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Dynamic seascapes predict the marine occurrence of an endangered species: Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*

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Summary

1. Categorical landscapes are powerful environmental partitions that index complex biogeochemical processes that drive terrestrial species distributions. However, translating landscapes into seascapes requires that the dynamic nature of the fluid environment be reflected in spatial and temporal boundaries such that seascapes can be used in marine species distribution models and conservation decisions.

2. A seascape product derived from satellite ocean colour and sea surface temperature partitioned mid-Atlantic coastal waters on scales commensurate with the Atlantic Sturgeon migration. The seascapes were then matched with acoustic telemetry records of Atlantic Sturgeon to determine seascape selectivity. To test for selectivity, we used real-time satellite seascape maps to normalize the sampling of an autonomous underwater vehicle that resampled similar geographic regions with time varying seascape classifications.

3. Our findings suggest that Atlantic Sturgeon prefer one seascape class over those available in the coastal ocean, indicating selection for covarying environmental properties rather than geographical location.

4. The recent listing of Atlantic Sturgeon as Endangered throughout much of their United States range has highlighted the need for improved understanding of marine habitat requirements to reduce interactions with anthropogenic stressors. Narrow dynamic migration corridors may enable seascapes to be used as a daily decision tool by industry and managers to reduce interactions with this imperilled species during coastal migrations.

Key-words: conservation, endangered species, habitat, seascape, spatial modelling.

Introduction

Identifying the spatial and temporal factors of protected species' occurrence is central to maximizing conservation and recovery actions. In particular, the observation and subsequent modelling of imperilled species distributions are effective tools for reducing interactions and anthropogenic sources of mortality (Noss 1990). Many organisms display strong habitat selection, leading to a disproportionate use of particular environments in comparison with available environments (Johnson 1980). These patterns can then be incorporated into the conservation decision-making process and utilized to develop actions that preserve critical habitats (Rondinini *et al.* 2006). Further, observed patterns in habitat selection create testable inferences regarding generality of spatial and temporal patterns, enabling application to other locations (Aarts *et al.* 2008) and different scales (Rondinini *et al.* 2006).

One imperilled species whose seasonal coastal migrations are difficult to predict is Atlantic Sturgeon *Acipenser oxyrinchus oxyrinchus*. Atlantic Sturgeon is a large, long-lived anadromous species found on the east coast of North America (Vladykov & Greeley 1963). Overfishing for caviar in the late 19th and early 20th century (Cobb 1900; Borodin 1925), combined with habitat loss and degradation, severely diminished Atlantic Sturgeon populations with little to no recovery despite a reduction in directed fishing pressure and improved water quality (Billard & Lecointre 2001). As a result, the National Marine Fisheries Service listed Atlantic Sturgeon under the Endangered Species Act (ESA) on 6 April 2012 (USOFR 2012). The ESA ruling has the potential to have major impacts on commercial fisheries, shipping and other industries that interact with Atlantic Sturgeon during their coastal migration.

Atlantic Sturgeon occupy marine waters for the majority of their adult life, only entering rivers to reproduce (Smith 1985). Both bycatch records (Stein, Friedland & Sutherland 2004a) as well as fisheries independent findings (Laney *et al.* 2007; Dunton *et al.* 2010; Erickson *et al.* 2011) suggest that Atlantic Sturgeon primarily occupy inshore areas with coastal features including inlets and the mouths of bays; a finding similar to Green Sturgeon *A. medirostris* in the Pacific Ocean (Erickson

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& Hightower 2007). Research using pop-up satellite archival transmitters placed on adult Atlantic Sturgeon in the Hudson River documented broad movements from Nova Scotia to Georgia; however, these estimates are too coarse to make practical management decisions (Erickson *et al.* 2011).

Large-scale coastal migrations of anadromous sturgeons increase their vulnerability to anthropogenic impacts along migration routes (Collins *et al.* 2000). Commercial bycatch of Atlantic Sturgeon occurs in a variety of gear types (Stein, Friedland & Sutherland 2004b; ASSRT 2007; Dunton *et al.* 2015) and has been identified as a major impediment to recovery (Collins *et al.* 2000; ASSRT 2007). Bycatch events are highest during coastal migrations in the fall, winter and spring (Stein, Friedland & Sutherland 2004b; Dunton *et al.* 2015). As a result of these threats, developing strategies that reduce human interactions with Atlantic Sturgeon in the coastal ocean are key to the conservation and recovery of this species (ASMFC 2007).

In terrestrial ecology, complex interactions between climate, soil, topography and vegetative cover are represented by categorical landscapes, which simplify analyses of species habitat use and selection. The underlying assumption is that a particular landscape class is representative of a complex, but spatially cohesive biogeochemical and ecological processes that are relevant to understanding species distributions (Noss 1990). Classification naturally leads to a loss in the quantification of environmental variation; however, the extracted landscape classes can be good predictors of species habitat use. Additionally, classifications, especially those used to group multiple continuous variables, increase parsimony in model development and ease interpretation while still accounting for a complex environment. Categorical approaches have been applied to the marine environment partitioning the global oceans into biogeochemical provinces based on latitude, prevailing winds, proximity to the coast and *in situ* chlorophyll fields (Longhurst 1998). Biome partitioning is very similar to previous work in the broad-scale eco-regions defined for terrestrial systems (Bailey 1983). Longhurst *et al.* (1995) suggested that temporally static provinces could be improved by capturing seasonal variability of dynamic marine seascapes using remote sensing.

The fusion of satellite remote sensing and species observations provides an oceanographic context to interpret habitat selection (Chassot *et al.* 2011). Remote sensing of ocean colour has been used to map the distribution of Loggerhead Turtles *Caretta caretta* and Albacore Tuna *Thunnus alalunga* (Polovina *et al.* 2001) enabling modifications in fishing practices to reduce bycatch (Howell *et al.* 2008). However, these species are likely selecting for multiple and complex aspects of the marine environment that are not well described by one or two continuous variables at fairly coarse scales. Simplifying complex global marine systems into classifications representative of varying biogeochemical properties (Reygondeau *et al.* 2013; Kavanaugh *et al.* 2014) can provide a simple framework for resource management and conservation at national and international scales (Spalding *et al.* 2007).

There is a long tradition in oceanography of using ocean colour and temperatures to classify ocean waters (Helland-Hansen 1916; Jerlov 1968) that continues into modern satellite observations. Satellite ocean colour has been used to infer the dynamics of river plumes, coastal upwelling zones and mesoscale eddies (Mcclain 2009; Geiger *et al.* 2011). Therefore, ocean colour and sea surface temperature (SST) have been used to partition the global ocean into spatially and temporally dynamic water types and seascapes (Devred, Sathyendranath & Platt 2009; Kavanaugh *et al.* 2014). The approach taken by Oliver & Irwin (2008) preserves coastal features, has been verified by *in situ* data, and correlates well with known global climate indices and flavobacteria community structure (Gómez-Pereira *et al.* 2010). Even though they are a simplified representation of a complex environment, seascape classes may serve as natural proxies for ecologically important oceanographic processes that dictate species distributions (Kavanaugh *et al.* 2014).

We tested the hypothesis that globally tuned, satellite-derived dynamic seascapes are predictors for the occurrence of Atlantic Sturgeon during their spring migration in the mid-Atlantic. Atlantic Sturgeon occurrence was obtained through acoustic telemetry and tested against publically available 1-, 3- and 8-day satellite composites of seascapes in the mid-Atlantic region of the United States. As an independent test of the relationship between seascapes and sturgeon occurrence, we deployed an autonomous underwater vehicle (AUV) to interrogate dynamic seascapes and habitat selection to verify that our findings did not result from the geographical positioning of a moored telemetry array.

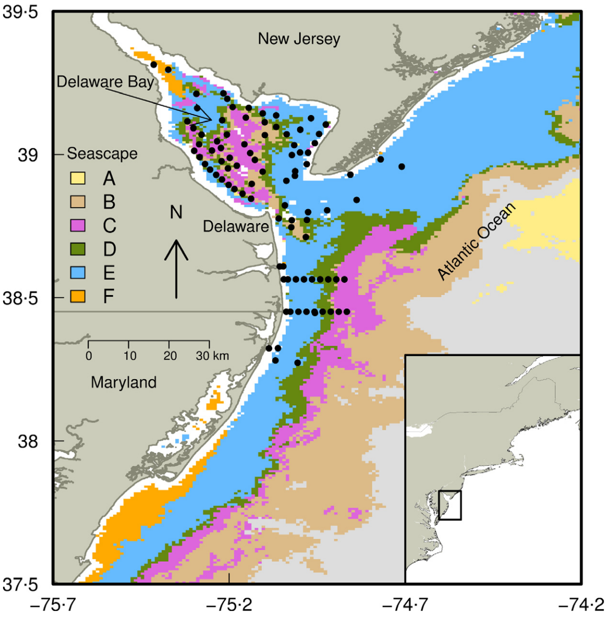

Fig. 1. Passive acoustic receiver locations (black dots) and example 8-day satellite seascape classes from 21 May 2009 (aggregated from May 18 to May 25) in the Delaware Bay and coastal Delaware, Maryland, and New Jersey. Seascape classes are listed as A–F.

Methods

Our study was conducted in Delaware Bay and nearby coastal waters (Fig. 1). Delaware Bay is a major coastal plain estuary and receives an average freshwater input of 920-m^3 s^{-1} from the Delaware River and its tributaries and has a major influence on the nearby coastal environment (Galperin & Mellor 1990).

SEASCAPES

The global seascape product used in this analysis was developed in Oliver *et al.* (2004) and Oliver & Irwin (2008), and is distributed daily for the Mid-Atlantic Regional Association Coastal Ocean Observing System, and is publically available (http://tds.maracoos.org/thredds/MODIS.html as Water Mass Classifications and available from 2009 to present). *In situ* hydrographic validation of this product is described in Oliver & Irwin (2008). Briefly, paired measurements of remote sensing reflectance (R_{rs}) (sr^{-1}) at 443 and 555 nm and daytime SST, taken by NASA's MODIS-Aqua (Moderate Resolution Imaging Spectroradiometer) satellite from 2002–2011, were standardized to their respective global mean and variance then partitioned into clusters (Table S1, Supporting information). Two clustering algorithms, Ward's linkage agglomerative clustering (Ward 1963) and K-means divisive clustering (Hartigan & Wong 1979), were used to create clusters of paired R_{rs} and SST. A Figure of Merit statistic (Yeung, Haynor & Ruzzo 2001) estimated how well each cluster centroid predicted all other members of its class, and the classification was determined complete when the addition of classes did not improve the predictive power for the other classes (Oliver & Irwin 2008). These classes were then applied to MODIS-Aqua data not involved in the clustering process in the following way. Level 1b MODIS-Aqua data were processed using the NASA SeaDAS program to 1 km Level 3 data using the standard NASA quality flags. These data were standardized to their global means and standard deviations from Oliver & Irwin (2008) (Table S1). These new standardized R_{rs} and SST data were assigned their seascape class by computing their nearest neighbour using Euclidean distances in standardized R_{rs} and SST space (see Data S1). The dominant seascape classes in our study area were assigned letters A–F. A MANOVA (manova, R package 'stats') showed these seascape classes to be significantly different from each other ($P < 0{\cdot}001$).

While contamination of the ocean colour radiance signal from bottom reflectance was possible due to the shallow water depth, this is not likely as the coastal waters in our study area are highly turbid year-round due to high chlorophyll concentrations (Xu *et al.* 2011). To overcome data loss from cloud cover and sunglint preventing observation of the sea surface, two additional temporal averages were made using daily R_{rs} and SST, which were then classified into seascapes. The first was an average over a 3-day period with assigned date being the 2nd day, and the second was an average over an 8-day period with the assigned date being the 4th day of the period.

ATLANTIC STURGEON

Atlantic Sturgeon locations were measured via implanted acoustic transmitters (V16-4 h and V16-6 h, 69khz; VEMCO Ltd. Halifax, NS, Canada) coupled with a passive acoustic receiver (VR2 and VR2W; VEMCO Ltd.) array (Fig. 1). Passive acoustic receivers use an omnidirectional hydrophone to detect, and log coded transmissions from transmitters when within the detection range of the receivers; typical ranges for VR2W receivers and V16 transmitters in our study area are ~700–1000 m depending on oceanographic conditions (Kilfoil 2014). Transmitters were implanted in adult Atlantic Sturgeon during April and May from 2009 to 2012 in the near-shore waters of the Atlantic Ocean near Bethany Beach, Delaware (collections were permitted under National Marine Fisheries Service Permit No. 16507).

Acoustic detections of Atlantic Sturgeon in the passive receiver array were reduced to unique detection locations by day (detection day), then spatial and temporally matched to the 1-, 3- and 8-day seascapes. We estimated the availability of each seascape class for individual Atlantic Sturgeon separately by summing the total number of days for each receiver station in each seascape class for the time interval bracketed by the first and last detection of an individual sturgeon (e.g. if an individual was first detected on April 1 and last detected on April 30, the available seascape proportion for that individual would be the sum of days each deployed receiver was matched to each seascape class divided by the sum of matched days to any seascape class from April 1 to 30). Detections and seascapes were censored to only cover April, May and June 2009–2012, the period of peak Atlantic Sturgeon spring migration. To facilitate analyses, we combined all seascape classes that represented <1% of the detection days into one remainder category.

GLIDER DEPLOYMENT

As an independent validation to the moored acoustic array analysis between seascapes and Atlantic Sturgeon, we deployed a generation two Slocum Electric Glider (Teledyne-Webb Research, Falmouth, MA, USA) in the mid-Atlantic coastal ocean from 10 April 2013 to 28 June 2013 (Fig. 2). The glider changes its buoyancy and weight distribution to glide in a sawtooth pattern under water while collecting data via a suite of sensors (Schofield *et al.* 2007). Pre-programmed missions allowed for the glider to be commanded over Iridium Satellite every 1–3 h. The glider was directed to sample across the 8-day aggregated seascape classes in the coastal Atlantic Ocean within ~25 km of the shoreline along a 120 km stretch of coastline between Bethany Beach, DE, and Chincoteague, VA. To detect telemetered Atlantic Sturgeon, two

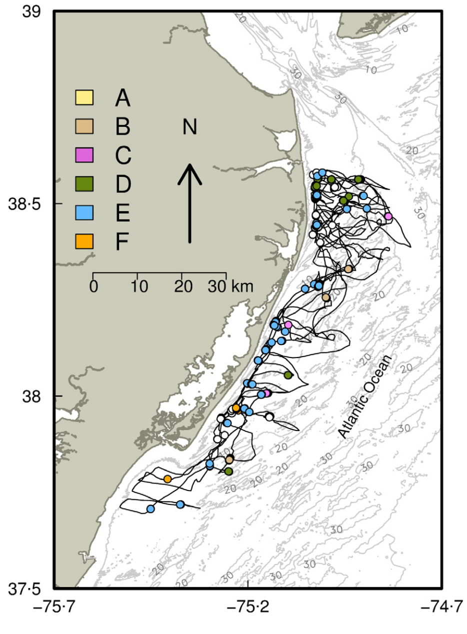

Fig. 2. Slocum Electric Glider mission path with Atlantic Sturgeon acoustic detections (coloured by 8-day seascape class). The mission lasted 79 days from 10 April 2013–28 June 2013 and covered 1440 km. Seascape classes are listed as A–F.

VEMCO VR2C acoustic receivers were integrated into the glider; one mounted dorsally and one ventrally to improve detection efficiency and reduce shadowing of acoustic signals by the body of the glider. Acoustic transmitter detection efficiency by the glider is very high (97%) within 250 m and diminished to 40% by 500 m (Haulsee *et al.* 2015), which is smaller than the ~1 km spatial resolution of the seascapes. The glider track was binned into hourly segments, which were then matched to 1-, 3- and 8-day seascape classes for the corresponding time and location. Likewise, Atlantic Sturgeon detections were binned hourly (detection hour) and matched to the assigned seascape class for that segment of track in which they were detected.

ANALYSES

To determine whether Atlantic Sturgeon detected by the passive acoustic array were selecting for certain seascapes, we conducted a compositional analysis (Aebischer, Robertson & Kenward 1993) of per cent habitat use (compana, R Package 'adehabitatHS', Calenge 2006) using seascapes as a surrogate for habitat type. Compositional analysis accounts for the differential sampling of seascape types by the acoustic receiver array and uses analysis of variance of the log ratios to test the significance of seascape selection (utilized) against the observed distribution of seascapes (available). Once analysed, seascape classes are ranked to determine order and significance of each seascape in comparison with the other available seascapes. To avoid pseudoreplication and problems associated with autocorrelation by individual behavioural effects (Aebischer, Robertson & Kenward 1993), each sampling unit was defined by an individual Atlantic Sturgeon and was comprised of the proportion of seascape classes used and available to that individual. We assigned a usage value of 0·01% to non-utilized seascape classes to prevent an invalid log-ratio transformation during the compositional analysis as recommended by Aebischer, Robertson & Kenward (1993).

The glider mission recorded a low number of repeated detections of individual Atlantic Sturgeon, and therefore, it was not appropriate to perform a compositional analysis on the glider mission data. However, we employed a chi-squared analysis and Manly selectivity ratio (selection ratio = used/available seascape) to test for preference and avoidance of seascapes (widesI, R Package 'adehabitatHS', Calenge 2006) (Manly, McDonald & Thomas 1993) on pooled detection hours from all Atlantic Sturgeon detected during the glider mission to determine if seascape use deviated significantly ($\alpha = 0{\cdot}05$) from what would be expected if no selection was occurring.

Results

SEASCAPES

Six seascape classes dominated the study area during this study and were labelled Seascapes A–F (Fig. 1). The fractional occurrence of the 8-day aggregated seascapes by location (number of seascape observations/number of 8-day satellite composites in our study period by pixel) in our study region shows that seascapes generally align parallel to the coast (Fig. 3). However, animating the seascapes at daily increments reveals a very dynamic environment over this study area (Fig. 1 and Movie S1; Fig. S1). Seascape E, the most frequent class in the passive receiver array, was associated with the coastline of Delaware Bay and Atlantic Ocean, and is defined by a mean temperature of 19·8 °C (SD = 8·0 °C) and had the second highest reflectance at both 443 nm (mean = 0·0073 sr^{-1}, SD = 0·0039 sr^{-1}) and 555 nm (mean = 0·0083 sr^{-1}, SD = 0·0011 sr^{-1}) of the seascapes (Table 1; Fig. 3e). The second most abundant seascape class was D with a mean temperature of 20·3 °C (SD = 10·4 °C) and mean reflectance 0·0054 sr^{-1} (SD = 0·0029 sr^{-1}: 443 nm) and 0·0063 sr^{-1} (0·00048 sr^{-1}: 555 nm: Table 1). The highest occurrence of Seascape D places it just offshore of Seascape E with a filament inhabiting a major portion of the Delaware Bay (Fig. 3d).

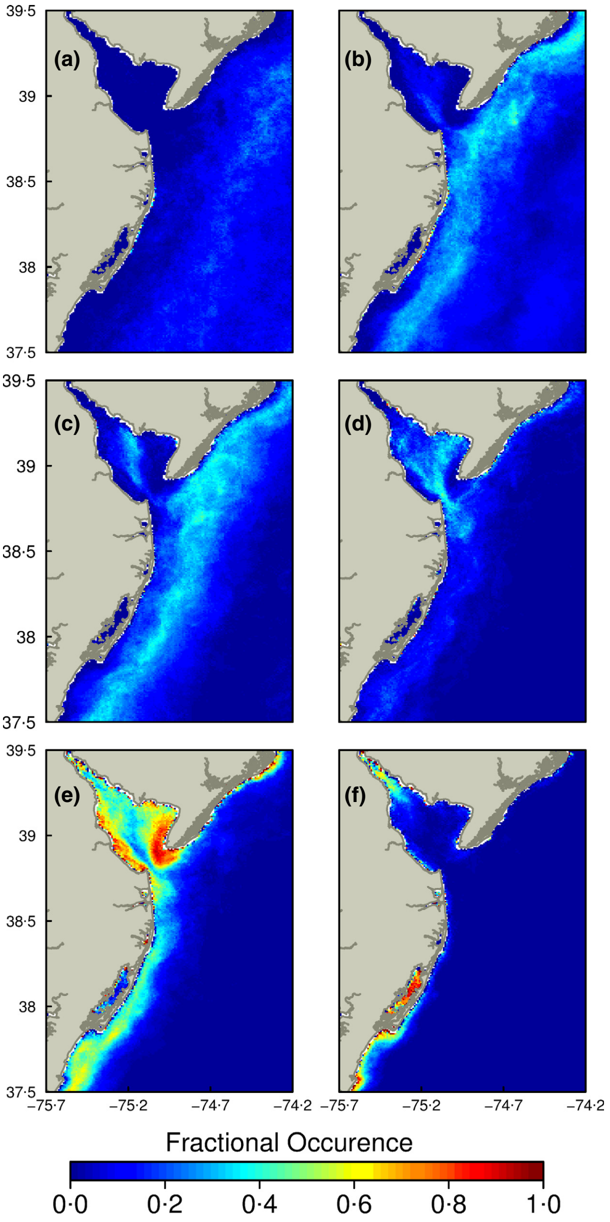

Fig. 3. Fractional occurrence 8-day averaged seascape classes in the Delaware Bay and coastal Atlantic Ocean for April, May and June 2009–2012. The mean (SD) pixel sample size is 306 (71).

FIXED RECEIVER ARRAY

Passive acoustic receivers were deployed at 94 stations during this study with coverage most limited in 2009 and increasing

Table 1. Global mean (standard deviation) for sea surface temperature (SST) and remote sensing reflectance (RRS) of the six seascape classes, and the total time each 8-day averaged seascape was observed by platform and detection days/hours (receiver array/glider) of Atlantic Sturgeon

Seascape	SST (°C)	R_{rs} 443 nm (sr^{-1})	R_{rs} 555 nm (sr^{-1})	Array days	Detect.days (array)	Glider hours	Detect. hours (glider)
A	15·2 (2·1)	0·0035 (0·0012)	0·0022 (0·00024)	165	45	–	–
B	6·7 (5·4)	0·0054 (0·0018)	0·0039 (0·00068)	1238	354	222	5
C	25·4 (4·2)	0·0048 (0·0022)	0·0036 (0·00076)	1767	286	234	8
D	20·3 (10·4)	0·0054 (0·0029)	0·0063 (0·00048)	2181	672	265	6
E	19·8 (8·0)	0·0073 (0·0039)	0·0083 (0·0011)	3890	2275	504	35
F	18·9 (9·8)	0·0091 (0·0035)	0·0133 (0·0021)	370	299	175	13
			Total	9911	3931	1400	67

each year until 2012. Within-year variability of receiver coverage was minimal and mainly resulted from equipment failure or loss. During the 4 years of the study, the 94 stations had a combined 14 617 monitoring days. Over this time frame, 240-telemetered Atlantic Sturgeon from the original tagging effort off of Bethany Beach, DE, were recorded on 90 of the 94 receiver stations for 14 049 detection days during April, May and June 2009–2012. Of the 14 617 monitoring days, 2047 were matched to 1-day seascape classes, 5323 to 3-day seascape classes and 9966 to 8-day seascape classes (Table 1). Atlantic Sturgeon detection days showed a similar pattern to that of the receiver monitoring days with 661 matched to 1-day seascape classes, 1897 to 3-day seascape classes and 4049 to 8-day seascape classes (Table 1). The six seascape classes defined above dominated both the receiver and Atlantic Sturgeon matches and accounted for >99% of the matches.

The compositional analysis of habitat selection on the passive receiver array revealed that Atlantic Sturgeon are associated with particular satellite-derived seascapes ($P < 0{\cdot}001$). Seascape class E was the seascape most preferred by sturgeon in all three averaging scenarios, and was the only seascape to be significantly preferred by Atlantic Sturgeon (Fig. 4). Subsequent to E, the ranking order varied among the three seascape averaging scenarios (Table 2). Analysis of 1-day averaged seascapes ranked seascape F second, followed by D, A, B and C, respectively. Analysis of the 3-day averaged seascape classes ranked D second, followed by F, B, A and C. Finally, for the 8-day average, the subsequent highest utilized seascapes were B, D and F, which were not significantly different from each other and had no indication of preference or avoidance. Seascape A was ranked significantly less than the top four, and Seascape C was ranked last being associated with sturgeon significantly less than all other seascape classes.

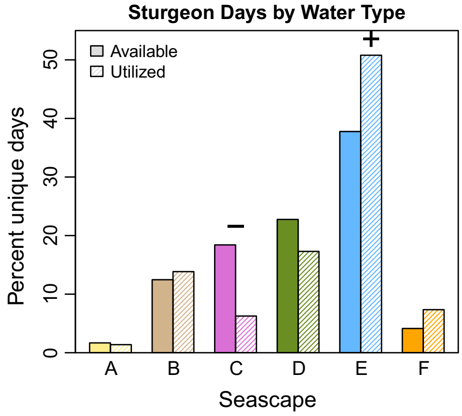

Fig. 4. Per cent available (solid bars) and utilized (striped bars) seascape detection days for Atlantic Sturgeon in the passive receiver array during the spring (April–June) of 2009–2012 (+ = significantly preferred; − = significantly avoided, α = 0·05).

GLIDER MISSION

The glider travelled 1420 km over the 1887-h deployment beginning on 10 April 2013 and ending on 28 June 2013; 1437 of the 1887 h were matched to the 8-day satellite seascape classes (Movie S2). The glider detected 62 Atlantic Sturgeon for 105 detection hours; of which 22 were from the original tagging effort off of Bethany Beach, DE, and 23 were subadult

Table 2. One-, 3-, and 8-day seascape class ranking for Atlantic Sturgeon detections on the acoustic receiver array. Preference is ranked from left to right/top to bottom. Symbol depicts preference (+) or avoidance (−) over corresponding seascape; three symbols depict a significant difference (α = 0·05) between corresponding seascapes

1-Day seascape	E	F	D	A	B	C
E	0	+++	+++	+++	+++	+++
F	−−−	0	+	+	+++	+++
D	−−−	−	0	+	+++	+++
A	−−−	−	−	0	+++	+++
B	−−−	−−−	−−−	−−−	0	+
C	−−−	−−−	−−−	−−−	−	0

3-Day seascape	E	D	F	B	A	C
E	0	+++	+++	+++	+++	+++
D	−−−	0	+	+++	+++	+++
F	−−−	−	0	+	+++	+++
B	−−−	−−−	−	0	+++	+++
A	−−−	−−−	−−−	−−−	0	+
C	−−−	−−−	−−−	−−−	−	0

8-Day seascape	E	B	D	F	A	C
E	0	+++	+++	+++	+++	+++
B	−−−	0	+	+	+++	+++
D	−−−	−	0	+	+++	+++
F	−−−	−	−	0	+++	+++
A	−−−	−−−	−−−	−−−	0	+++
C	−−−	−−−	−−−	−−−	−−−	0

Atlantic Sturgeon collected during the spring and fall of 2010–2012 near Rockaway, NY. The remaining 17 transmitters were implanted by other researchers as part of unrelated projects; nine in the James River, VA [M.T. Balazik (7), VCU/Rice Rivers Center & A. Wright, Rice Rivers Center (2)], four in the Long Island Sound (T.F. Savoy, CTDEP), two in the Roanoke River, NC [J.E. Hightower & H.J. Flowers, NCSU, (1) (Flowers 2014), & M. Loeffler, NCDENR (1)], and two in the Combahee River, SC (B. Post, SCDNR).

Five of the six seascape classes identified in the passive array (Seascape classes B–F) were dominant during the glider mission and accounted for >99% of the matched data. Of the 105 detection hours during the glider mission, only 15 were matched to the 1-day seascape classes, 27 were matched to the 3-day seascape classes, and 67 were matched to the 8-day seascape classes (Fig. 2).

Deployment of the Slocum Glider allowed for directed sampling of seascapes for telemetered Atlantic Sturgeon as they migrated through the mid-Atlantic region in 2013 (Movie S2). By resampling, the same geographic areas under different environmental conditions, and thus different seascapes, the association of Atlantic Sturgeon with Seascape E were further supported. In the initial stages of the glider mission, we sampled off the coast of Delaware, Maryland and Virginia from ~2–18 km from shore, in an area where we expected to encounter Atlantic Sturgeon. However, we did not detect our first Atlantic Sturgeon until the 7th day of the mission, coinciding with the first sampling of Seascape E (Movie S2). This pattern continued with detections of Atlantic Sturgeon occurring more often in Seascape E despite repeated sampling of geographic areas on different dates throughout the mission, indicating a significant spatial and temporal coupling between seascape E and Atlantic Sturgeon.

The chi-squared analysis of Atlantic Sturgeon detection hours during the glider mission matched to the 8-day aggregated seascapes aligns with the findings on the passive acoustic receiver array with the exception of Seascapes B and D where significant avoidance was observed during the glider mission compared to no preference found in the fixed receiver array. Overall, the distribution of seascape classes was significantly different from random for the 8-day averaged seascape classes ($P = 0\cdot0016$) with Seascape E used significantly more than random ($P = 0\cdot022$), while Seascape B ($P = 0\cdot002$) and Seascape D ($P = 0\cdot005$) were significantly avoided (Fig. 5). Use of the seascape classes C ($P = 0\cdot16$), and F ($P = 0\cdot20$) were not significantly different from random for the 8-day aggregate. The limited number of detection hours matched to the 1 and 3-day seascape aggregates contributed to the lack of significant findings when compared to a random distribution (1-day $P = 0\cdot44$ and 3-day $P = 0\cdot054$).

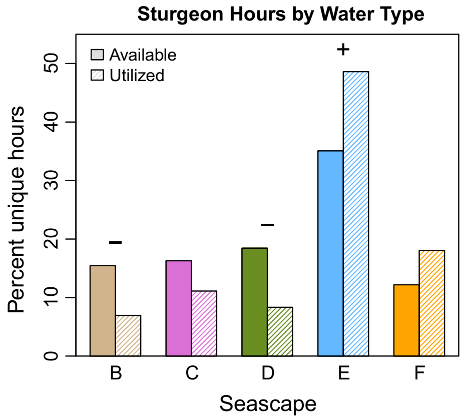

Fig. 5. Per cent available (solid bars) and utilized (striped bars) seascape detection hours for Atlantic Sturgeon during the Slocum Electric Glider mission, the mission lasted 79 days from 10 April 2013–28 June 2013 and covered 1440 km. (+ = significantly preferred; – = significantly avoided, $\alpha = 0\cdot05$).

Discussion

Our findings strongly suggest that Atlantic Sturgeon are exhibiting habitat selection based, at least, on seascapes during their spring coastal migrations. Sturgeon detected by the passive receiver array and the Slocum Glider preferred a specific seascape, providing evidence that managers can utilize seascape products as a simple monitoring tool for understanding the distribution and movement of marine species in a dynamic environment. The overwhelmingly preferred seascape class (E) was found most often near the mouth of the Delaware Bay and along the coast south of the Delaware Bay in the Atlantic Ocean, with reflectance values likely a result of terrigenous input from the Delaware Coastal Current (Sanders & Garvine 1996). This seascape class is the same seascape class that was associated with Atlantic Sturgeon in the original proof of concept test of glider feasibility in detecting telemetered fishes (Oliver *et al.* 2013).

Landscape partitioning and species distribution models have been used in terrestrial ecology to describe species distributions and occurrences (Forman & Godron 1981; Stinnett & Klebenow 1986) and plan conservation measures (Rondinini *et al.* 2006). However, the use of species distribution models in the marine environment has lagged behind the terrestrial realm (Robinson *et al.* 2011). Previous studies of sturgeons have substituted substrate or bathymetry for landscape class to perform similar analyses in the marine and estuarine environment with some success (Fox, Hightower & Parauka 2002; Huff *et al.* 2011; Breece *et al.* 2013); however, temporally static attributes such as landscape classes have their limits when applied to the dynamic coastal ocean. Classifying the fluid in which marine organisms live in, rather than the bottom in which they live over, may improve our ability to estimate species occurrence in the aquatic environment, as migratory marine organisms, even benthic ones such as Atlantic Sturgeon, are often tied to the fluid rather than the substrate (Manderson *et al.* 2011). Atlantic Sturgeon appear to be a species in which this simple, class based relationship, holds true.

The seaward extent of Seascape E varies significantly with time, distance, and direction from the Delaware Bay (see Movie S1). The narrow seaward extension of Seascape E off the coast of New Jersey follows the patterns of Atlantic Sturgeon detections, indicating that sturgeon may be constricted to a narrow corridor that is spatially coincident with seascape availability. There is large interannual variation in the seaward extension of Seascape E, which also is congruous with Atlantic Sturgeon detections. Importantly, the presence of Seascape E does not guarantee high detections, but where Seascape E is in low proportions, there are relatively few Atlantic Sturgeon detections (Fig. S2).

Mouths of estuaries and inlets have been known to concentrate Atlantic Sturgeon in the coastal ocean (Laney *et al.* 2007; Dunton *et al.* 2010; Erickson *et al.* 2011), and Atlantic Sturgeon migrate among these locations using relatively narrow corridors along the coast (Dunton *et al.* 2010). This study confirms these findings using both the passive acoustic array and glider. Further research linking surface measurements to physiology and ecology of Atlantic Sturgeon, or in relation to benthic habitat processes, such as the location of sediment deposition, will be required to reveal the mechanisms driving this association and their consistency throughout the year.

Full understanding of the processes driving the association of Atlantic Sturgeon to seascape E is not yet known; however, it appears we can use this global product to estimate spatial occurrence without requiring direct observation of individuals to inform coastal ocean users during spring migration. Verified daily estimates of species occurrences in a dynamic environment promote a greater understanding of environmental factors that influence migration patterns and habitat use explaining why, in some locations, Atlantic sturgeon can be found further offshore than others. Users of the coastal ocean could apply this knowledge to reduce interactions with Atlantic Sturgeon by avoiding preferred seascapes.

The seascape classification product utilized in our study is a relatively simple, publically available global product that can be used for the delineation of habitat preferences and comparisons between habitat uses for many other marine species. These classifications can also be employed to help reduce detrimental impacts to protected species such as fisheries bycatch (Dunton *et al.* 2015), vessel strikes (Simpson & Fox 2009; Fisher 2011) and dredging (Smith & Clugston 1997). The use of seascape classes may also prevent the need for broad spatiotemporal fisheries closures that might have adverse economic effects on industry and would likely be highly opposed. Near real-time seascape maps would allow coastal ocean users to self-mitigate risks of encountering species such as Atlantic Sturgeon. For example, the large-mesh gillnet fisheries in the mid-Atlantic encounter sturgeon at increased rates compared to other fisheries (Collins *et al.* 2000; ASMFC 2007) and could benefit from a seascape based avoidance tool. Displacement of fishing effort from seascape classes strongly associated with Atlantic Sturgeon should reduce the incidence of bycatch and associated mortality events. This effort displacement could come in the form of offshore shifts during times when Seascape E is historically prevalent or, in a more complex approach, individual fishers with access to the satellite seascape classes could make daily decisions to avoid certain seascape classes to reduce interactions, affording themselves a longer fishing season without reaching seasonal Atlantic Sturgeon incidental take limits. The use of seascape classifications may facilitate the development of an alternate approach to marine species distribution models that rely on continuous data. In the dynamic seascape approach presented here, a single categorical variable is used as a proxy for a complex marine system. While models tuned to specific species and continuous predictors typically have a better fit to species occurrence data, their use can create complex models that may not be as easily appropriated by managers or stakeholders.

We integrated multiple technologies in a compositional seascape analysis to determine the habitat preferences of an endangered species. Relying on satellite remote sensing, acoustic telemetry and an AUV, we revealed an association between Atlantic Sturgeon and seascape classes that could have major benefits in conserving and protecting this imperilled species. Daily satellite passes allow a continually updating seascape map that can be easily visualized by managers and stakeholders to avoid interactions thereby fostering recovery. The dynamic, fluid nature of the coastal ocean poses many challenges in the study of marine species. While the classification of the ocean into seascapes may result in some information loss, the benefits of this approach allow for the simple identification of habitat preferences and are directly applicable to management and conservation.

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Data accessibility

Utilized and Available data for each Atlantic Sturgeon in the passive acoustic array matched to 1-, 3- and 8-day seascapes are located as a.Rdata file (Data S1). The level 3 satellite channels to reproduce the seascapes are archived at http://oceandata.sci.gsfc.nasa.gov/MODISA/. Additionally, the processed seascapes are available at http://tds.maracoos.org/thredds/MODIS.html and can be reproduced with other sources of satellite ocean colour and SST using the Supplemental R script. The glider path and associated Atlantic Sturgeon detections are available via the Ocean Tracking Network at www.datacite.org http://dx.doi.org/10.14286/2015BREECEMEE.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Global mean and standard deviation of R_{rs} 443, R_{rs} 555, and sea surface temperature for all seascapes defined by Oliver & Irwin (2008).

Fig. S1. Two examples of 8-day satellite seascape classes with detections of Atlantic Sturgeon (solid black dots) varying seascape class with the passive acoustic receiver locations (hollow circles).

Fig. S2. Detections per day of Atlantic Sturgeon (left vertical axis, bars) and proportion of receiver time in Seascape E (right vertical axis, lines) by distance from shore for the Delaware Coast in 2011 (top) and 2012 (middle), and the New Jersey Coast for 2009–2012 combined.

Movie S1. Daily images of 8-day seascape classes in the Mid-Atlantic during the spring of 2012.

Movie S2. Daily images of 8-day seascape classes and the slocum electric glider mission path with Atlantic Sturgeon acoustic detections (coloured by seascape class). The mission lasted 79 days from 10 April 2013–28 June 2013 and covered 1440 km.

Data S1. R script and example data set.