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Long term expansion of a deep *Syringodium filiforme* meadow in St. Croix, US Virgin Islands: the potential role of hurricanes in the dispersal of seeds

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Abstract

Automated image classification techniques were applied to aerial photographs of a deepwater (10–20 m) *Syringodium filiforme* bed in Buck Island Channel, St. Croix, US Virgin Islands to quantify change in its extent from 1971 to 1999. An increase in seagrass coverage from 1.33 km^2 of sea bottom to 4.34 km^2 was documented. Ninety-two percent of the area already covered in 1971 was still occupied in 1999. In addition, the relative contribution of horizontal expansion of existing beds in 1971 versus that of seed dispersal and growth were estimated. Fifty-four percent of the new seagrass area in 1999 was within the distance of possible horizontal growth of 1971 patches, whereas the rest was outside of this distance suggesting that only dispersal, germination, and subsequent growth of seeds could be responsible for this new colonization. New seagrass patches were not spread randomly throughout the channel; rather they were concentrated near patch reefs but beyond the usual sand halo typical of reef/seagrass interfaces. The current period of increasing meadow extent is coincident with a greater frequency of hurricanes in the region. Since no other causal mechanism could be identified, we suggest that this higher hurricane frequency enhanced seed and seagrass fragment dispersal.
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Keywords: Aerial photography; Hurricane; Patch dynamics; Seagrass; *Syringodium filiforme*

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1. Introduction

Seagrass meadows are an important feature of many coastal areas due to their role as primary producers (Kenworthy and Schwarzchild, 1998), since they provide habitat to a variety of fish and invertebrates (Kenworthy et al., 1988; Nagelkerken et al., 2000), and also because of their ability to influence coastal geomorphology by damping wave energy (Fonseca and Cahalan, 1992) and trapping and stabilizing sediment (Ward et al., 1984; Gacia et al., 1999). Monitoring the changes in the distribution of these often dynamic benthic features is critical to understanding and predicting their impacts on ecosystem composition, fisheries production, and even coastal erosion.

Changes in seagrass cover are caused by a variety of biological and physical mechanisms. For example, grazing by fish and invertebrates has been shown to eliminate seagrass and other vegetation from a sandy 'halo' around reefs that are close to seagrass meadows (Ogden, 1976). Dense populations of manatees, dugongs, sea turtles, or even sea urchins have been known to strip wide swaths of seagrass from some areas (Camp et al., 1973). In addition to these biological factors, physical processes including erosion from waves and burial from sediment deposited during storm events (Patriquin, 1975; Williams, 1988), disturbance from boat anchors and propellers (Dawes et al., 1997; Creed and Amado Filho, 1999), and algal shading following eutrophication (Cambridge et al., 1986; Kendrick et al., 2002) have all been identified as causes of seagrass loss over extensive areas.

Seagrass can also cover new areas or be re-established in former meadows. This is done through two primary means: horizontal expansion of existing beds and colonization of new areas through seed dispersal (Johnson and Williams, 1982; Duarte and Sand-Jensen, 1990; Gallegos et al., 1994; Orth et al., 1994). The relative contribution of each of these mechanisms to the enlargement of seagrass meadows is difficult to quantify (Kendrick et al., 1999). Most studies of seed dispersal and patch growth are conducted under average flow conditions and short timescales which, while necessary as a first step, offer only a limited temporal perspective on patch dynamics (Fonseca and Kenworthy, 1987). Long term influences of extreme events such as hurricanes remain poorly documented and understood (Patriquin, 1975; Williams, 1988).

A database of historical aerial photographs has accumulated over recent decades for many coastal areas that now allow a landscape-scale perspective for analysis of long term changes in distribution of seagrass meadows and other benthic features at some sites (Ferguson et al., 1993; Kendrick et al., 1999; Kendrick et al., 2002). In the present study, aerial photos from 1971 and 1999 were analyzed and the results compared to determine the extent of change in the distribution of the seagrass *Syringodium filiforme* (Kützing) in Buck Island Channel, St. Croix, US Virgin Islands (Fig. 1). In recent decades, the study area has been subjected to increased frequency of hurricanes although other parameters such as community structure of marine organisms have remained relatively constant. Analysis of aerial photos of this

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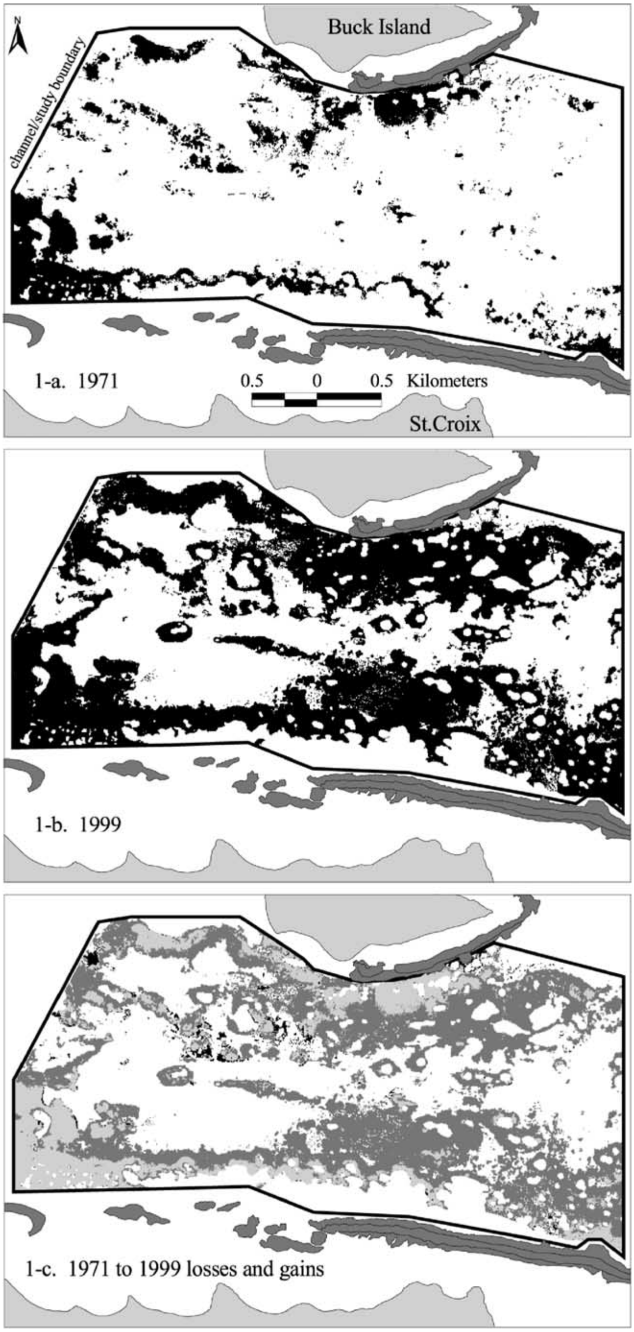
Fig. 1. (a–c) Changes in coverage of *S. filiforme* from 1971 to 1999. The center of the study area is located at 17.77° N, 64.62° W. Outside the study boundary, land is light gray and emergent reef crests are dark gray. Bare sand and patch reefs within the study boundary are in white. In (a) and (b), coverage of *S. filiforme* is in black. In (c), areas in the study area colonized by seagrass in 1971 only are in black, seagrass areas from 1999 only are in dark gray, and seagrass areas present in both 1971 and 1999 are in light gray.


N
Buck Island
channel/study boundary
1-a. 1971
0.5 0 0.5 Kilometers
St.Croix
1-b. 1999
1-c. 1971 to 1999 losses and gains

area places the extent and dynamics of the seagrass meadows within the channel into their wider historical and ecological context.

Our objectives were to quantify the losses, gains, and overall change in extent of *S. filiforme* meadows in Buck Island Channel from 1971 to 1999, to calculate the possible contribution of horizontal expansion of existing beds through vegetative growth versus propagation through seed dispersal to enlargement of seagrass meadows during this period, and to discuss the alternative mechanisms that may be responsible for the observed changes such as differences in intensity of herbivory, environmental conditions, and frequency of hurricanes.

2. Methods

The study region for this analysis is a roughly rectangular area locally known as Buck Island Channel. This region extends from the fringing reef along the north shore of St. Croix northward approximately 2 km to the fringing reef along the southern shore of Buck Island (Fig. 1). The Channel runs east–west between Buck Island and St. Croix for a distance of approximately 5 km. In the channel, the depth range is from 10 to 20 m; however, the substrate is generally flat and is on average ∼15 m deep. There are three primary bottom types in this area: sand, seagrass, and patch reefs. Seagrass meadows in this area are clearly dominated by *S. filiforme* but contain several species of algae and other seagrass including *Thalassia testudinum* (König). The patch reefs generally have a low relief and rise at most 1–2 m above the substrate. Tidal fluctuations in this region are negligible for water of this depth and do not significantly influence spectral signatures and classification.

Color aerial photographs acquired by the NOAA National Ocean Service in 1971 and 1999 were used in this analysis. The 1999 photos were collected at a scale of 1:48,000 specifically for the purpose of benthic mapping and therefore were acquired under clear atmospheric and water conditions. The 1971 imagery was acquired at a scale of 1:40,000 for charting airport obstructions although the photographer's notes indicate "deep clear water". This notation along with careful examination of the images indicates that water turbidity was low and atmospheric conditions were excellent for identifying benthic features. Furthermore, in both the 1999 and 1971 imagery, it was possible to discern all of the patch reefs and other permanent features across the full range of depths in the study area. This indicates that bottom type including seagrass was detectable throughout the study area for both years of imagery. Photographs were taken in November in 1971 and in February in 1999. This difference of three months in the season of acquisition is assumed to minimally impact our results since seasonal differences in seagrass cover are small at this site (pers. obs.) and both sets of photos were acquired during the winter weather pattern. Additional parameters for each photo are described in Table 1.

The 1999 photographs of the area were mosaiced to support a benthic mapping project in the region (Kendall et al., 2002). This mosaic was created in geoTIF format with 2.2 m pixels in the WGS84 datum, UTM Zone 20 projection. This format results in 8 bit data with three values per pixel; red, green, and blue brightness (0–255), respectively. The 1971 photos were rectified to the 1999 mosaic using 12 image to image tie points. By selecting shoreline features and patch reefs common to the two years of imagery, a root mean square

Table 1
Summary of parameters for aerial photographs used to conduct change analysis

	November 20, 1971	February 20, 1999
Frames	1123–1125	770–773
Roll	71LC31	99ACN03
Time (GMT)	15:05	16:17
Scale	1:40000	1:48000
Sun angle (°)	50.5	61.8
Turbidity	low	low
Clouds/haze	none	none

error value of 0.69 pixels was obtained based on the 12 tie points, a result which indicates strong geometric correspondence between images. To account for the difference in scale between the 1999 (1:48,000) and 1971 (1:40,000) photographs, scans of the 1971 images were re-sampled using the nearest neighbor method to match the pixel size of the 1999 mosaic. This process was assumed to make the resolution of the two sets of photography comparable since the finer scale 1971 imagery was simplified to match the resolution of the 1999 imagery prior to analysis.

Before classification of the images, pixels forming Buck Island Channel were masked to isolate them from land and other non-channel pixels which resulted in an area of 9.08 km^2 for analysis (Fig. 1). In addition, since the objective of the analysis was to evaluate seagrass change, pixels of reef cover were also eliminated. This was necessary since seagrass and reef pixels at this depth and resolution of imagery are spectrally very similar. All patch reefs in the area were visible in both sets of imagery. Size and dimensions of reefs were not observed to change during preliminary analysis of the imagery. Therefore, the same mask, derived from ground truth data and visual interpretation of the 1999 mosaic, was applied to both years of imagery to eliminate reef pixels from the analysis. Even though reef and seagrass pixels are spectrally similar, reef areas are visually identifiable in the imagery due to sand halos around these features caused by grazing of reef-associated herbivores (Ogden, 1976). This masking process resulted in only sand and seagrass pixels available for image classification.

An iterative self-organizing data analysis technique (ISODATA) was independently applied to both years of imagery (Jensen, 1996). This unsupervised technique was used rather than visual interpretation or supervised techniques to minimize human bias during classification of sand and seagrass pixels. For both years of images, photomosaics were segmented into areas of homogenous depth and illumination characteristics to facilitate ISODATA clustering. The ISODATA algorithm was applied independently on these segments and, depending on the area, was limited between 2 and 10 clusters, 12 iterations, and a 5% convergence threshold. Therefore, if less than 5% of the pixels in each category were reattributed during any iteration, the clustering process was terminated, otherwise the algorithm continued until all 12 iterations were complete. Two to ten clusters were requested during classification to accommodate tonal differences in sand based on water depth and those of seagrass areas based on depth and shoot density. All clustering runs were completed in less than 10 iterations. Once the classification process was complete, clusters were recombined for each image segment into either sand or seagrass categories only using a combination of field data and visual interpretation. No attempt was made to define areas of different shoot density. Finally, an image smoothing algorithm was applied to eliminate isolated pixels of sand or seagrass caused by dust or other irregularities in the film or scan. The filter consisted of a 3×3 pixel moving window that used the majority rule in assigning a new value to the focal pixel. For example, if a single pixel labeled sand was in the center of a 3×3 group of seagrass pixels, its value would be changed to seagrass.

Qualitative assessment of classification accuracy was conducted for the final 1999 seagrass map based on field data and existing benthic maps of the region (Kendall et al., 2002). These maps were created by visual interpretation of the same images from 1999 used in this project. Since a 1 acre minimum mapping unit was used in that work, and individual pixels ($4.84\,\mathrm{m}^2$) were classified in the present study, quantitative comparison was not possible; however, visual comparison of the two maps and the data from eight ground truth points indicated excellent correspondence of classifications among the three data sources. Unfortunately, no historical data are available for even qualitative evaluation of the 1971 imagery, however, since the same methods were used to create seagrass maps from that time period it is believed that the thematic accuracy for that year is similarly acceptable.

The differences in seagrass cover over the 30 years between aerial photos were quantified in the classified images by counting the number of pixels changing from sand to seagrass and vice versa. In addition, to calculate the amount of expansion of seagrass beds that could be explained by horizontal patch growth, a buffer was placed around the outer edge of the 1971 meadow boundaries based on *S. filiforme*'s horizontal growth rate for a patch edge and compared to the extent of meadows in 1999. The area of new seagrass in 1999 that was within this buffer distance from the outer edge of the 1971 beds was quantified and labeled as potentially being generated from horizontal extension alone. Seagrass in 1999, that was outside of this buffer, was quantified and labeled as potentially resulting from seed dispersal and subsequent growth since 1971.

Buffer distance was determined by multiplying the edge extension rate by the 27.25 years between acquisition dates of the 1971 and 1999 photographs. Published estimates of *S. filiforme's* rhizomatic growth rate as summarized by Marbà and Duarte (1998) have an average of 123 cm per year and range between 52 and 182 cm per year. This wide variability is due to the different locations, environmental conditions, and resulting growth rates of the meadows examined. It is important to recognize, however, that the rate of horizontal advancement for an entire patch edge is slower than the rhizome growth rates listed above. Rhizomes do not occupy 100% of an advancing patch edge; they must branch and interweave considerably before the entire patch edge is observed to advance (Marbà and Duarte, 1998). Following this consideration, Fonseca et al. (in press) used field data (Kenworthy et al., 2002) to calculate a 123 cm per year advancement rate for patch edges based on recovery rates from experimental excavations in the Florida Keys. Coincidently, this edge advancement rate matches the average rhizome growth rate reported by Marbà and Duarte (1998). Clearly, the local environmental conditions will determine the edge advancement rate for individual seagrass beds. The 123 cm per year advancement rate calculated by Fonseca et al. (in press) is currently the only available estimate for entire patch edges and will therefore be used to evaluate meadow expansion in our study. Based on this value, over the 27.25 year period covered in this study, a total possible distance of horizontal meadow extension was calculated as 33.5 m (1.23 m per year × 27.25 years).

3. Results

A dramatic expansion of *S. filiforme* beds was quantified from 1971 to 1999 in Buck Island Channel. In 1971, seagrass covered 1.33 km^2 or 15% of the bottom in the study area (Fig. 1a). By 1999, seagrass meadows covered 4.34 km^2 or 48% of the area (Fig. 1b), about a three-fold increase.

Specific changes in seagrass distribution are presented in Fig. 1c. Of the 1.33 km^2 of area covered with seagrass in 1971, 1.22 km^2 or 92% was still occupied in 1999. An area of only 0.11 km^2 colonized in 1971 was no longer occupied by 1999. This small loss of seagrass since 1971 is in contrast with the large area of new growth observed by 1999. An area of 3.12 km^2 of previously bare sand was colonized with seagrass by 1999.

Increases in seagrass distribution by 1999 were probably due both to the horizontal expansion of meadows existing in 1971 and the dispersal and germination of seeds some distance away from 1971 meadows. Fifty-four percent or 1.69 km^2 of the 3.12 km^2 of new seagrass area in 1999 was within the distance of possible 1971 patch growth based on the horizontal extension rate currently available. Forty-six percent or 1.42 km^2 of new seagrass area was outside of this distance suggesting that only dispersal, germination, and subsequent growth of seeds or viable plant fragments could be responsible for new seagrass in these areas.

4. Discussion

The extent of *S. filiforme* meadows in Buck Island Channel increased dramatically from 1971 to 1999, a finding in contrast to the numerous long term studies that report seagrass decline. The limited areas of seagrass loss in the Channel were more than compensated for by new growth through horizontal expansion of existing beds and seedling recruitment with subsequent bed formation. Approximately, half of 1999 seagrass could have resulted simply from expansion of existing beds and the rest is probably due to seed dispersal. This suggests that both these mechanisms are important for increasing seagrass coverage at this site. Confidence intervals around these estimates are not yet possible due to the limited data on patch extension rates for this species. The relative importance of vegetative growth versus seed dispersal is suspected to have considerable latitudinal and interspecific variation (McMillan, 1981; Johnson and Williams, 1982; Rollón et al., 2003) and could be examined in other areas using a similar approach to that described here to quantify the contribution of each expansion mechanism in other environmental conditions.

Changes in the dynamics of seagrass certainly occurred at a finer temporal scale between 1971 and 1999 than were quantified by this study. However, qualitative evaluation of aerial photographs of the study area from 1977 and 1992 reveal a consistent pattern of incremental increases in seagrass extent that is intermediate between 1971 and 1999 distributions. This indicates that we have quantified a gradual meadow expansion rather than two random snapshots in a rapidly fluctuating landscape. Unfortunately, lower quality of the 1977 and 1992 images due to moderate turbidity prevented quantitative analysis using the same methodology as was used for the 1971 and 1999 images.

Although separated by the usual narrow sand halo, seagrass beds in 1971 were primarily located along the fringing reefs to the north and south of the Channel and around patch reefs in the middle of the channel. These initial beds could have been the only surviving meadow fragments following a storm event, somehow protected from the deleterious effects of the storm by their proximity to reefs. Alternatively, the location of these beds could be the result of higher seed deposition or germination rates around reefs relative to flat sand plains. By 1999, the many circular patch reefs in the channel are clearly visible and are evenly surrounded by the expanding seagrass meadows. Eddies and turbulent flow around reefs may simply improve seed deposition close to these topographic features, or perhaps some other interaction with reef environments promotes growth. A few studies on the distances of propagule dispersal have been conducted (Orth et al., 1994; Lacap et al., 2002) but not within topographically complex environments.

Growth since 1971 is not spread randomly throughout the Channel either. New growth is concentrated near pre-existing beds, but extends farther away from them than can be explained by vegetative advance alone. This suggests that seed dispersal and growth is most common within a short distance away from parent beds rather than more widely and randomly spread throughout the Channel. Studies of seed dispersal in another seagrass species with negatively buoyant seeds indicate that dispersal distances are relatively short (only a few meters) and that future seagrass distributions can be predicted well by the initial biogeographical distribution of mature meadows (Orth et al., 1994). Additionally, studies on dispersal distances of seagrass seeds with initially positive buoyancies indicate that once the outer seed coat is lost and the seed becomes negatively buoyant, travel distances across the sediment surface are only a couple of meters (Lacap et al., 2002).

Hurricanes play a primary role in altering the benthic landscape in St. Croix by rearranging sediments, eroding or burying seagrass meadows, creating and dispersing seagrass fragments that result in vegetative propagation, breaking individual coral colonies, and even moving large volumes of reef material over tens of meters during particularly intense storms (Rogers et al., 1982; Williams, 1988; Bythell et al., 1993). Sediments and seagrass meadows even in deep water (20 m) such as that found in the study area can be affected by storms (Williams, 1988). The last severe hurricanes to pass nearby St. Croix before the 1971 photography were four decades earlier i.e. in 1928 and 1932 (Table 2; Rogers et al., 1982; Bythell et al., 1993) making it unlikely that the large area of bare sand in Buck Island Channel in 1971 was a result of either storm induced erosion or burial.

Table 2
Number of tropical cyclones according to the Saffir Simpson intensity scale that passed nearby (within 0.5 decimal degrees or 56 km) the study site by decade since 1920. Source: Caribbean Hurricane Network

Decade	1920	1930	1940	1950	1960	1970	1980	1990
Hurricanes								
Category 5	●							
Category 4							●	●
Category 3								
Category 2		●						●
Category 1								
Tropical storm/depression	●	●				●	●	●
Total storms	2	2	0	0	0	3	2	4

After the 1971 photography was acquired, the hurricane frequency in the region has increased, with numerous hurricanes and tropical storms either directly hitting or passing near the study area (Table 2). In the 1970's, three tropical storms passed within 30 nautical miles (56 km) of Buck Island Channel and Hurricanes David and Frederick damaged coral reefs while passing to the south and north of St. Croix, respectively (Rogers et al., 1982). In 1989, a direct hit by Hurricane Hugo had a dramatic influence on the southern fringing reef around Buck Island, a feature which is also the northern limit of this study (Bythell et al., 1993; Rogers and Beets, 2001), although no deleterious effects could be detected on the seagrass meadow based on 1992 imagery. More recently, Hurricanes Luis and Marilyn in 1995, Georges in 1998, and Lenny in 1999 have all affected the coral benthos around St. Croix although changes in seagrass and soft bottom areas were not documented. Typically, hurricanes are documented as one of the major causes of meadow reduction; however, we speculate that these storms may stimulate growth under certain conditions. Indeed, the beds in the present study area have been expanding during a period of increased storm frequency. Since these beds are in moderately deep water, storm energy and currents may be dampened such that meadow erosion is not widespread but still sufficiently strong to have enhanced pollination and seed dispersal along with shifting sediment farther than found previously under normal flow conditions (Fonseca and Kenworthy, 1987; Orth et al., 1994). This hypothesis of 'storm stimulus' provides the most plausible explanation for the dramatic expansion of the meadow during the current period of increased hurricane activity.

Several alternative explanations to account for the increase in seagrass extent were considered but could not be supported with convincing evidence. For example, a decline in the abundance of seed predators, herbivorous fishes, or sea turtles coincident with the increase in meadow extent could not be documented. The dramatic region-wide decline in abundance of these organisms occurred over one hundred years prior to this study (Jackson, 1997). We also considered the possibility that some change in environmental conditions other than the higher frequency of hurricanes discussed above, such as higher water clarity or better nutrient availability resulted in improved growth, however, there is neither empirical nor inferential evidence to support such a possibility.

Due to the importance of seagrass as a nursery habitat to fisheries species, as a sediment stabilizer shielding reefs from sedimentation (Ward et al., 1984; Kenworthy et al., 1988), and the scientific value of an expanding meadow with long term monitoring potential, the large area of seagrass identified within Buck Island Channel should be protected and maintained. Although not currently documented to be impacting the study area, human threats to seagrass in this region include anchor damage from large vessels, eutrophication induced by point source discharge and seepage of treated and untreated sewage, and runoff of sediment and other pollutants as St. Croix is increasingly developed (Short and Wyllie-Echeverria, 1996). Now that a baseline inventory of seagrass in the area is available, the impact of these activities on long term patch dynamics can be investigated.

The changes observed in this study suggest that monitoring in St. Croix and in similar Caribbean sites could be conducted on a decadal basis to reliably detect long term changes with additional surveys conducted specifically to evaluate hurricane impacts or other discrete events. With the quantification of historical and current seagrass distribution and the establishment of the simple approach described here, future research should be focused on regularly monitoring changes in distribution of seagrass meadows and identifying the mechanisms that drive the observed patterns. Specifically, the edge advancement rates of seagrass patches in a variety of environments and water quality conditions, seed dispersal around topographically complex bottom features such as patch reefs, and the influence of hurricanes on distances of seed dispersal and patch dynamics will all require greater scrutiny to understand changes in seagrass meadows on ecologically meaningful scales of time and space.

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