical features on organisms at the land-, river-, and seascape scales is a challenge. In commonly used animal habitat methodologies, regularly occurring physical conditions

that can be sampled at any location within the study system (e.g., temperature, current velocity, depth, substrate for aquatic organisms) are often measured in a systematically or randomly sampled design using transects or grids (e.g., Manly et al. 2002, Newcomb et al. 2007, Fisher et al. 2013). In these approaches, unusual or irregularly distributed physical features (i.e., spatial discontinuities) that would be classified as not available, rather than zero, are often avoided to satisfy statistical assumptions (e.g., avoidance of empty cells, inadequate replication, unbalanced designs; Quinn and Keough 2002). In a landscape ecology approach, these unusual features are quantified as distance variables (distance to the nearest feature) or densities (number of features within a given distance or distance weighted numbers) to smooth out rare habitats (Cushman et al. 2008). Our combined use of habitat and landscape ecology approaches showed that uncommon but important features can influence spatial patterns of mobile organisms.

### Spatial discontinuities as drivers of striped bass distribution

Striped bass were aggregated at sites with sandbars. Sandbars are soft-bottomed depositional areas that juxtapose shallow, slow-water edges with deeper, narrower areas through which flow may be accelerated. This spatial and temporal flow variation may be especially important in an estuary, where depth changes dramatically throughout the tidal cycle. The arrangement of sandbars can be relatively simple or the highly complex labyrinth observed in PIE. Sandbars have rarely been considered as a habitat type that drives fish distribution, and are more often considered as a featureless habitat category to which targeted three-dimensional structures like oyster reefs are compared (Harding and Mann 2003). Our results suggest that the role of sandbars has been underestimated.

Striped bass were concentrated in the middle *region* of PIE where river and ocean influences converge. The lower region is marine in character and defined by extreme conditions (e.g., few small confluences, very deep channels, very large drop-offs, strong currents). The upper region is dominated by the Parker River. However, the middle region contains a varied collection of habitat types (e.g., smaller confluences, the larg-

er Rowley River, a large salt marsh island, and numerous, reticulate sandbars). Others have also argued for the inclusion of spatially explicit locational parameters, like our variable *region* (e.g., Torgersen and Close 2004).

Numbers of striped bass increased with *confluence diversity*. Confluences or intersections of a tributary with a larger body of water are discontinuities at which flow is disrupted, channel morphology is altered, and physical complexity can be increased (Kiffney et al. 2006, Bigelow et al. 2007, Wallis et al. 2008). Elsewhere confluences affect fish biodiversity in general (Kiffney et al. 2006, Osawa et al. 2011) and anecdotally influence striped bass (Tupper and Able 2000). Surprisingly, these ecological networks were not the dominant habitat feature that aggregated striped bass in the PIE estuary. In fact, in PIE, the variety of confluences at a site was more important than the presence or absence of a confluence. Because confluences were extremely common throughout PIE, other irregularly distributed discontinuities that did not occur everywhere (e.g., sandbars) may have been the determinants of consumer habitat use (Kennedy 2013). Although network geometry has been emphasized in other disciplines (Benda et al. 2004), in research seeking to link consumers to physical habitat, little is known about the role of confluence complexity.

*Channel proximity*, *median depth variation*, and *median drop-off size* interacted with geographic *region* and *percent sandbar* to concentrate striped bass. Channel intersections are the underwater equivalent of tributary confluences, where strong currents meet to create variable bathymetric and hydrodynamic conditions. In PIE, more individual striped bass occurred at sites closer to channel intersections, probably for the same reasons that confluences increase heterogeneity (Benda et al. 2004, Kiffney et al. 2006, Wallis et al. 2008). *Median drop-off size* and *median depth variation*, by themselves, were minor players. Previous research has shown that striped bass can have an affinity for channels, deeper water, drop-offs, and an uneven bottom (Ng et al. 2007). In our research, sites that attracted a large number of striped bass were neither flat nor associated with extreme drop-offs. Our goldilocks approach to "just right" intermediate conditions could prove useful elsewhere.

We have tested new ideas about the ecological role of discontinuities. Existing studies have only looked at one type of discontinuity (e.g., dams, waterfalls; Robinson and Rand 2005, Kiffney et al. 2006) or whether a discontinuity is present or absent (Stanford and Ward 2001, Robinson and Rand 2005). Our results suggest that variation within (type, size, configuration, location) and between discontinuities should be considered in organism–environment relationships. In our quantitative ensemble approach (Oppel et al. 2012), similar results emerged from two statistical approaches (MLR and CART), which increased confidence that our trends resulted from an ecological signal not a specific statistical analysis. MLR is a powerful statistical approach for identifying the relationship between regressors and continuous response variables. However MLR cannot uncover complex ecological interactions and has restrictive assumptions. By looking for thresholds through an iterative approach, our second statistical approach, CART, complemented the MLR (De'ath and Fabricius 2000).

### Striped bass and additive heterogeneity

A combination of discontinuities explained why striped bass predators were concentrated. Sites in PIE with multiple discontinuities attracted more predators, possibly because increased physical heterogeneity provided more habitat options for striped bass as the hydrodynamics in the estuary changed throughout the tidal cycle. Creating effective complexity indices is challenging (Smith and Mather 2013). Existing indices have proven useful but often only measure a few variables, use qualitative variables, do not explain why a particular set of variables were chosen, or simply do not predict distribution better than individual habitat features (Clark et al. 2004, Gratwicke and Speight 2005, Anlauf et al. 2011, França et al. 2012, Kovalenko et al. 2012). Our three indices that combined individual discontinuities showed how habitat heterogeneity was linked to striped bass distribution.

### Management implications

Understanding patterns and drivers of distribution is critical for population, community, and ecosystem ecology, as well as for effective resource management. The distribution of predators affects the functioning of ecosystems via direct and indirect effects on prey communities (e.g., Heithaus et al. 2002, Fischer et al. 2012) and top-down ecosystem impacts (e.g., Heithaus et al. 2008, Estes et al. 2011, Altieri et al. 2012, Casini et al. 2012). Heterogeneity in the spatial distribution of predators also has broader conservation impacts such as biodiversity (e.g., Sergio et al. 2005). In PIE, irregularly distributed physical features (e.g., discontinuities) consistently concentrate striped bass predators and may set the stage for top-down effects at the "hotspots" that we identified. Across coastal systems, some combination of the physical features that we measured here are likely important for concentrating foragers, although the specific features and relative importance will vary across sites. In PIE, sandbars were particularly important, but elsewhere confluences, oyster reefs, or deep channels may drive consumer aggregations.

Animals within seascapes respond to patch mosaics in complex and important ways that are not yet completely understood (Boström et al. 2011). Research on mobile animal distribution and movement pathways can provide insights into these information gaps (Pittman 2013). Our research links the distribution of a mobile predator to physical features across an estuarine seascape in a way that starts to relate spatial pattern to process and has the potential to establish new definitions of functional connectivity. We use the term "seascape" to promote the perspective that when a mobile organism inhabits a heterogeneous ecosystem, physical features need to be examined at a larger spatial scale in order to detect the impact of rare influential features. This spatially explicit approach can also be useful to resource managers who require new approaches for conserving aquatic ecosystems at larger scales [ecosystem-based fisheries management (Rosenberg et al. 2000), spatial planning (Madden et al. 2005), and marine protected areas (Greenlaw et al. 2011)].

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## SUPPORTING INFORMATION