Understanding uncertainty in seagrass injury recovery: an information-theoretic approach

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Abstract. Vessel groundings cause severe, persistent gaps in seagrass beds. Varying degrees of natural recovery have been observed for grounding injuries, limiting recovery prediction capabilities, and therefore, management's ability to focus restoration efforts where natural recovery is unlikely. To improve our capacity for predicting seagrass injury recovery, we used an information-theoretic approach to evaluate the relative contribution of specific injury attributes to the natural recovery of 30 seagrass groundings in Florida Keys National Marine Sanctuary, Florida, USA. Injury recovery was defined by three response variables examined independently: (1) initiation of seagrass colonization, (2) areal contraction, and (3) sediment in-filling. We used a global model and all possible subsets for four predictor variables: (1) injury age, (2) original injury volume, (3) original injury perimeter-to-area ratio, and (4) wave energy. Successional processes were underway for many injuries with fast-growing, opportunistic seagrass species contributing most to colonization. The majority of groundings that exhibited natural seagrass colonization also exhibited areal contraction and sediment in-filling. Injuries demonstrating colonization, contraction, and in-filling were on average older and smaller, and they had larger initial perimeter-to-area ratios. Wave energy was highest for colonizing injuries. The information-theoretic approach was unable to select a single "best" model for any response variable. For colonization and contraction, injury age had the highest relative importance as a predictor variable; wave energy appeared to be associated with second-order effects, such as sediment in-filling, which in turn, facilitated seagrass colonization. For sediment in-filling, volume and perimeter-to-area ratio had similar relative importance as predictor variables with age playing a lesser role than seen for colonization and contraction. Our findings confirm that these injuries naturally initiate seagrass colonization with the potential to recover to pre-injury conditions, but likely on a decadal scale given the slow growth of the climax species (*Thalassia testudinum*), which is often the most severely injured. Our analysis supports current perceptions that sediment in-filling is critical to the recovery process and indicates that in order to stabilize injuries and facilitate seagrass recovery, managers should consider immediate restorative filling procedures for injuries having an original volume >14–16 m^3.

Key words: Florida Keys National Marine Sanctuary; Halodule: information-theoretics; seagrass gap dynamics; seagrass recovery; Syringodium; Thalassia; vessel groundings.

INTRODUCTION

Natural disturbances have the ability to produce open spaces (gaps) within an otherwise continuous seagrass meadow (see review by Short and Wyllie-Echeverria 1996, Holmquist 1997, Fonseca and Bell 1998, Townsend and Fonseca 1998, Rose et al. 1999, Nelson and Lee 2001, Nakaoka et al. 2006). These Type I patches (sensu Sousa 1985) are common features in many seagrass landscapes (den Hartog 1971, Patriquin 1975, Bell et al. 1999, Tewfik et al. 2007) and represent the lower end of a range of patchiness often associated with physical disturbance of seagrasses by waves and

currents (den Hartog 1971, Patriquin 1975, Fonseca et al. 1983, Fonseca and Bell 1998). Our knowledge of the role of these gaps in seagrass ecosystems has improved by comparisons to terrestrial examples. Sprugel (1976), Reiners and Lang (1979), Sprugel and Bormann (1981), and Iwasa et al. (1991) discuss the role of wind-mediated canopy gap dynamics in high-altitude balsam fir forest ecosystems where vegetation gradients resulting from "wave regeneration" bear substantial similarity to successional processes associated with wave/current-generated "migrating" seagrass blowouts (e.g., Patriquin 1975, Tewfik et al. 2007). Similarly, physical displacement or burial of vegetation by mound-building organisms in serpentine terrestrial grasslands creates small-scale gaps (Wu and Levin 1994) akin to ghost shrimp excavation mounds in seagrass beds (Suchanek 1983, Duarte et al. 1997, Dumbauld and Wyllie-Echeverria 2003). Bioturbation activities such as these

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can substantially influence plant population dynamics and landscape patterns (Suchanek 1983, Hobbs and Mooney 1985, 1991, Wu and Levin 1994, Duarte et al. 1997, Dumbauld and Wyllie-Echeverria 2003), illustrating similarities in gap dynamics across ecosystems.

Field studies on the persistence and recovery dynamics of both natural and anthropogenic seagrass landscape gaps have considered the influence of many factors including hydrodynamics (Patriquin 1975, Kirkman 1985, Whitfield et al. 2002), gap orientation (Patriquin 1975, Whitfield et al. 2002), competitive interactions among seagrass species (Kirkman 1985), contributions of different seagrass species (Olesen et al. 2004), roles of clonal vs. sexual propagation (Peterken and Conacher 1997, Olesen et al. 2004, Whitfield et al. 2004), rates of belowground biomass recovery (Di Carlo and Kenworthy 2008), seagrass morphological plasticity (Nakaoka and Aioi 1999), as well as initial gap size (Bell et al. 1999). Manipulative studies, generally conducted over small spatial extents, have also provided additional data regarding limits to seagrass gap closure, including the role of nutrient and light availability (Williams 1987, 1988a, 1990), competitive interactions among seagrass species (Williams 1990), recruitment limitation arising from gap geometry (Kenworthy et al. 2002, Fonseca et al. 2004, Hammerstrom et al. 2007), gap size (Rollon et al. 1998, Creed and Amado Filho 1999), the comparative capacity for recovery among seagrass species (Williams 1988a, Holmquist 1997, Uhrin et al. 2005), and the importance of sexual vs. vegetative colonization (Rasheed 1999, Olesen et al. 2004).

From these studies, a number of generalizations can be made regarding seagrass Type I gap recovery. Small, shallow gaps tend to recover faster than large, deep gaps (Rollon et al. 1998, Bell et al. 1999). In tropical seagrass communities, gap colonization typically follows the long-standing paradigm of seagrass succession (Williams 1990, Rollon et al. 1998, Kenworthy et al. 2002). Regrowth of the climax species is often disrupted along gap edges (Kenworthy et al. 2002, Whitfield et al. 2002, Olesen et al. 2004, Hammerstrom et al. 2007, Di Carlo and Kenworthy 2008), while the most effective gap colonizers are species present in the margins (border effect) with high rates of rhizome elongation (Nakaoka and Aioi 1999, Olesen et al. 2004, Hammerstrom et al. 2007). Even so, these colonizing species appear effective only in the near term (months to years) and for small gaps (<10 m^2; Bell et al. 1999, Olesen et al. 2004); complete recovery of large gaps will rely upon the eventual recruitment of fragments or seedlings from the local climax species into the gap center and may require many years (Inglis 2000, Kenworthy 2000, Olesen et al. 2004, Whitfield et al. 2004). Moreover, chronic high-wave energy conditions can form and maintain a landscape of physically unstable "migrating" seagrass blowouts (sensu Patriquin 1975) and, depending upon the orientation of gaps with respect to prevailing flow,

can scour and further destabilize existing gaps, exacerbating bed fragmentation (Whitfield et al. 2002; A. V. Uhrin, *unpublished data*).

A number of human-induced disturbances create gaps in seagrass landscapes as well, and consideration of both natural processes and manipulative studies provide heuristic guidance as to how such disturbances may recover; understanding and forecasting recovery from anthropogenic disturbances is of great interest to many decision-makers. Common gap-forming anthropogenic activities include dredge and fill operations, dock and boat-mooring installation (Walker et al. 1989, Short et al. 1991, Burdick and Short 1999), anchor/chain drags (Williams 1988b, Walker et al. 1989, Francour et al. 1999), certain fishing practices (Fonseca et al. 1984, Peterson et al. 1987, Orth et al. 2002, Neckles et al. 2005), trampling (Eckrich and Holmquist 2000), propeller scarring by outboard motors (see review by Sargent et al. 1995, Dawes et al. 1997), and motorized-vessel-grounding events (Sargent et al. 1995, Kenworthy et al. 2002, Olesen et al. 2004, Kirsch et al. 2005, SFNRC 2008). For this study, we focused on the seagrass beds of the Florida Keys National Marine Sanctuary (FKNMS), where >600 motorized-vessel groundings occur annually, causing widespread damage to subtropical seagrasses (Sargent et al. 1995, Kirsch et al. 2005, SFNRC 2008). These disturbances create some of the most severe Type I gaps that can occur in seagrass beds (Kenworthy et al. 2002, Kirsch et al. 2005).

Vessel-grounding events result in readily identifiable injury features (Fig. 1), occurring singly or in combination, including: (1) propeller scar (narrow, excavated trench caused by propeller penetration into the sediment while the vessel is still moving); (2) blowhole (deep excavation caused by propeller wash as the operator attempts to free the vessel); and (3) berm (excavated material ejected from the blowhole by propeller wash that is deposited over, and often buries the seagrass surrounding the blowhole). By directly removing above- and belowground seagrass biomass, vessel groundings cause acute environmental modification on a local scale, which has been shown to result in sediment instability, loss of organic matter and nutrients, and progressive erosion of adjacent seagrass habitat far beyond the extent of the original injury (Kenworthy et al. 2002, Whitfield et al. 2002, Di Carlo and Kenworthy 2008; A. V. Uhrin, *unpublished data*). Vessel-grounding events clearly have the potential to increase the frequency of persistent gaps in seagrass beds beyond that of natural conditions, creating concern that for a given wave energy climate, a critical level of fragmentation could result that would lead to a collapse of the bed to a new stable state, if not complete erosion (sensu Fonseca and Bell 1998). Given the potential for cumulative injuries to any given location and injury expansion, and the slow recovery rates exhibited by the most frequently injured seagrass species (*Thalassia testudinum*; Zieman 1976, Williams 1990, Durako et al. 1992, Dawes et al. 1997, Kenworthy et al.

2002), persistent degradation and widespread loss of seagrass habitat has been demonstrated for South Florida (Sargent et al. 1995, SFNRC 2008). As such, gap-generating vessel groundings in highly vulnerable habitats such as the *Thalassia testudinum*-dominated shallow seagrass ecosystems of the FKNMS are of special interest for managers concerned with potential cumulative impacts to natural resources.

In this study, we investigated natural seagrass recovery (i.e., gap closure) in severe Type I patch disturbances associated with vessel groundings in the FKNMS. We utilized an information-theoretic (IT) approach to determine the relative importance of physical and temporal attributes of vessel-grounding injuries with respect to observed levels of natural seagrass recovery, selecting environmental factors that may be measurable under current assessment and enforcement capabilities. We also evaluated the extent of seagrass species substitution occurring during the natural recovery process in the context of successional theory in seagrass ecosystems (den Hartog 1971, Williams 1990).

METHODS

Site selection

Study sites were located in the inshore waters of the Gulf of Mexico and Atlantic Ocean in the Florida Keys, Monroe County, Florida, USA (Fig. 2). The region is a carbonate sediment-based, subtropical marine environment consisting of inshore and offshore coral reefs, scattered mangrove islands, and extensive seagrass beds (Fourqurean et al. 2001). Three seagrass species are vulnerable to vessel groundings due to their prominence in shallow waters: *T. testudinum*, *Syringodium filiforme*, and *Halodule wrightii*. *T. testudinum* is the most frequently injured, due to its ability to form elevated banks, effectively creating shallow water that is frequented by vessels operating along bank margins and outside of navigable channels (Kenworthy et al. 2002).

Sites were chosen from a database of documented seagrass vessel groundings in the FKNMS provided by the National Oceanic and Atmospheric Administration, Damage Assessment Center (NOAA DAC). Forty-four sites where restoration had yet to be implemented were evaluated as potential candidates for our study. The widespread geographic distribution of the grounding sites (over ~150 km) made it necessary to limit the number of sites to a manageable subset while capturing the range of environmental conditions, landscape settings, and injury characteristics. Sites were initially grouped by quartiles for injury age (years since time of occurrence) and representative wave energy (RWE; in joules/m). While not a part of current seagrass injury assessment protocols in the FKNMS, we felt it important to utilize RWE during the site selection process in order to help eliminate possible bias for recovery potential as exposure to wind wave events has been shown to drastically alter the geometry of
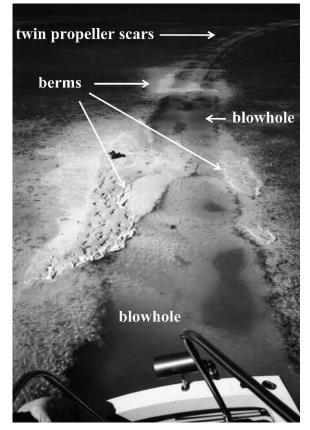

FIG. 1. Oblique photo of an actual vessel-grounding injury on a shallow seagrass bank in Florida Keys National Marine Sanctuary (FKNMS). Twin propeller scars, numerous berms, and two distinct blowhole injury features are visible. For scale, the rectangular object resting on the left-hand berm is a cement block, ~39.5 cm in length. The divots in that same berm are footprints made by the assessment team. Photo courtesy of NOAA/FKNMS.

grounding injuries (sensu Whitfield et al. 2002). RWE was computed by the application of the Wave Exposure Model (WEMo; Malhotra and Fonseca 2007) for the time period beginning from the date of the first injury assessment through present day. Within each age × RWE quartile, we attempted to obtain a minimum of two grounding sites; in some instances, this was not possible due to the absence or limited number of sites meeting these criteria. In total, 30 sites were included in our investigation (Fig. 2, Table 1).

Injury recovery assessments

The 30 sites were previously assessed by NOAA DAC personnel shortly after the time of occurrence of each injury using established techniques (Kirsch et al. 2005). These protocols included site mapping with a differential global positioning system (DGPS), bathymetric surveys, and characterization of injured habitat vs. adjacent uninjured habitat using visual assessment methods.
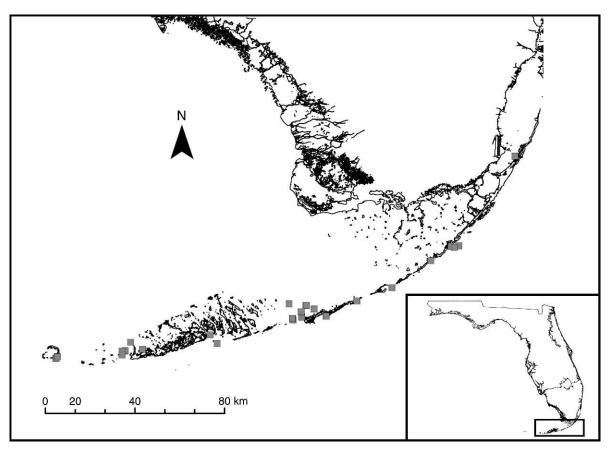
FIG. 2.   Location of the 30 vessel-grounding sites examined in the study (gray squares) in the Florida Keys, Florida, USA.

During the summer of 2004 and spring of 2005, each of the injury grounding sites were revisited and reassessed duplicating the methods of Kirsch et al. (2005). Given the severity of blowholes relative to other injury features (i.e., complete removal of above- and below-ground biomass with acute changes to landscape grade), we limited our investigation to these features. Hereafter, "injury" refers only to blowholes and does not consider the associated berms or propeller scars (Fig. 1). *T. testudinum* was the most abundant species at 26 sites, occasionally interspersed with *S. filiforme* and *H. wrightii*. The remaining four sites were dominated by *S. filiforme*.

Site mapping.—For shallow sites, injury features were mapped by walking the perimeter of each feature using DGPS (Trimble GPS Pathfinder Pro XR receiver and Trimble TSC1; data collector, Trimble Navigation, Sunnyvale, California, USA), following Kirsch et al. (2005). Where deeper water precluded walking, the DGPS unit was mounted on a small inflatable boat that was then maneuvered around the injury perimeter by a snorkeler. Injury feature coordinates were downloaded to Trimble GPS Pathfinder Office 3.0 software (Trimble Navigation 2003) and then exported to ESRI's ArcMap 9.2 software (ESRI 2006) for calculation of injury area (m^2) and perimeter-to-area ratios (P:A).

Bathymetric survey.—Following Kirsch et al. (2005), a Lowrance LCX-15MT depth sounder (Navico International, formerly Lowrance Electronics, Tulsa, Oklahoma, USA) integrated with the DGPS was mounted on the stern of the inflatable boat. Geo-referenced depth soundings (0.1 m vertical accuracy) were logged while the boat was slowly guided back and forth across the injury by investigators. The resulting bathymetry file was downloaded to Trimble GPS Pathfinder Office software and then exported to ArcMap, where an inverse distance-weighting function (IDW) was used to create a bathymetric grid layer enabling the calculation of blowhole volume (m^3) using the ArcMap 3-D Analyst Extension.

Habitat characterization.—A modified Braun-Blanquet technique (Braun-Blanquet 1932, Kenworthy et al. 1993, Fourqurean et al. 2001) was used to assess seagrass species composition and percent cover in the blowhole and the surrounding undisturbed seagrass bed (sensu Kirsch et al. 2005). Replicate 0.25-m^2 quadrats were haphazardly tossed both in the blowhole and in the seagrass immediately adjacent (hereafter referred to as the "reference") and assigned a Braun-Blanquet cover-abundance scale value by visual inspection: 0 = not present, 0.1 = solitary specimen, 0.5 = few specimens (<5), 1 = numerous but <5% cover, 2 = 5–25% cover, 3

TABLE 1. Dependent and independent variable summary for 30 vessel-grounding sites in the Florida Keys National Marine Sanctuary (FKNMS), Florida, USA.

Site	Seagrass colonization	Contraction	Filling	Injury age (yr)	Perimeter : area	Original volume (m^3)	RWE (joules/m)
1	1	1	1	3.13	0.96	10.0	10 544.8
2	0	0	1	1.82	0.88	17.6	741.7
3	0	1	0	1.95	2.07	16.7	3330.8
4	0	0	0	1.75	1.06	70.4	2194.6
5	0	0	0	3.01	1.17	11.5	1567.6
6	0	1	1	1.65	2.17	1.5	609.8
7	0	0	0	2.14	1.43	4.5	2293.1
8	1	1	1	3.45	0.58	52.1	77.8
9	1	1	1	2.97	0.98	17.2	2196.7
10	0	⋯	1	2.07	1.22	10.9	649.7
11	0	0	1	1.37	1.83	3.0	333.4
12	0	0	0	1.09	1.00	7.2	405.7
13	0	0	1	1.31	1.25	15.6	142.8
14	0	0	0	1.85	0.63	72.3	1500.1
15	1	0	1	2.82	2.43	3.4	6451.2
16	1	0	0	2.04	0.58	17.8	6571.4
17	1	1	1	1.43	2.15	2.7	369.8
18	1	1	1	3.24	1.01	7.2	318.7
19	1	1	1	2.92	0.83	50.5	554.7
20	0	0	0	3.46	0.70	37.8	4360.2
21	1	1	1	2.78	1.16	4.9	970.4
22	1	1	1	2.86	1.13	6.9	2658.0
23	1	1	1	2.07	1.26	21.4	1388.5
24	0	1	⋯	3.24	0.73	⋯	1718.0
25	0	1	0	3.39	0.11	17.1	1132.0
26	0	0	0	2.09	0.82	5.6	1034.0
27	0	0	0	1.89	1.04	87.5	1015.6
28	1	1	1	1.82	0.99	6.7	6989.4
29	1	1	1	1.84	2.14	3.6	837.5
30	0	0	0	1.83	1.32	16.5	3705.5

Notes: In columns 2–4, "1" indicates a positive response (presence or yes), while "0" indicates a negative response (absence or no). Missing values ("⋯") are those sites where either no change in the area occurred (Site 10) or no original volume data were available (Site 24) because the injury occurred prior to the development of the bathymetric survey technique. RWE stands for representative wave energy.

= 26–50% cover, 4 = 51–75% cover, and 5 = >75% cover. For continuity, the number of quadrats sampled from within the blowhole and its associated reference area was kept the same as was sampled during the original assessment.

Species substitution.—Currently, the desired endpoint of seagrass vessel-grounding restorations in the FKNMS is the attainment (within the injury) of reference levels of aboveground percent cover for each seagrass species encountered in the adjacent, uninjured community (NOAA and FDEP 2004). Here, we assumed the injury and reference area to be in spatial equilibrium (Parker and Wiens 2005) with a narrow window of temporal variation (Di Carlo and Kenworthy 2008). We also assumed that the reference area has not been disturbed prior and that once the injury attains reference levels, it is considered to be recovered.

A seagrass abundance estimate (*A*) was calculated for: (1) the dominant reference species from the original assessment data, (2) the dominant reference species from the original assessment data but sampled from within the injury at the time of the reassessment, and (3) the primary colonizing species within the injury at the time of the reassessment. These were tabulated to determine the extent of species substitution (if any) during the natural recovery process. Abundance was calculated from Braun-Blanquet cover estimates as follows:

$$A_i = \sum_{j=1}^{n} S_{ij}/N_i$$

where A_i is the abundance of species i; j is the quadrat number from 1 to n, the total number of quadrats sampled per injury feature; S_{ij} = the Braun-Blanquet score for species i in quadrat j, and N_i is the number of quadrats within the injury feature in which species i was present (Kenworthy et al. 1993, Fourqurean et al. 2001).

Model development

Predictor variables.—Three injury characteristics and one physical parameter were considered in the model: injury age (AGE; in years), original injury volume (VOL; as m^3), original injury perimeter-to-area ratio (P:A), and RWE. The injury characteristics are included in established injury assessment protocols (Kirsch et al. 2005), reflecting their influence on seagrass gap closure dynamics (Fonseca et al. 2004, Olesen et al. 2004, Hammerstrom et al. 2007), and exposure to wind wave events has been shown to drastically alter the geometry

of grounding injuries (sensu Whitfield et al. 2002). Injury age was computed from the date of the first assessment of the injury to the date of the reassessment. The volume of excavated blowholes was obtained directly from the original bathymetric survey data, while the P:A for each blowhole was calculated from the original DGPS perimeter files. RWE was computed by the application of the Wave Exposure Model (WEMo; Malhotra and Fonseca 2007) for the time period beginning from the date of the first injury assessment through the date of the reassessment, yielding the average RWE over the life of each injury.

Response variables.—Over time, and barring further disturbance, seagrass grows inward from the undisturbed injury perimeter, creating a progressive band of clonal expansion that leads to a reduction in injury area (Olesen et al. 2004). Regrowth of seagrass into experimental gaps has been shown to track the sediment deposition trajectory (Hammerstrom et al. 2007). Thus, we defined and evaluated natural recovery of seagrass grounding injuries using three binary, dependent variables: (1) seagrass colonization (recorded as presence/ absence of seagrass, all species combined, within the boundaries of the original injury area, indicating that at least the recovery process had initiated), (2) areal contraction (measured as decrease/increase in injury area and recorded as yes/no), and (3) sediment in-filling (measured as decrease/increase in injury volume and recorded as yes/no). Each response variable was modeled separately.

To create the seagrass colonization variable (COLONIZE), we reduced the Braun-Blanquet data to a dichotomous outcome (Kleinbaum and Klein 2002, Podani 2006). Although solitary shoots or a handful of individuals (Braun-Blanquet values of 0.1 or 0.5) indicate some seagrass colonization, we did not regard those levels as sufficient to unequivocally signal persistent, long-term establishment; whereas Braun-Blanquet values > 1.0 suggest recruitment and propagation with measureable cover ($>5\%$). Consequently, we reclassified Braun-Blanquet cover abundance scale values of 0.1 and 0.5 as equivalent to zero (absence), while all other scale values were designated as "1" (presence).

Injury contraction (CONTRACT) was calculated as the difference between the original blowhole area (m^2) and the area at the time of the reassessment. A positive difference would indicate contraction (yes), while a negative difference would indicate expansion (no). The area for one injury remained unchanged, preventing calculation of contraction, leaving $n = 29$.

Sediment in-filling (FILL) was calculated as the difference between the original blowhole volume (m^3) and the volume at the time of the reassessment. A positive difference would indicate in-filling (yes), while a negative difference would indicate scouring (no). Original volume data was lacking for one injury that occurred prior to the development of the bathymetric

survey technique, thus preventing calculation of in-filling for this site, leaving $n = 29$.

We modeled each of the three response (dependent) variables separately by evaluating a global model that included all four predictor (independent) variables and all possible nested subsets, resulting in a candidate model set of $R = 2^3 = 16$, including the intercept-only model (Burnham and Anderson 2002). Although Burnham and Anderson (2002) suggest limiting model structural parameters to $n/10$ (here, 3), we considered models with up to five parameters, one for each predictor variable and one for the intercept-only variable. Given the relevance of the predictor variables in the seagrass injury assessment process and in terms of seagrass gap dynamics, we felt it was important to retain all four despite the potential for increased model "noise." Despite using all possible predictor variable combinations, R was smaller than n (here, 30), as recommended by Burnham and Anderson (2002). We did not consider interactions among the predictor variables. Following a priori variable selection and analyses, we conducted exploratory, judgment-based analyses and model selection with respect to the relative importance of each predictor variable (sensu Burnham and Anderson 2002). Variables with negligible predictive value (our judgement, relative importance weight < 0.3) were removed in order to both simplify the model and to amplify the predictive capabilities of the remaining variables.

Model selection

Traditional statistical tests rely on probability statements (P values) about data given a null hypothesis, with no information regarding the probability of the alternative hypothesis. Unlike null hypothesis testing, the information-theoretic approach does not rely upon probabilities to evaluate a single model. Rather, inferences are made from a set of candidate models developed a priori and evaluated relative to each competing model given the data at hand. Models can then be grouped into three categories: (1) a single best model, (2) models that are obviously inadequate when compared to the best model and have little utility, and (3) models that do not fit the data as well as the best model but cannot be ignored (Holl et al. 2003). The more nuanced consideration of multiple categories can be more informative than a single decision to accept or reject a null hypothesis.

We compared models based on Akaike's information criteria (AIC; Akaike 1973, Burnham and Anderson 2002) estimated via PROC LOGISTIC (SAS Institute 2002). AIC is defined as

$$\text{AIC} = -2 \log(\mathfrak{L}(\hat{\theta} \mid y)) + 2K$$

where $\log(\mathfrak{L}(\hat{\theta} \mid y))$ is the numerical value of the maximized log-likelihood over the estimated model parameters ($\hat{\theta}$) given the data (y) and the approximating model. K is the number of estimable parameters in the

approximating model. A second-order bias adjustment was made for small sample size (AIC$_c$; Hurvich and Tsai 1989). The model with the smallest AIC$_c$ is considered the "best approximating" model and remaining models are ranked and ordered relative to the best model using AIC$_c$ differences (Δ_i) and Akaike weights (w_i). As a general rule, models having Δ_i within 1–2 of the best model have substantial support, those within 4–7 have less support, and those >10 either have no support or fail to explain a substantial portion of the variation in the data (Burnham and Anderson 2002).

An Akaike weight of at least 0.9 is required for any one model to be accepted as clearly the best (Burnham and Anderson 2002). When no single model is definitively the best, and many parameters (variables) appear in more than one model, model averaging is used to base inferences on the entire set of models (Burnham and Anderson 2002). Weighted averages of model parameter estimates (obtained from PROC LOGISTIC; SAS Institute 2002) were computed by multiplying each estimate by the model's associated Akaike weight and then summing across all models where the parameter occurred (Buckland et al. 1997). For each model average, estimators of unconditional variance and unconditional standard errors were calculated following Buckland et al. (1997).

As an indicator of how many models have some plausibility, the w_i were summed sequentially beginning with the best model until the sum was ≥ 0.95, resulting in a 95% confidence set of models, also referred to as the "prediction set" (Burnham and Anderson 2002). To measure the relative importance of each independent variable as compared to all others, we summed the w_i for all models that contained a given independent variable.

Evidence ratios were used to compare the estimated best model to each of the remaining competing models and were calculated as w_1/w_j, where w_1 is the Akaike weight for the best model and w_j is the Akaike weight for the subordinate model in question. As evidence ratios increase, so does support for the best model (Edwards 1992). Evett and Weir (1998) suggested the following rules of thumb for interpreting evidence ratios: 1–10 = limited model support; 10–100 = moderate model support; 100–1000 = strong model support; and >1000 = very strong model support. What is important to consider is that the evidence ratio is constant among applications; a ratio of 10 represents the same strength of evidence in all contexts, but its implications will vary according to the application (Royall 1997).

RESULTS

Injury recovery summary

Of the 30 sites examined, 13 (43.3%) had initiated seagrass colonization with measurable cover (Braun-Blanquet score ≥ 1.0) and 17 (56.7%) had not (Fig. 3). Of the 13 sites with initiated colonization, contraction and filling of blowholes was widespread (Fig. 3). Of the 17 sites where seagrass had yet to colonize, there was a tendency for blowholes to have expanded and deepened (Fig. 3). The average percent decrease in injury area for sites having seagrass present and experiencing contraction was 76.8% (range 10.6–100%); these sites had an average original injury area of 69.3 m^2. The average percent increase in area for sites without seagrass recolonization and experiencing expansion was 218.9% (range 13.9–587.4); these sites originally averaged 90.4 m^2. The average percent decrease in injury volume for sites both having seagrass and experiencing in-filling was 61.6% (range 9.5–100%); these sites had an average original volume of 15.5 m^3. The average percentage increase in volume for sites without seagrass recolonization and experiencing deepening was 221.3% (range 10.9–568.7%); these sites had an average original volume of 31.5 m^3.

Species substitution.—*T. testudinum* was the dominant reference species for 10 of the 13 injuries that had measurable seagrass colonization, but only two of those had *T. testudinum* as the primary recovering species (Table 2). Even so, the contribution of *T. testudinum* to injury contraction at these two sites was slight (20%; Table 2). Of the three injuries where reference samples were dominated by *S. filiforme*, two were primarily recovering with *S. filiforme* (Table 2). No reference samples were dominated by *H. wrightii*, yet this species was the primary recovering species for five of the 13 injuries with measurable colonization (Table 2).

Model selection

Seagrass colonization.—Overall, sites having measurable colonization appeared to be older, shallower, and have slightly larger P:A than those not experiencing seagrass colonization (Table 3). In addition, sites with measurable colonization exhibited considerably higher RWE (Table 3). The full complement of a priori information-theoretic criteria for the global model including all four predictor variables is given in the Appendix. Given its low relative importance as a predictor variable ($\sum \omega_i = 0.2465$; Appendix), VOL was removed from the analyses and judgment-based model selection proceeded using AGE, P:A, and RWE. As a predictor variable, AGE had the highest relative importance ($\sum \omega_i = 0.7090$; Table 4).

The weight of evidence (w_i) for all models considered ranged from a high of 0.2067 down to 0.0487, indicating considerable model uncertainty. The highest ranked model included AGE alone; however, the low Akaike weight (w_i) and evidence ratios indicated that the weight of evidence in favor of this model being the "best" was not convincing (Table 4; Evett and Weir 1998, Lukacs et al. 2007). The top five models were tentatively supported given each had $\Delta_i < 2$ (Table 4; Burnham and Anderson 2002). To reach a >95% confidence interval required the inclusion of the top six models, indicating that each of these models have some plausibility and that model uncertainty is high (Burnham and Anderson 2002).
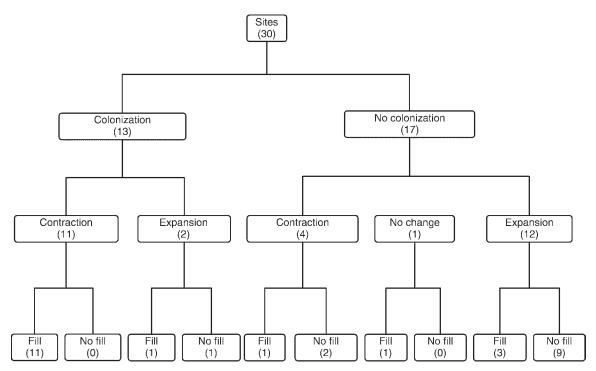
Fig. 3. Hierarchical relationship among dependent variables irrespective of independent variable effects. One injury did not have original volume measurements and so was eliminated from the comparison. No colonization was observed at this site. As such, the "fill/no fill" level is reduced by 1 in this case.

Model averaging resulted in a predicted estimate of the effect of AGE on COLONIZE of 1.1918, which was similar to the predicted estimate based on the fitted best model (0.9680). However, the corresponding standard errors (SE) were 1.8637 and 0.5690, respectively. This substantial increase in SE reflected uncertainty in the AGE-alone model with regard to its estimated effect on COLONIZE.

Areal contraction.—Where contraction occurred, injuries appeared to be older, shallower, and had slightly higher P:A, but RWE was similar (Table 3). The full complement of a priori information-theoretic criteria for the global model including all four predictor variables is given in the Appendix. Given its low relative importance as a predictor variable ($\sum\omega_i = 0.2973$; Appendix), RWE was removed from the analyses and judgment-based model selection proceeded using AGE, VOL, and P:A. As a predictor variable, AGE again had the highest relative importance ($\sum\omega_i = 0.8690$; Table 4).

Model uncertainty was apparent as the Akaike weights ranged from 0.2735 to 0.0231 (Table 4). The top four models were tentatively supported given each had $\Delta_i < 2$ (Table 4; Burnham and Anderson 2002). The top-ranked model included the predictor variables AGE

TABLE 2. Shifts in seagrass species abundance (shown in parentheses), calculated from Braun-Blanquet cover estimates, for 13 vessel-grounding sites having measurable seagrass cover during reassessment sampling.

Site	Abundance of dominant species in reference	Abundance of first species recovering in injury	Abundance of reference dominant species observed in injury
1	*Thalassia* (2.2)	*Thalassia* (1.75)	*Thalassia* (1.75)
8	*Syringodium* (2)	*Halodule* (2)	*Syringodium* (0)
9	*Syringodium* (1.9), *Thalassia* (1.8)	*Syringodium* (1.8)	*Syringodium* (1.8), *Thalassia* (1)
15	*Thalassia* (1.9)	*Halodule* (1.6)	*Thalassia* (0.67)
16	*Thalassia* (1.9)	*Syringodium* (1.1)	*Thalassia* (0.7)
17	*Syringodium* (2.5)	*Syringodium* (3.6)	*Syringodium* (3.6)
18	*Thalassia* (2.3)	*Syringodium* (1.75)	*Thalassia* (1.25)
19	*Thalassia* (3.8)	*Thalassia* (1)	*Thalassia* (1)
21	*Thalassia* (2.1), *Halodule* (2)	*Halodule* (5)	*Thalassia* (0)
22	*Thalassia* (2.9)	*Halodule* (4.6)	*Thalassia* (0.1)
23	*Thalassia* (2)	*Syringodium* (1)	*Thalassia* (0.6)
28	*Thalassia* (1.7)	*Syringodium* (1.25)	*Thalassia* (0.75)
29	*Thalassia* (2.5)	*Halodule* (1.8)	*Thalassia* (0.4)

Note: Abundance was calculated from Braun-Blanquet cover estimates as described in *Methods: Species substitution*.

TABLE 3. Mean values of predictor variables for each of the three seagrass recovery-dependent variables on the basis of whether or not recovery was occurring.

Variable	AGE (yr)	VOL (m^3)	P:A	RWE (joules/m)
Colonization				
Yes	2.57	15.7	1.25	3071.5
No	2.11	24.7	1.14	1572.6
Contraction				
Yes	2.58	15.6	1.22	2246.5
No	2.03	26.5	1.15	2308.3
In-filling				
Yes	2.33	13.8	1.35	2107.9
No	2.21	30.4	1.00	2425.9

Note: The predictors are: injury age (AGE), original injury volume (VOL), original injury perimeter-to-area ratio (P:A), and representative wave energy (RWE). See *Model development: Predictor variables* for more information.

and VOL ($w_i = 0.2735$). Evidence ratios suggested weak support for this model, particularly when compared to the second best model (AGE), which had a nearly identical Akaike weight (0.2711) and the third model (AGE and P:A), which had a similar weight of evidence (0.2224; Table 4). An approximate 95% confidence interval was reached by summing the Akaike weights for

the top five models (0.9468), indicating that each of these models have some plausibility, reinforcing model uncertainty (Burnham and Anderson 2002).

The model-averaged estimate of the effect of AGE on CONTRACT was very similar to the predicted estimate based upon the best model (1.385 vs. 1.2904). The substantial increase in the unconditional standard error

TABLE 4. Information-theoretic criteria for all models in rank order based upon AIC$_c$ model selection methods.

Model	K_i	AIC$_c$	Δ_i	ω_i	ER	$\sum \omega_j$
Seagrass colonization						
INTERCEPT ONLY	1	43.0540				
AGE	2	42.3444	0	0.2067	1.00	0.7090
AGE, P:A	3	42.5171	0.1727	0.1896	1.09	
RWE	2	42.6094	0.2650	0.1810	1.14	0.5550
AGE, RWE	3	42.7521	0.4077	0.1686	1.23	
AGE, RWE, P:A	4	43.0650	0.7206	0.1441	1.43	
P:A, RWE	3	44.7751	2.4307	0.0613	3.37	
P:A	2	45.2344	2.8900	0.0487	4.24	0.4437
Areal contraction						
INTERCEPT ONLY	1	42.1680				
AGE, VOL	3	40.1190	0	0.2735	1.00	
AGE	2	40.1365	0.0175	0.2711	1.01	0.8690
AGE, P:A	3	40.5330	0.4140	0.2224	1.23	
AGE, VOL, P:A	4	42.0907	1.9717	0.1021	2.68	
VOL	2	42.6345	2.5155	0.0778	3.52	0.4764
P:A	2	44.5285	4.4095	0.0302	9.07	0.3776
VOL, P:A	3	45.0650	4.9460	0.0231	11.86	
Sediment in-filling						
INTERCEPT ONLY	1	41.3360				
VOL	2	40.0095	0	0.2679	1.00	0.5877
P:A	2	40.5315	0.5220	0.2064	1.30	0.5908
AGE, P:A	3	41.0250	1.0155	0.1612	1.66	
VOL, P:A	3	41.3050	1.2955	0.1402	1.91	
AGE, VOL	3	42.0510	2.0415	0.0965	2.78	
AGE, VOL, P:A	4	42.3517	2.3422	0.0831	3.23	
AGE	2	43.5905	3.5810	0.0447	5.99	0.3855

Notes: Abbreviations are: K_i, number of estimable parameters in the model including the intercept; Δ_i, AIC difference; ω_i, Akaike weights; ER, evidence ratios; and $\sum \omega_j$, relative variable importance weight. The best model will have an AIC difference (Δ_i) = 0. Models having Δ_i within 1–2 of the best model have substantial support. The larger the Akaike weight (ω_i), the greater the evidence that model i is the best model out of the candidate set. As evidence ratios (ER) increase, so does the support for the estimated best model over the model it is indexed against. The larger the $\sum \omega_j$, the more important variable j is relative to the other variables. See Table 3 and *Model development: Predictor variables* for more information.

(2.4331) over the conditional standard error from the best model (0.6238) reflects considerable model uncertainty in the estimated effect of AGE on CONTRACT. The model-averaged estimate of the effect of VOL on CONTRACT was very similar to the predicted estimate based upon the best model vs. (−0.0292 vs. −0.0326). The unconditional standard error (0.0409) nearly doubled over the conditional standard error from the approximated best model (0.0238), which reflected considerable model uncertainty in the estimated effect of VOL on CONTRACT.

Sediment in-filling.—Injuries where natural sediment in-filling occurred appeared to be much shallower and have higher P:A than those where in-filling did not occur (Table 3). The means for AGE were similar in comparing sites with in-filling vs. those without, as were the means for RWE (Table 3). The full complement of a priori information-theoretic criteria for the global model including all four predictor variables is given in the Appendix. Given its low relative importance as a predictor variable ($\sum \omega_i = 0.2646$; Appendix), RWE was removed from the analyses and judgment-based model selection proceeded using AGE, VOL, and P:A. As predictor variables, P:A and VOL had similar relative importance weights (0.5908 and 0.5877, respectively), which were greater than the importance of AGE (Table 4).

Model uncertainty was reflected in the range of Akaike weights (0.2679–0.0447; Table 4). The top four models were tentatively supported given each had $\Delta_i < 2$ (Table 4; Burnham and Anderson 2002). The highest ranked model included the single variable VOL with an Akaike weight of 0.2679 (Table 4). However, evidence ratios suggested that the top model was not convincingly the best (Table 4). The second model, which included P:A alone, had an Akaike weight of 0.2064 (Table 4). It required six models to reach a >95% confidence interval (0.9553), indicating that each of these models have some plausibility and reflecting model uncertainty (Burnham and Anderson 2002).

The predicted and model-averaged parameter estimates of the effect of VOL on FILL were nearly identical (−0.0349 and −0.0316, respectively). The unconditional standard error (0.0520) was more than double the conditional standard error (0.0202) from the approximated best model.

DISCUSSION

There was considerable model uncertainty when making inferences regarding seagrass injury recovery leading to weak, but not uninformative, predictions. For seagrass colonization, the model including AGE alone was selected as the best approximating model and AGE was the variable with the highest relative importance, suggesting that gaps created by vessel groundings in South Florida do not necessarily persist into perpetuity but can colonize, mostly with pioneering species when those species are available for recruitment into the disturbance (Duarte and Sand-Jensen 1990, Thayer et al. 1994, Bell et al. 1999, Whitfield et al. 2002, Di Carlo and Kenworthy 2008), but also when those species (e.g., *H. wrightii*) were not obviously available. To describe injury areal contraction, there was support for models combining AGE with either VOL or P:A, as well as for a model including AGE alone. For sediment in-filling, the best approximating model included VOL alone, but was closely followed by the model that included P:A alone; both variables had similar relative importance.

The majority of blowholes that had some measurable natural seagrass colonization taking place also exhibited areal contraction and sediment in-filling (Fig. 3). These recovering injuries were on average, smaller in area from the start than those injuries where recovery was not occurring, a tendency that has been observed elsewhere for small vs. large gaps in seagrass beds (Rollon et al. 1998, Bell et al. 1999). Recovering injuries were also initially shallower than injuries that showed little or no recovery. Hammerstrom et al. (2007) reported that regrowth of *T. testudinum* into experimental excavations tracked the sediment filling trajectory, a trend that was observed in the current study as well, with 70% of naturally filling sites demonstrating measurable seagrass colonization, largely with pioneering species. Conversely, large, deep blowholes demonstrated reduced capacities for colonization, contraction, and in-filling, particularly for *T. testudinum*, given the tendency of such deep injuries to exhibit steep edges that can impede seagrass regrowth (Kenworthy et al. 2002, Whitfield et al. 2002, Hammerstrom et al. 2007, Di Carlo and Kenworthy 2008). Although a few injuries with natural sediment accumulation did not experience measurable colonization, the mean reduction in volume for those injuries was half that exhibited by injuries with measurable seagrass cover, suggesting that natural in-filling processes play a role in facilitating subsequent seagrass colonization. Substrate stabilization is critical to the recovery process (McNeese et al. 2006), and it is possible that these sites may have been too dynamic for effective seagrass colonization. Filling of injuries with crushed limestone rock is a recommended course of action in many restoration plans for vessel groundings in the FKNMS (NOAA ORR 2009). However, the high number of expanded injuries observed in our study suggests that a protracted lag time between injury occurrence and restoration implementation may leave the site vulnerable to secondary disturbance (i.e., storms; Whitfield et al. 2002). Given that some of our blowholes were able to begin to naturally fill with sediment and sustain seagrass coverage over the course of one to three years post-occurrence, management would be best served by implementing restoration fill activities as quickly as possible, especially for blowholes greater than 14–16 m^3 (average volume of injuries experiencing colonization, contraction, and natural in-filling; Table 3).

P:A ratios were slightly higher for recovering sites, a trend consistent with simulation models by Fonseca et al. (2004) that examined recovery as a function of injury P:A. Those injuries exhibiting recovery tended to be older, similar to small, naturally occurring and experimentally created seagrass gaps (Williams 1990, Rollon et al. 1998, Rasheed 1999, Kenworthy et al. 2002, Olesen et al. 2004, Uhrin et al. 2005, Hammerstrom et al. 2007, Di Carlo and Kenworthy 2008). Consistent with previous studies, it appears that, over time and barring further disturbance, seagrass is expected to grow inward from the undisturbed injury perimeter, creating a progressive band of clonal expansion that leads to a reduction in injury area (Marba and Duarte 1998, Creed and Amado Filho 1999, Rasheed 1999, Olesen et al. 2004; A. V. Uhrin, W. J. Kenworthy, and M. S. Fonseca, *personal observation*).

Wave energy (RWE) was a moderately important variable with regard to seagrass colonization, but not so for areal contraction or sediment in-filling; sites exhibiting seagrass colonization had nearly double the wave energy of those not exhibiting colonization. We expected that as a first-order response, RWE would contribute negatively, not positively, to seagrass colonization, suggesting that our assessments captured a second- or third-order response. We posit that seagrass colonization was not directly enhanced by wave energy, but by the influence of wave energy in preparing the site for colonization by accelerating sediment in-filling. Similarly, we suspect that RWE did not adequately explain sediment in-filling because sediment movement probably commenced at RWE intensities that were either reached routinely, or occurred in one episodic event (we have observed extremely large blowholes in the back reef environment of the FKNMS to in-fill with sediment in a matter of hours during exposure to a tropical storm event; M. S. Fonseca, *personal observation*). Thus, areal contraction may be a third-order response to RWE after sediment in-filling and the initiation of seagrass colonization, which would also explain the low predictive strength of RWE.

Vessel groundings often disrupt seagrass belowground biomass (Di Carlo and Kenworthy 2008), impeding recovery and creating persistent gaps similar to those resulting from natural-disturbance events (tropical storms [Birch and Birch 1984, Poiner et al. 1989], manatee grazing [Lefebvre et al. 2000]). The blowholes examined in our study persisted for a number of years as documented for other vessel-grounding injuries in the region (Sargent et al. 1995, Whitfield et al. 2002, 2004, SFNRC 2008) and consistent with modeled recovery rates that predict full recovery on a decadal scale (Uhrin et al. 2009). However, in *H. wrightii*-dominated beds in Tampa Bay, Bell et al. (1999) observed high rates of natural gap closure and limited gap expansion, with gaps rarely persisting beyond six months; a response not unexpected for a species with high rhizome extension rates and therefore rapid colonization capabilities

(Fonseca et al. 1987, Gallegos et al. 1994, Kenworthy et al. 2002). Similarly, dugong feeding areas in Moreton Bay, Australia, were found to completely recolonize with *Zostera capricorni* within one year post-disturbance (Peterken and Conacher 1997). *Z. capricorni* forms seed banks, and dugong grazing activities essentially plow the sediment leading to seed burial and abrasion of seed coats, which has been shown to stimulate germination (Conacher et al. 1994). In contrast, vessel-grounding injuries in the FKNMS typically occur in areas where the climax species, *T. testudinum*, dominates (Kenworthy et al. 2002). In the current study, *T. testudinum* was the most abundant seagrass species for 26 of the 30 injuries. *T. testudinum* is adapted to grow vertically upward rather than downward, according to the branching architecture of its dimorphic rhizomes (Tomlinson 1974). This species has strongly lignified, inflexible rhizomes, with inherently slow elongation rates (Marba and Duarte 1998), and apical meristems that are inhibited by exposure to light, showing very little tendency to reorient downward along the steeply graded margins exhibited by blowholes (Kenworthy et al. 2002, Whitfield et al. 2002).

Much of the observed natural seagrass colonization was dominated by *H. wrightii* and another early colonizer, *S. filiforme*, which is consistent with the current paradigm of Caribbean seagrass bed succession (Williams 1990, Gallegos et al. 1994, Kenworthy et al. 2002, Di Carlo and Kenworthy 2008), as well as other studies that have examined gap colonization in seagrass beds (den Hartog 1971, 1977, Walker et al. 1989, Rasheed 1999, Olesen et al. 2004). These two species have flexible rhizomes with rapid rates of rhizome elongation (Marba and Duarte 1998) that permit downward vegetative colonization into blowholes. Because these species are less sensitive to blowhole edge height and steepness (as compared with *T. testudinum*), the sensitivity of the COLONIZE variable was potentially obscured as pioneer species colonization likely began before the injury edges were sufficiently smoothed to accommodate *T. testudinum*. Restoration plans designed for vessel-grounding injuries in the FKNMS often incorporate what is termed "compressed succession" (Derrenbacker and Lewis 1982, Fonseca et al. 1987), whereby pioneering seagrass species such as *H. wrightii* are planted in the injury footprint (following restoration fill activities) to rapidly stabilize sediments and contribute to the establishment of functional seagrass habitat (NOAA ORR 2009). Despite the abundance of *H. wrightii* and *S. filiforme* in naturally colonizing injuries, *T. testudinum* was present in small quantities, suggesting that full recovery was underway. This initial trajectory of pioneering species recovery has been offered as evidence that injuries may indeed recover to full baseline values (from a seagrass cover standpoint), given time measured in decades (Fonseca et al. 2008, Uhrin et al. 2009). Indeed, it would appear as if the majority of the injuries examined in this study are

recovering naturally, but probably in episodic stages (Uhrin et al. 2009) and, in terms of the injured reference species, quite slowly, particularly regarding the associated belowground components (Di Carlo and Kenworthy 2008).

Just as gaps in terrestrial grasslands may serve as potential seed recruitment sites (Grubb 1977), fragment or seedling recruitment into seagrass injuries may result in a scattered distribution of plants and clonal fragments that could speed the recovery process (Olesen et al. 2004, Whitfield et al. 2004). Seeds of *S. filiforme* and *H. wrightii* are more persistent than those of *T. testudinum*, which may allow for the accumulation of substantial seed banks (see review by Orth et al. 2000); germination of *Halodule* spp. sediment seed reserves has led to rapid recolonization in areas with extensive, natural seagrass loss (Robblee et al. 1991, Inglis 2000). Although *T. testudinum* seedlings have been shown to recruit, survive, and grow in vessel-grounding injuries in FKNMS, said recruitment has been found to sometimes be highly episodic with low survivorship (Whitfield et al. 2004). Recruitment of *T. testudinum* seedlings also appears to be limited by injury size with reduced seedling densities in smaller injuries (Kaldy and Dunton 1999, Whitfield et al. 2004), a response that invokes gap size-dependent recruitment limitations as seen for other marine ecosystems (Sousa 1985). In the present study, two injuries had expanded but also had initiated seagrass colonization, suggesting recruitment. However, we did not observe individual seedlings of any seagrass species in any of our injuries. Therefore, the observed colonization at these two sites was either due to fragment recruitment or represents seedlings that had begun to branch and form small patches, indicating that gap closure of our vessel-grounding sites is proceeding almost exclusively from vegetative propagation of adjacent, undisturbed seagrass sources (but see Whitfield et al. 2004).

At this time, injury recovery assessments for seagrass injuries in the FKNMS do not consider the influence of post-injury disturbances (Kirsch et al. 2005). Nonetheless, severe wind events have demonstrated the capacity to both further erode injuries (Whitfield et al. 2002; A. V. Uhrin, *unpublished data*) as well as to cause low to moderate sediment accumulation (United States v. Kane Fisher and Salvors 1997, Whitfield et al. 2002; A. V. Uhrin, *unpublished data*). In fact, in 2005, following our reassessment surveys, our sites experienced a procession of tropical storms and hurricanes that resulted in both erosion and accumulation of sediment in various injuries (A. V. Uhrin, *unpublished data*), supporting our suspicion that episodic, extreme storm events may also be drivers of sediment accumulation in gaps (sensu Bell et al. 1999, Whitfield et al. 2002, Bell et al. 2006, Fonseca et al. 2008), which in turn appears to be the key factor promoting seagrass colonization in vessel-grounding injuries. However, because our understanding of the linkages between site recovery and wind event characteristics remain to be resolved (i.e., first-, second-, or third-order interactions), we do not recommend that RWE be added to the seagrass injury assessment process at this time.

Management implications

Restoration plans in the FKNMS currently call for a five-year schedule of monitoring to assess the success of seagrass primary restoration, which is the minimum recommended monitoring period (Fonseca et al. 1998, NOAA ORR 2009). This is based on the expectation that a short period of monitoring will accurately depict the beginning of a recovery process that may otherwise be decades in duration. The initial shape of the recovery curve (percent recovery as a function of time) will have profound consequences for the remainder of the trajectory; therefore, determining whether colonization and injury contraction are underway are important milestones. Without having achieved these initial stages of recovery within the five-year period following injury formation, we have limited expectation of long-term recovery and in fact, may instead be witnessing a new, enduring landscape pattern. Our data suggest that to arrest gap expansion and set vessel groundings on a trajectory for recovery, it is critical that sediment elevations in blowholes be quickly restored to the level of the adjacent, undisturbed grade, especially for those blowholes with a volume >14–16 m^3. Reconstruction of sediment elevation is critical because recovery, when measured as injury contraction, was governed exclusively by in-growth from the undisturbed, adjacent seagrass bed (vs. seed or fragment recruitment) and even small differences in elevation across colonizing faces have been shown to retard seagrass colonization (Rasheed 1999, Kenworthy et al. 2002, Hammerstrom et al. 2007). Because claims cases often do not result in sufficient resources to sustain five years of restoration, we also suggest that monitoring be limited to subsampling of representative injuries to derive guidance on restoration performance.

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APPENDIX

Information-theoretic criteria for all a priori models (*Ecological Archives* A021-063-A1).