3b2 v7 AQC : 610 PROD.TYPE: COM ED: UMA
pp.1–18 (col.fig.: NIL) PAGN: DORTHY SCAN: MALLIK

AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. **14**: 000–000 (2004)
Published online in Wiley InterScience
(www.interscience.wiley.com). DOI: 10.1002/aqc.610

Use of two spatially explicit models to determine the effect of injury geometry on natural resource recovery

MARK S. FONSECA[a,*], PAULA E. WHITFIELD[a], W.J. KENWORTHY[a], DAVID R. COLBY[a] and BRIAN E. JULIUS[b]

[a] *National Ocean Service, NOAA, National Centers for Coastal Ocean Science, Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Rd, Beaufort, NC 28516-9722, USA*

[b] *National Ocean Service, NOAA, Damage Assessment Center, SSMC4 Room 10218, 1305 East–West Highway, Silver Spring, MD 20910, USA*

ABSTRACT

1. Disturbance to sessile communities has been evaluated in a wide variety of terrestrial and marine settings, but, to our knowledge, recovery has not explicitly considered the effects of injury shape, except in an exploratory fashion. Therefore, we have developed a simple, but spatially explicit relationship between the geometry of a disturbance and the recovery rate in the context of natural resource damage assessment.

2. Here, grounding of motor vessels in shoalgrass (*Halodule wrightii*), manatee grass (*Syringodium filiforme*), and turtlegrass (*Thalassia testudinum*) habitats results in a variety of injury shapes whose recovery must be evaluated to assign penalties and restoration costs to the party responsible.

3. We developed two spatially explicit, cellular automata modelling techniques to evaluate injury recovery trajectory. Techniques in both SAS® and ArcINFO® were developed and applied to injuries of varying perimeter but fixed area.

4. The SAS method utilized either a simple Boolean or probabalistic interrogation of the status of adjacent pixels using the matrix language component of the software. ArcINFO utilized a cost/distance module to evaluate proximity of unfilled to filled (colonized) pixels and then applied a decision rule that governed conversion from unfilled to a filled state. As expected, the greater the perimeter/area ratio, the faster the recovery; and modelling approaches yielded almost identical results.

5. A case study involving $\sim 1200\,m^2$ of almost monotypic *T. testudinum* revealed that both models predicted that 100% recovery of above-ground components of the injury would not occur for approximately 60 years. This model is now being used routinely in the assessment of vessel groundings in seagrass beds within the Florida Keys National Marine Sanctuary and has been used successfully by the Government to prevail in US Federal Court challenges. Both methods have substantial, untapped capabilities to explore the effect of numerous ecological effects on the processes influencing recovery from disturbance.

Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS: seagrass; injury geometry; disturbance; recovery; cellular automata; assessment

*Correspondence to: Dr M.S. Fonseca, National Ocean Service, NOAA National Centers for Coastal Ocean Science Center for Coastal Fisheries and Habitat Research, 101 Pivers Island Rd., Beaufort, NC 28516-9722 USA. E-mail: Mark.Fonseca@noaa.gov

Copyright © 2004 John Wiley & Sons, Ltd.

Received 15 November 2002
Accepted 1 June 2003

UNCORRECTED PROOF

INTRODUCTION

One of the most widespread and serious injuries to shallow water, marine natural resources is the damage done to seagrass beds by propeller scarring and vessel groundings (Sargent *et al*., 1995; Kenworthy *et al*., 2002; Whitfield *et al*., 2002). These actions are violations of the Federal Water Pollution Control Act (33 U.S.C. 1251 *et seq*.) and River and Harbors Act of 1899 (33 U.S.C. 401 *et seq*.), and, depending on the location, may be in further violation of other state and federal laws, such as the National Marine Sanctuaries Act (16 U.S.C. 1431 *et seq*.).

A typical vessel injury in a seagrass bed consists of a simple, linear propeller scar. More complex injuries arise when vessels, especially large ones powered with twin propellers, create a blowhole (a propeller-washed excavation of the seagrass and underlying substrate; Figure 1). To our knowledge, Zieman (1976) provided the first qualitative recovery estimates for the dominant tropical species *Thalassia testudinum*, predicting recovery from single propeller scars in approximately 6 to 7 years. More recent experimental manipulations of disturbance and quantitative studies of propeller scar recovery in seagrasses (Kenworthy *et al*., 2002) and transplanting studies (Fonseca *et al*., 1987) confirm the slow recovery rate for *T. testudinum*

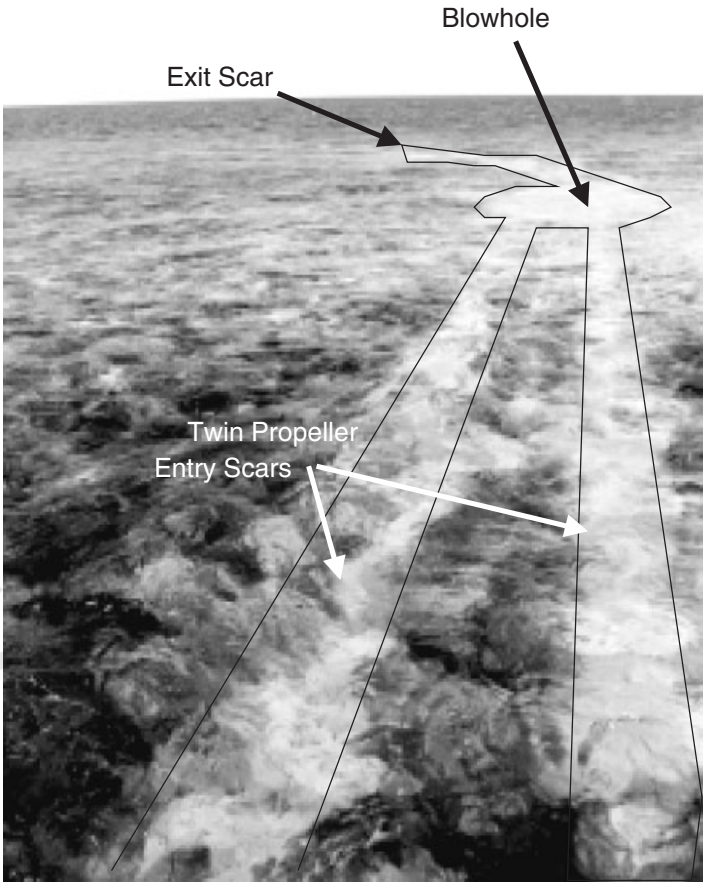

Figure 1. Typical grounding scar on shallow *Thalassia testudinum* bank in the Florida Keys National Marine Sanctuary. Note the twin entry scars caused by the vessel's propellers and the grounding blowhole at their terminus, marking where the hull settled onto the seagrass and efforts were made to power the vessel off the bank. Exit scars can be discerned above the blowhole.

Copyright © 2004 John Wiley & Sons, Ltd.

in the Caribbean (Williams, 1990), Tampa Bay (Durako *et al*., 1992; Dawes *et al*., 1997) and the Florida Keys National Marine Sanctuary (FKNMS; Kenworthy *et al*., 2002). Recovery estimates range from 3.5 to 26 years for a limited range of propeller scar sizes. Although *T. testudinum* is probably the seagrass most frequently injured by scarring in the FKNMS, two sympatric species with higher colonization rates, *Halodule wrightii* and *Syringodium filiforme*, also experience damage from motor vessels. Recovery rates for these two species, based on small experimental excavations (Williams, 1990; Fonseca *et al*., 1994; Kenworthy *et al*., 2002), simulated propeller scars (Durako *et al*., 1992), a pipe drag scar (Fonseca *et al*., 2000) and transplanting experiments (Fonseca *et al*., 1987), suggest full recovery of these injuries may often occur in less than 3 years.

Even when data are sufficient to contemplate quantification of injury recovery, studies of the recovery process have been conducted primarily where the injury was a geometrically simple shape, such as a narrow, rectangular propeller scar (Figure 1); but, as we stated above, the grounding can be much more complicated. A vessel grounding typically homogenizes the above- and below-ground structures of the plants within the scar, and may excavate sediments down several decimetres. With large vessels, propeller scars (often parallel scars for twin engine vessels) frequently terminate in full-scale hull groundings, where the vessel has lost momentum and settled onto the seagrass bed. When the vessel operators attempt to recover from such a grounding, they characteristically power up the engine(s) to manoeuvre to deeper water, forming blowholes (Figure 1). As the blowholes are excavated, they suspend and cast aside sediments and seagrasses, the extent of which depends on the size and power of the vessel and the behaviour of the operator (Whitfield *et al*., 2002). The ejected sediment often forms thick, geometrically variable berms alongside what may be geometrically erratic blowholes and may kill the underlying benthic community. In some instances, salvors that assist a grounded vessel may also prop-scar the seagrass bed, adding to the original injury. Thus, the net result of the grounding event is often a geometrically complicated injury composed of several different shapes that range from continuous to isolated in their distribution within the seagrass bed.

Because of their complicated geometry, many groundings pose problems for predicting recovery because of the varying levels of perimeter per unit area of injury. If we assume that recovery rate is positively related to the amount of edge (*sensu* Paine and Levin, 1981), then an injury with high perimeter-to-area ratio should recover faster than another injury of the same area but lower perimeter. The shape of a disturbance and other geometric attributes, such as slope and aspect of the injury, as well as local conditions such as substrate composition, exposure to waves, etc., have all been shown to be relevant parameters that may influence recovery (*sensu* Paine and Levin, 1981; Miller, 1982; Sousa, 1985).

Variation in injury geometry as the result of vessel groundings is essentially a modification of the landscape pattern (e.g. shape, contiguity and spatial extent). Extensive work on the ecological consequences of landscape pattern has been conducted in terrestrial systems (Watt, 1947; Whittaker and Levin, 1977; Levin, 1978; and reviews by various authors in Pickett and White (1985)). However, disturbance and recovery in marine systems have, in general, received far less attention than terrestrial systems (but see Williams (1987, 1990)). Historically, marine work was conducted on rocky intertidal ecosystems (e.g. Connell and Slatyer, 1977; Sousa, 1979, 1985; Paine and Levin, 1981; Connell and Keough, 1985). More recently, studies have focused on the effects of disturbance distribution, frequency, return interval (reciprocal of frequency), size, and intensity, particularly with regard to fauna and associated changes in landscape pattern arising from groundings in seagrass beds (Bell *et al*., 2002; Uhrin and Holmquist, in press). Such changes have been implicated as a controlling factor for a number of critical ecological processes in seagrass ecosystems, including colonization, migration, prey detection, and predator avoidance to name but a few (Bell and Hicks, 1991; Irlandi, 1994, 1996, 1997; Irlandi *et al*., 1995, 1999; Irlandi and Crawford, 1997; Bell *et al*., 2001; Guichard *et al*., 2001; Hovel and Lipcius, 2001).

Studying similar processes in non-marine systems provides guidance as to how to approach the problem of modelling recovery in spatially complex seagrass injuries. For example, the process of gap closure

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

(Loucks *et al.*, 1985; Sousa, 1985; where gaps are either open areas within an otherwise occupied landscape; Type I patch, or *vice versa*, Type II) provides a template with which to evaluate recovery of seagrass beds. Paine and Levin (1981) provided a concise mathematical basis for the influence of simple injury geometry on recovery rates of Type I patches in Pacific-coast mussel communities. They concluded that the change in the area of a gap (open patch) over time could be described not only by the rate of advance of the community back into the gap but also by the shape (eccentricity; length/width) and gap area. Because the shape of the gap and, likely, the amount of edge (and implicitly, the edge-to-area ratio) will change over time, gap filling will likely be a non-linear process. The obvious key to this computation is having robust, empirical information on the rate of coverage advance and injury geometry. More recently, attention has been focused on gap processes in seagrass beds (Bell *et al.*, 1999), documenting the temporal and spatial dynamics of gap formation. The existence of comparative data, such as that of Bell *et al.*, (1999), provides important verification and context for quantifying the recovery of the bed from disturbance (Fonseca *et al.*, 2000; Kenworthy *et al.*, 2002).

The objective of our study was to perform a spatially explicit (where spatial information is contingent upon conditions or information flowing laterally across the landscape) computation to determine the influence of an injury shape (open gap) on the recovery time within a seagrass bed. Specifically, we set out to evaluate the effect of gap geometry on the recovery (to 100% of pre-injury conditions), a process that is achieved through lateral extension of rhizomes and shoots of seagrass surrounding the injury site. Here, we do not model rhizome advance *per se*, but rather the movement of the quality of 100% of pre-injury conditions across the sea floor. Via what is essentially a cellular automata approach, our methods incorporate the unique effects of geometry on recovery for each individual injury, rather than relying on generalized geometric representations (e.g. modelling an injury as a circle). Moreover, we desired to create a modelling process that could ultimately incorporate other environmental factors, such as slope, aspect, depth of the injury, hydrodynamic setting, sediment types and various recolonization strategies, so that the process could be broadly applicable across a wide variety of injured resources, and not just seagrass. This also means that the geometric complexity and extent of an injury could be consistently evaluated in terms of recovery time (or severity of the injury). By imposing costs on vessel operators that are scaled to the severity of the disturbance they create, in the future, vessel operators and salvors would hopefully become educated to minimize post-grounding disturbance and agree to pursue available, low-impact options for removing the vessel from the area. Therefore, in this paper we address what we consider to be the first-order issue: an evaluation of the effect of injury geometry on the seagrass recovery process.

METHODS

Approach

The space domain used here was two-dimensional because, at present, little is known about the influence of topographical features (third dimension) on the rate of lateral extension of seagrass. The approach was essentially deterministic, yielding a liberal estimate of recovery because seagrass mortality was implicit in the recovery rates and was not manipulated to determine the role of varying mortality (such as from storms (*sensu* Whitfield *et al.*, 2002)). To test that we did not reach conclusions that were driven by inherent software limitations, we developed this technique using two fundamentally different approaches and software, namely ArcINFO® and SAS®.

Here, we present: (1) the background information needed to convert the results of injury geometry modelling to real-world recovery rates; (2) an operational description of the two modelling procedures (ArcINFO and SAS); (3) the effects of varying injury geometry on the recovery function; and (4) a comparison of the two models in a case study regarding an actual grounding event in Puerto Rico.

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

Adjusting the time scale in injury geometry models to empirical recovery rates

For actual percentage recovery rates (i.e. recovery to 100% of pre-injury conditions), we had three sources of empirical data (Table 1): (1) excavation experiments in *T. testudinum*, *S. filiforme* and *H. wrightii* in

Table 1. Source data for computation of recolonization rates

Source	Recruiting faces	Scar width (m)	Time (years) adjusted to 2 recruiting faces	Time (years) to close a 1 m gap with 2 recruiting faces
Thalassia testudinum				
Experimental excavations, Florida Keys (Kenworthy *et al*., 2002)	4	1	10.5	10.5
Great Lakes model of actual scar (Fonseca *et al*., 2000)	2	1	17	17
Artificial scar in Tampa Bay (Durako *et al*., 1992)	2	0.25	5 (3.6–6.4)	20
Artificial scar in Tampa Bay (Dawes *et al*., 1997)	2	0.25	7.6	30.4
Artificial scar in Tampa Bay (Dawes *et al*., 1997)	2	0.25	3.9 (3.5–4.3)	15.6
Lignumvitae actual scar (Kenworthy *et al*., 2002)	2	0.44	7.5 (5.4–9.6)	17.05
Mean				15.09 years *or* 7.55 years m^{-1} for 1 face *or* 0.133 m $year^{-1}$ for 1 face
Halodule wrightii				
Experimental excavations, Florida Keys (Kenworthy *et al*., 2002)	4	1	1.9	1.9
Artificial scar in Tampa Bay (Durako *et al*., 1992)	2	0.25	1.95 (1.3–2.6)	7.8
Mean				4.85 years *or* 2.43 years m^{-1} for 1 face *or* 0.412 m $year^{-1}$ for 1 face
Syringodium filiforme				
Experimental excavations, Florida Keys (Kenworthy *et al*., 2002)	4	1	1.5	1.5
Great Lakes model of actual scar (Fonseca *et al*., 2000)	2	2	3.5	1.75
Mean				1.63 years *or* 0.81 year m^{-1} for 1 face *or* 1.23 m $year^{-1}$ for 1 face
Average for *H. wrightii* and *S. filiforme*				0.821 m $year^{-1}$

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

Tampa Bay and the FKNMS (Durako *et al*., 1992; Fonseca *et al*., 1994; Dawes *et al*., 1997; Kenworthy *et al*., 2002); (2) actual measurements of recovery rates for *T. testudinum* in 10 m segments of randomly chosen scars at Lignumvitae Key, FKNMS (Kenworthy *et al*., 2002); and (3) pipe scar recovery measurements in the FKNMS (Fonseca *et al*., 2000). It is important to note that these studies all involve linear recruitment faces, which greatly simplified data reduction. As a form of additional corroboration, we compared the rates of ingress from the aforementioned studies with rates of expansion of seagrass from transplant studies of the same seagrass species in Tampa Bay and the FKNMS (Fonseca *et al*., 1987, 1996). Because the data from the first three experiments were composed of geometric shapes with differing numbers of parallel recruiting faces, it was necessary to standardize the data to a common unit basis. First, we recomputed the data to represent the time in years for recovery based on two opposite and parallel recruiting faces 1 m apart and averaged this among experiments. Here, we assumed that the contribution to recovery of a long linear shape by any seagrass growing in from either end would be trivial. For square injuries, the four recruiting faces were considered to have the same influence as two parallel faces, because if the rate of advance of each face was assumed to be equal, then two faces would close a two-dimensional surface as fast as four. Next we divided this value for time in years for recovery by two to yield years per metre, and then we took the inverse of this value (metres per year) as our final expression of recovery rate (Table 1).

Measurements of actual scars in the FKNMS predicted that ~11 to 17 years were required for 100% recovery of a 1 m wide scar, a situation with two recruiting faces (Kenworthy *et al*., 2002). Both of these rates estimate a much slower recovery than would be obtained by using the rhizome extension velocity directly — which has been reported to be as great as 0.5 m year^{-1} for *T. testudinum* and 2.5 m year^{-1} for *H. wrightii* (Marba and Duarte, 1998). There are several reasons for not using rhizome extension rate as the explicit metric of encroachment. One reason is because such a simple estimation of recovery time presumes every pixel along the edge of an injury to be occupied by a rhizome apical (which is not the case; apical densities are typically an order of magnitude less than shoot densities; pers. obs.). A second reason for not utilizing simple extension rate data is that seagrasses branch as they extend their rhizomes across the sea floor; thus, they divert some of the forward advance into a recursive growth pattern that fosters consolidation of the space being colonized. Discrepancies may also arise from varying injury depth. Kenworthy *et al*. (2002) suggest that recovery may be highly dependent on excavation depth, and we suspect that our excavations were deeper than the average 2–10 cm depth of the 15 Lignumvitae Key scars. For *T. testudinum*, excavation depth may control how rhizome apical meristems grow when they reach a steep vertical gradient (Kenworthy *et al*., 2002; Whitfield *et al*., 2002). Also, these scars typically accumulate macroalgae and organic matter that may create conditions that are unfavourable for seagrass growth (pers. obs.). Though the depths of the excavated scars were not unlike that of actual groundings, it appears (authors' pers. obs.) that deeper scars yield a slower recovery rate.

We were also concerned that computing recovery for injuries with multiple recruitment faces may not be directly proportional to the number of recruitment faces. For example, we assume that rhizome extension from a linear front could not be extrapolated to compute the time of encroachment into a 1 m × 1 m excavation surrounded by seagrass as simply four times the extension velocity, because some competitive interactions among seagrasses may occur as they encounter recruitment from other recruitment faces, potentially slowing the recovery (i.e. a density-dependent relationship). In contrast, a lone recruiting face or two opposing faces would logically be free of intraspecific competition until most of the injury was colonized, and thus recover more rapidly (which is another reason to disregard the contribution of four recruiting faces in favour of only two). Although this awaits experimental verification, we will use the higher recovery rate estimates (i.e. based on either one or two recruiting faces) to the benefit of the responsible party (RP). This higher rate will be applied to all recruiting faces in the injury geometry models, thus ignoring any potential competitive effects that could slow recovery.

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

To summarize, in the following computations, we have attempted to model the net movement of occupied space across the sea floor, of which rhizome extension rate is only one factor that contributes to the actual pace of colonization. Moreover, we do not include the negative effects of biological disturbance, storms, excessive injury depth, competition, etc. on the recovery rate — factors that we must ultimately incorporate into injury assessments as the empirical data set grows. In contrast, we also do not include recolonization by seeding (but see Whitfield *et al.*, 2002). On balance, we consider our modelling assumptions to be highly conservative, and thus biased to the benefit of the RP.

Scaling for Thalassia testudinum

If we take the average of the time in years to close a 1 m gap based on two recruiting faces, halve it to obtain the value for a single recruiting face and then take the inverse (metres per year), this becomes the average time to achieve 100% recovery of a 1 m distance of injury, or the velocity of horizontal recovery to pre-injury conditions (Table 1). Because we suspect that these values represent recovery rates from scars of differing injury depths, shapes, sediment types, etc., use of the average value (0.133 m year^{-1}) as the initial estimate for *T. testudinum* is an appropriate compromise. However, findings by Kenworthy *et al.* (2002) suggest that separation of recovery rates into injury depths greater or less than ~20 cm excavation depth may be appropriate, with deeper excavations recovering much more slowly than shallow ones.

Scaling for Halodule wrightii *and* Syringodium filiforme

These data arise primarily from the excavation experiments in the FKNMS (Kenworthy *et al.*, 2002). Both *S. filiforme* and *H. wrightii* achieved 100% injury recovery over a 1 m distance from two recruiting faces in ~2 years. Further north, in Tampa Bay, Fonseca *et al.* (1996) found similar results, in that they computed it would take planted *H. wrightii* 3.6 years to return a 1 m gap to 100% of ambient bed densities, rates further supported by transplanting data (Fonseca *et al.*, 1987) that demonstrate coalescence of plantings on 1 m centres in a similar time frame. The average horizontal velocity from both these species combined is 0.514 m year^{-1} (Table 1).

Modelling approaches

ArcINFO®

For a given injury shape, a binary raster grid (1 = occupied; 0 = unoccupied) was created. Euclidean geometry was combined with a cost/distance function to calculate the shortest distance from each unoccupied cell representing the injured area to the closest uninjured (occupied) cells in the grid. The value in the cells is the cost factor, which must be multiplied by the distance travelled to obtain the impedance to travel. The value in a cell is the accumulated cost by the lowest cost route through the landscape. Although the cost/distance function can be weighted by direction, we did not utilize directional weighting in this model version because it will allow us later to incorporate relevant ecological data that may strongly influence recovery, such as injury depth or slope. Cost can be conceptualized to represent the biological and physiological cost accrued by adjacent uninjured plants to colonize adjacent open space created by an injury. The output from each iteration of the cost/distance surface computation was automatically reapplied as the input data for the next iteration, where each iteration consisted of the entire series of computations across the injured area.

To evaluate the effect of injury geometry, a series of geometric shapes of constant area with differing perimeter/area ratios was converted into a grid in ArcINFO and the cell size set to 1 m^2 (Figure 2(a) and (b)). The model is an iterative process that begins with the Euclidean distance function in ArcINFO (Figure 2(a) and (b)). The source grid (the seagrass bordering the injury area coded as '1' or 'source cells') was evaluated by the Euclidean distance function (EUCDIST) to output a grid whereby every injury cell (cells

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

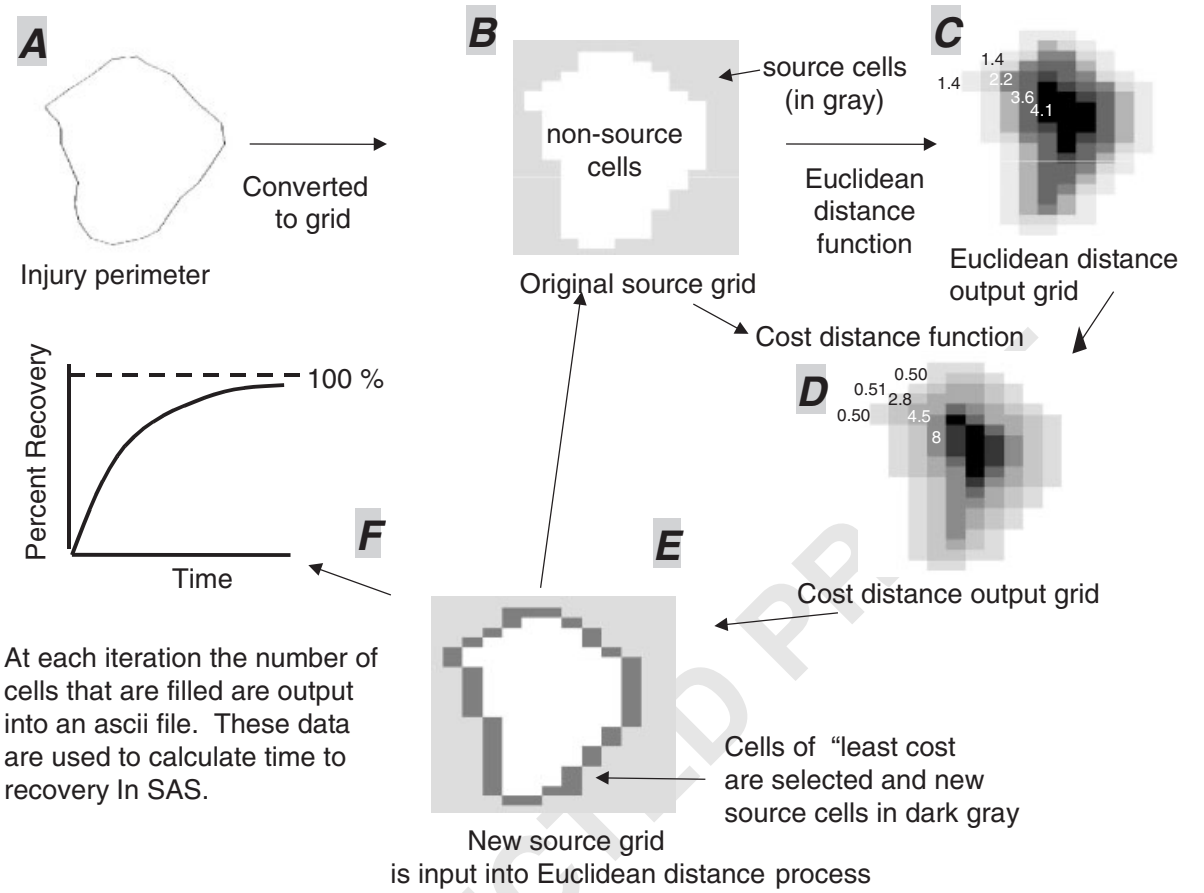

Figure 2. Diagram illustrating the steps involved in the ArcINFO modelling approach.

within the injury area coded as '0') was designated a value that represents the closest distance of each non-source cell to the closest source cell (Figure 2(c)). The next step in the process utilizes the cost/distance function. This function incorporated both the original source grid and the output grid from the EUCDIST function to create a second output grid of values that represents cost (Figure 2(d)). Each cell value in this grid represents the cost of moving through each cell in cost per unit distance. In this case, the cost grid was actually representing time to recovery because it is based solely on distance and no other weighting factor, such as injury depth. The greater the distance of the non-source cell to the source cells, the longer it will take for the seagrass (source) to recover into this area, implying the aforementioned physiological cost of the plant to grow into the injured area.

Next, because the cells nearest to a source cell always had a common lowest value across the entire grid, cells with that (known) lowest common value were automatically selected and reclassified as 'source cells'. These new source cells were merged with the original source grid, creating a 'new source grid' (Figure 2(e)). At this point, the whole process, beginning with the EUCDIST function, started over (Figure 2(b)) with the new source grid and continued until all of the cells were designated as being filled. For each iteration of the model (here scaled to time), the number of cells occupied was output into an ASCII text file (Figure 2(f)). The percentage of the injury that has recovered and the remaining years to complete recovery were

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

calculated at each time step. For example, if the cell size was 1 m then we used rates as years per metre from Table 1 to scale each iteration as a time step, thereby calculating time (in years) to 100% recovery. Specifically, a seagrass recovery value in years per metre would be used as follows:

$$\text{Percentage recovery} = \frac{\text{no. of cells filled at each time step}}{\text{total no. of injured (non-source cells)}} \tag{1}$$

$$\text{Years to recovery} = \text{no. of iterations} \times \text{rate of growth (years m}^{-1}) \tag{2}$$

Percentage recovery was then plotted by years to recovery to derive the recovery horizon for the entire injury (Figure 2(f)).

SAS®

This model begins by invoking Proc IML, the interactive matrix language in SAS. The value and utility of Proc IML was that we could readily address each element (cell in the simulation space) of a matrix, asking whether a particular cell P_{ij} at a particular time $t = t'$ was vegetated (i.e. whether the corresponding matrix element has a value of unity) or unvegetated (has a value of zero). We next used Proc IML to create an $n \times n$ matrix P with each element set to zero. The next step was to create the initial conditions for the simulation. This meant surrounding the hypothetical square injury with vegetated cells by setting appropriate elements of P to a value of unity. Because the contribution of seeds to the recovery process is not empirically quantified (Whitfield *et al.*, 2002) seeds have not yet been incorporated into the model.

The next step was to initiate a series of repetitive computations by invoking a user-defined module in Proc IML (named 'RECOVERY'). During each successive time step, RECOVERY examined each cell within P where value is zero to determine whether there was a vegetated border cell. If so, then the open cell was converted into a filled, or colonized state (value of unity). Thus, the more irregular the shape of the injury boundary, the more unoccupied cells are bounded by occupied cells and the more cells are converted to 'filled' per iteration of the module. Before the time step was incremented and the whole process repeated, the elements of P were copied into SAS data sets for later use in plotting various aspects of the sequential recovery process, also allowing one to depict graphically the invasion process advance with successive iterations.

We also developed another version of this model where the decision to colonize an adjacent, unfilled cell was made in a probabilistic fashion, by choosing a random number between zero and one and testing it against a probability function as a decision criterion for colonization. However, because other ecological factors, such as natural mortality or disturbance regimes, were not incorporated into the model, scaling of model iterations to time was performed *post facto*, making the effect on colonization rate not unlike that of the aforementioned, strictly deterministic approach. Although the probabilistic approach leaves open the possibility of incorporation of ecologically interesting processes, it was not needed to meet the goals of natural resource damage assessment and was not used for the modelling exercises herein.

Effects of injury geometry

In this simulation study, injury area was held constant to isolate the effects of shape. We did not vary cell size in the model, because this would be offset by the concomitant change in the time step represented by each cell (i.e. given that rhizome extension or colonization velocities are held constant, then higher resolution modelling would necessarily decrease the period of time required for the colonization of a cell). For this exercise, we used an area of 900 cells, arranged as a series of geometric forms (circle (unsmoothed), square and five different size rectangles) with increasing perimeter/area ratio P/A. The sizes ranged from widths of 1 to 10 cells (Table 2).

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

Table 2. Relationship between shape of a patch with fixed area (900 cells) and time to 100% recolonization (recovery) of that patch using ArcINFO model. Patch shape (at time zero, prior to recovery) was defined as eccentricity $E_c =$ patch length/patch width. P/A ratio is the ratio of the length of the patch perimeter to its area

Shape description	Eccentricity E_c	P/A ratio	Iterations to 100%
Circle (900 cells)	1.0	0.1180	19.0
30×30 square	1.0	0.1333	15.0
90×10 rectangle	9.0	0.2000	6.0
150×6 rectangle	25.0	0.3467	5.0
225×4 rectangle	56.25	0.5089	4.0
450×2 rectangle	225.0	1.0044	3.0
900×1 rectangle	900	2.0022	2.5

By holding injury area and model resolution constant, and varying initial eccentricity (E_c: length/width) and P/A of an injury, we examined the relationship of recovery rate of Type I gaps in seagrass coverage as a function of their geometry. We then examined whether these different modelling approaches yield different results. We also sought to determine whether we could collapse the general response of recovery to some simple-to-measure shape attributes, such as P/A or E_c. For purposes of clarity, we present only the results of the ArcINFO-based model in this exercise.

Case study application

During Hurricane Georges (1998) a fuel barge broke loose from its moorings at Naval Station Roosevelt Roads, Puerto Rico, and grounded on a seagrass bed composed largely of *T. testudinum*. The barge remained stranded for several days, in full contact with the sea bed. Upon removal, several large propeller scar tracks were created, in addition to the footprint of the barge grounding, creating a complex injury geometry (Figure 3). The scar area was mapped on 29, April 2000, using a Trimble Pro XRS differential global positioning system (GPS) with 0.10 m nominal spatial accuracy. This scar area was exported from Trimble's Pathfinder Office into an ArcINFO polygon coverage. A boundary was added to create a border of cells with a value of unity, and the cells representing the scar area were set to zero. Both the ArcINFO- and SAS-based modelling approaches were then applied to this polygon coverage. Outputs from both modelling approaches were combined in an SAS program that put both sets of results on the same axis scales and fit those results to a simple quadratic equation.

RESULTS

Effects of injury geometry

We found that the number of ArcINFO model iterations required to reach 100% recovery decreased with increasing P/A ratio or E_c (Table 2). The percentage recovery was plotted for each P/A ratio as a function of model iterations (Figure 4). The decrease in iterations to 100% recovery was then plotted against E_c (Figure 5). Both Figures 4 and 5 suggest that the models have strong predictive capability; however, Figure 4 can accommodate more spatially explicit information (P/A ratio), whereas Figure 5 uses a simpler geographic metric (E_c). Therefore, we expect that the approach using P/A ratios or, where possible, the precise geometry of the particular injury will yield the most accurate prediction of recovery. Being strictly deterministic, with no losses to mortality or subsequent disturbance, the results of the modelling exercise reasonably describe an expected recovery rate and function as influenced by injury geometry. Both Figures 4 and 5 suggest that injury geometry effects might be categorized into two simple groups: one for $P/A < 0.2$

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

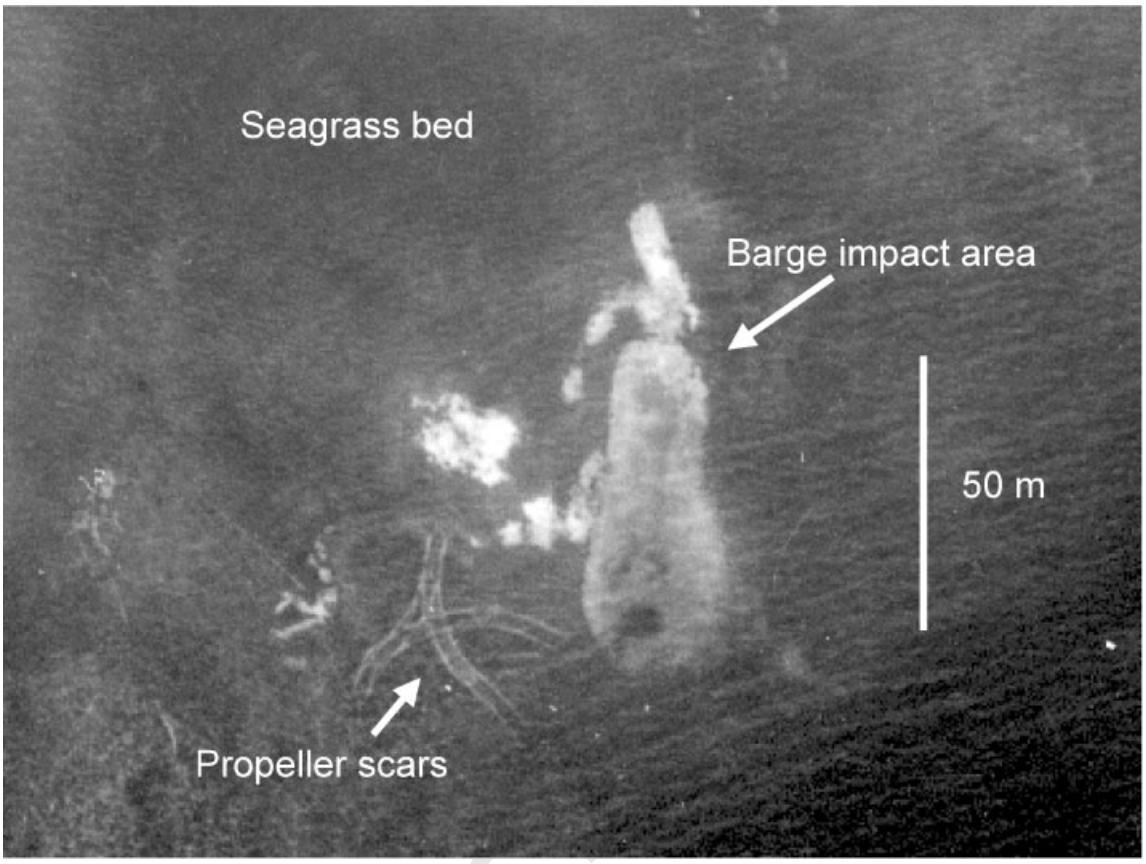

Figure 3. Plan view of fuel barge grounding site in Puerto Rico. The twin propeller scars of the vessel used to retrieve the barge can be clearly seen in the lower left of the photograph.

and $E_c < 10$ (termed here 'wide gap group' or (WGG)) and the ratio for $E_c \geqslant 10$ ('narrow gap group' (NGG)), respectively. The WGG would be typically applied to blowholes as seen in Figure 1, whereas the NGG would typically be applied to the propeller-scarred areas or areas where a deep V-hull scoured the bottom clean of seagrass. The model results from the deterministic approach suggest that most propeller scars would require no adjustment for geometric effects as their geometry is fairly constant across a grounding site (authors' pers. obs.). This is in contrast to blowholes and their associated sediment berms, which would require substantially more adjustment of the recovery function to account for temporal changes in injury geometry.

Case study

The fuel barge grounding, including both propeller scars from vessels attempting to capture the barge and the area where the barge itself grounded, covered an area of approximately 1200 m^2. Because the area was almost monotypic *T. testudinum*, we modelled recovery using a value of 0.133 m $year^{-1}$ from Table 1. The percentage of the injury that had recovered was plotted against time in years (Figure 6). Both models indicate that 100% recovery of above-ground components of the injury would not occur for approximately 60 years.

UNCORRECTED

Copyright © 2004 John Wiley & Sons, Ltd.

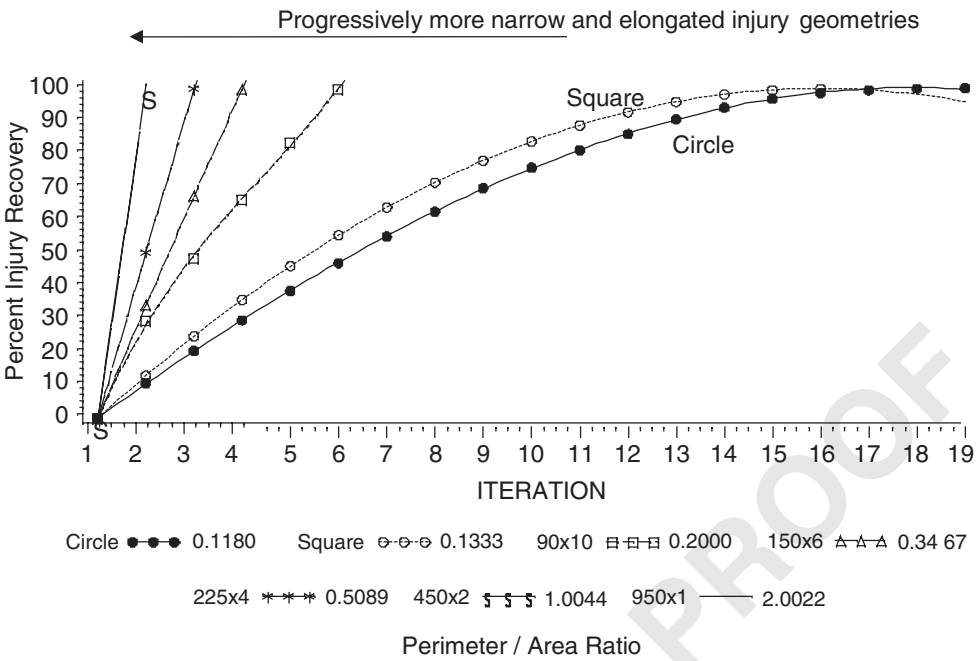

Figure 4. Recovery functions showing number of ArcINFO model iterations to 100% recovery as a function of injury perimeter/area ratio.

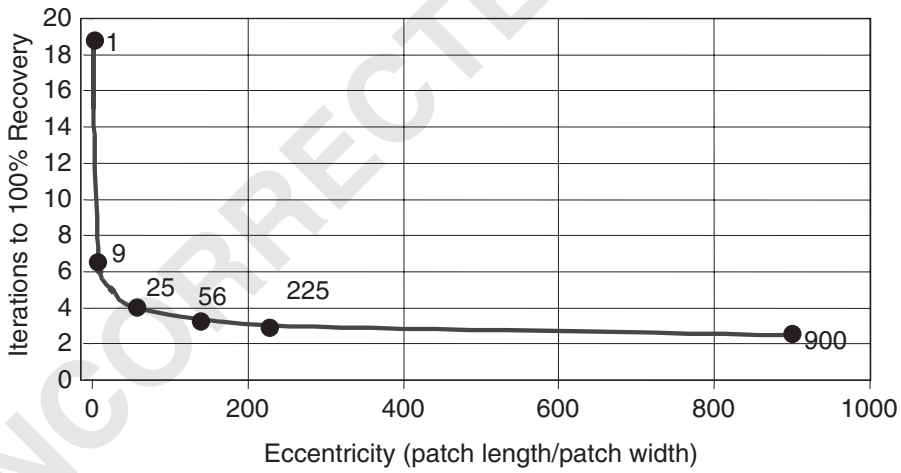

Figure 5. Plot of the number of ArcINFO model iterations to achieve 100% recovery as a function of injury eccentricity, E_c.

UNCORRECTED PROOF

DISCUSSION

Effects of injury geometry

The proximal reason for creating such recovery models was our need to provide a fair and reasonable assessment of injuries to seagrass beds (particularly to very old and slow-spreading *T. testudinum*) in the

Copyright © 2004 John Wiley & Sons, Ltd.

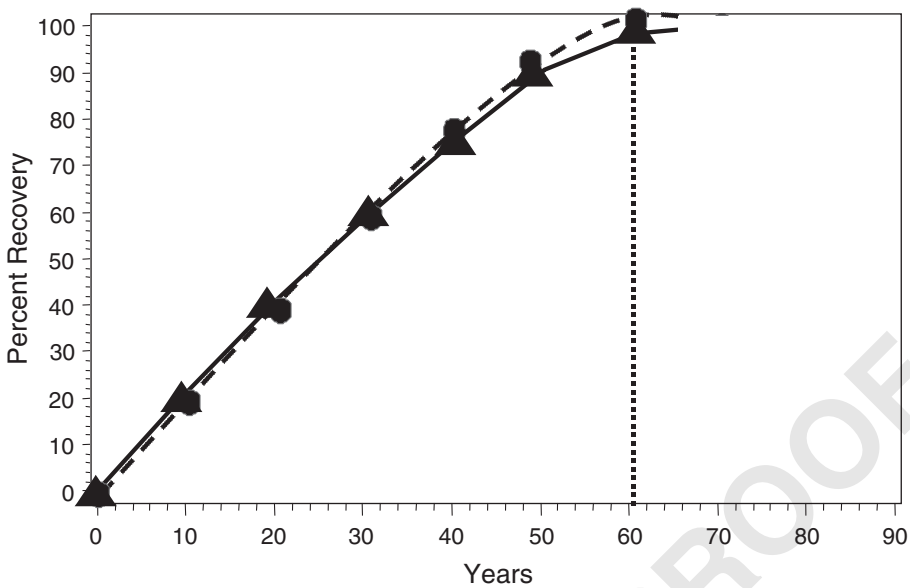

Figure 6. Comparative recovery functions for the fuel barge grounding using both the ArcINFO-based method (solid line with circles) versus the SAS-based method (dashed line using symbols with triangle). Vertical dashed line intercepts X axis (years) at the averaged 100% recovery for both methods.

UNCORRECTED PROOF

FKNMS (Fonseca *et al*., 2000). To accomplish this, the literature was reviewed for pertinent data regarding the recolonization rates of three tropical seagrass species found in the FKNMS. These literature data were combined with the results of field experiments (e.g. Durako *et al*., 1992; Dawes *et al*., 1997; Kenworthy *et al*., 2002) to produce vegetative recolonization rates that could be used to parameterize spatially explicit models describing the recovery process irrespective of the initial geometry of the injury.

As would be expected based on previous work in intertidal marine environments (Connell and Slatyer, 1977; Sousa, 1979, 1985; Paine and Levin, 1981; Connell and Keough, 1985), the geometry of an injury (expressed either as E_c or as P/A ratio) strongly influenced the recovery function in a non-linear fashion (Figures 3 and 4) . Simple linear injuries, such as propeller scars, will recover much more rapidly because of their high E_c and P/A ratio, whereas squares and circles of an identical area (but much lower E_c and P/A ratio) recover much more slowly. Though not unexpected, these differences in recovery rate suggest that, in order to represent the severity of the injury fairly (vis a-vis time to complete recovery), the unique geometry of the injury should be captured in order to provide a reasonable assessment of the recovery potential. Both models shown here can capture unique geometry in a straightforward manner; and when the empirical recovery rate data are applied, a process is created wherein a rapid and accurate assessment of recovery can be attained. Lacking trained surveyors, a differential GPS with sub-metre accuracy, or metric aerial photography geo-corrected (all of which would yield a spatially explicit injury shape), a rough estimate of E_c can be obtained during field surveys, but this represents a comparatively coarse assessment of injury geometry and, thus, characterization of the recovery scenario. Accuracy is expected to decline linearly with increasing P/A ratio of the injury.

In both the ArcINFO and SAS models, the recovery is essentially deterministic because each iteration of the model equals a 1 m forward step of encroachment. The SAS model differs from the ArcINFO version only in that each cell is examined for the presence of a vegetated neighbour upon each iteration of the model, rather than computing a cost/distance value as is done in the ArcINFO model. A consistent

Copyright © 2004 John Wiley & Sons, Ltd.

characteristic of the model simulations is that the number of boundary cell edges initially increases as the complexity of the injury boundary increases (not shown). This is because we have started with geometrical objects (circles, square, and rectangles) with relatively simple boundaries, but with different P/A ratios. However, that need not be the case. This simulation approach can likely accommodate an injury of any shape and with a very rough, irregular boundary as well. In both cases, the more convoluted (more perimeter or edge) an injury is, the faster the recovery is, and the simulation models are unlimited in their spatial or temporal dimensions, are entirely flexible with regard to rate of change, and can theoretically accommodate any set of initial conditions in terms of size, shape and boundary complexity of a hypothetical injury or a real injury. However, such scaling does not account for ecological realities, such as susceptibility of a site to subsequent disturbances, that can quickly reset the colonization process to zero, such as extreme storm events or additional groundings.

Case study

The case study described here demonstrates the convergence of these two modelling approaches (Figure 6). While the propeller scars would heal rather rapidly, the footprint of the fuel barge on the seagrass bed has created a fairly large area with moderately complex margins. We presume, based on the model responses (Figures 3 and 4; Table 2), that the long recovery here is driven by the extent of the injury and that the effects of the moderately convoluted edges are small in facilitating the recovery process. In any event, users of this approach can choose to apply either the SAS- or ArcINFO-based versions of the model (a choice likely driven by the user's familiarity with these software packages) with the confidence that, at the current level of model sophistication, either approach will yield virtually identical results.

Balancing fair and reasonable with biological reality

Despite seagrass beds being a comparatively simple structure when compared with other nearby communities, such as coral reefs, the recovery of seagrass bed injuries has several issues that must be considered in order to develop and implement these models as part of the injury assessment and restoration process. Because application of these models will result in enforcement action that may be challenged in litigation, careful attention must be paid to the standard of 'fair and reasonable', which is a general metric applied by the courts. Although numerous additional ecological factors could be explicitly considered if empirical information were available, the reasonableness standard dictates a less complicated approach. Because our goal was to establish a robust, but understandable process for injury assessment, we chose not to include or manipulate many factors that have great interest to research ecologists (e.g. mortality); the product was designed to be consistent with the needs of resource managers, at the expense of pursuing more scientifically challenging issues. Below, we discuss the potential influence of several ecological factors on the application of these spatially explicit models to real-life assessment of seagrass injuries.

Scar depth

The excavation experiment data predict linear recovery rates of *T. testudinum* averaging 10.5 years for two recruiting faces (on opposite sides of a 1 m scar) to yield 100% recovery of above-ground portions of the seagrass (Kenworthy *et al.*, 2002). These rates were much slower than rates reported in the literature for *T. testudinum* in Tampa Bay (Durako *et al.*, 1992). However, the work in Tampa Bay was in shallow excavations and a firmer substrate of different mineral composition (siliceous in Tampa Bay versus carbonate in the FKNMS). The rates for *T. testudinum* (Kenworthy *et al.*, 2002) are also much slower than suggested by Zieman (1976) for Florida Bay, although there were little quantitative data in that paper to support the recovery estimates. However, it seems clear that the depth to which an injury occurs may strongly influence the ability of certain seagrass species to recover if they have only a limited capability for

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

vertical growth. All the recovery rate data input into the model are compiled from fairly shallow scars, most with scar depths less than 0.2 m. Our preliminary findings from ongoing research in the FKNMS indicate that, when scar depth is >0.2 m in a *T. testudinum* meadow, the recovery rate is reduced dramatically, perhaps to as little as 25% of the rates we are using (Kenworthy *et al*., 2002). This may be due to changes in the sediment geochemistry, which may negatively affect growth. Recent findings by Terrados (1997) suggest that exposure to light inhibits seagrass rhizome apical extension, and this is precisely the situation that would occur as *T. testudinum* rhizomes emerge from the wall of a scar while colonizing an injury site. Therefore, the data we have used most likely overestimate the actual recovery rate in deeply excavated scars.

Above- versus below-ground recovery

Our models are based on recovery of above-ground components of the seagrass (Fonseca *et al*., 2000). In the case of frequently injured, climax species, *T. testudinum*, the living below-ground component may be four times that of the above-ground portion being modelled here. The generation of this extensive rhizosphere mass appears to lag far behind that of the above-ground portions (Kenworthy, unpubl. data) as, typically, it is destroyed during the scarring and grounding process, especially at sites with deep excavations (Whitfield *et al*., 2002). Pioneering species, such as *H. wrightii* and *S. filiforme*, do not have as large an above- to below-ground ratio and do not exhibit this lag of below-ground development nearly as dramatically as the climax species (pers. obs.).

Application of this model in a vessel grounding on a mixed-species community would require additional adjustments to the results based on the species composition of the seagrass. We can give credit for recolonization by pioneering species (e.g. *H. wrightii* and *S. filiforme*) when the injury has been in the climax, *T. testudinum*-dominated beds and these pioneering species are found in the adjacent, undisturbed population (>1% of the population). This credit may be determined by rerunning the spatial recovery models at the higher recovery rates (Table 1), and the benefit of this rapid recolonization is set against the slower *T. testudinum* recovery after weighting for differences in the above-below-ground ratios of the species. If this weighting were not performed, then we would be granting 100% recovery of a *T. testudinum* bed by pioneering species (not the dominant species that was injured) and with comparatively little below-ground biomass.

Disturbance events

The 'realism' of the model could be improved by incorporating random mortality of seagrass cells that might arise from various sources, such as bioturbation or aperiodic storms (*sensu* Whitfield *et al*., 2002). The seasonality of seagrass growth, although not a large factor in recovery of FKNMS seagrass resources (Fonseca *et al*., 1987), was not considered. However, it would be relatively simple to introduce seasonality to the process by systematically varying an embedded selection threshold (chosen from a probability function) over the number of time steps specified for a year. We plan to explore a stochastic simulation approach arising from this work that will incorporate mortality estimates, disturbance events, and various ecological factors (e.g. light, sediment type, bottom slope) that, at this time, await empirical evaluation for their effects on the recovery function. However, we expect that many of these factors would tend to slow recovery over the recovery predicted by our models, suggesting that application of the current model structures represents optimistic recovery scenarios.

Effects of seed recruitment on recovery

Recruitment of *T. testudinum* seedlings has the potential to hasten the recovery process but was not included in our modelling efforts. Recent empirical observations at some grounding sites suggest a potentially important role of seedlings (authors' pers. obs.); however, this is a highly variable process. The

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

passage of storms was seen to virtually eliminate seedlings that recruited within 4–5 years prior to a Category Two hurricane (Whitfield *et al.*, 2002). Therefore, we saw no compelling reason to build this into the model given that scar depth, below-ground recovery and disturbance were absent as well. This is not to say that seedlings could never enhance the recovery process; but, as a rule, increased recovery arising from seedling colonization for the tropical species are not well described (Fonseca *et al.*, 1998). Thus, the role of seedling recolonization in restoration efforts is still being evaluated (Whitfield *et al.*, 2002).

Fair versus reasonable

Seagrass ecosystems are an important natural resource for which the National Oceanic and Atmospheric Administration (NOAA) has stewardship authority in the FKNMS and other areas under federal jurisdiction. As part of its responsibility, NOAA is mandated to pursue compensation from the RP that has damaged natural resources. An estimate of the recovery rate for injured resources is required in order to compute compensatory restoration, justify recovery of a claim sufficient to institute effective restoration and, if necessary, prevail in litigation (Fonseca *et al.*, 2000). We have cited several ecological factors that would alter the recovery beyond that which is incorporated into the models that we have developed. In addition, we note one factor (seeding) that could accelerate the recovery. However, Whitfield *et al.* (2002) demonstrated that periodic disturbance events can eliminate any gains from seeding events. On the whole, it appears that we err heavily on the side of the RP if the model is applied without incorporation of these various factors. This work awaits further analysis to determine whether any differences resulting from inclusion of the aforementioned ecological factors are substantial enough to elicit different levels of compensatory restoration in the face of discounting techniques utilized in the computation of Habitat Equivalency Analysis (Fonseca *et al.*, 2000), an injury assessment tool that has emerged as the mainstay of NOAA's damage assessment strategy. Nonetheless, given the favourable bias towards the RP, this model is now being employed in the assessment of groundings in seagrass beds within the FKNMS.

Application to other trust resources

The models discussed thus far consider the colonization of an injury as arising only from lateral extension of shoots and rhizomes into uncolonized cells. As long as the rate at which colonization occurs can be determined, then the models apply directly to any resource exhibiting similar colonization strategies. Moreover, these models could easily be modified to incorporate propagules, such as from seeding events or recruitment of vegetative fragments transported into an injury site. Candidate habitats for application of these models include corals, salt marsh, macroalgal communities and mangroves. Thus, this approach should be amenable to simulating combined propagule and vegetative encroachment if needed.

ACKNOWLEDGEMENTS

We would like to thank Manuel Merello, Kamille Hammerstrom and Art Schwarzschild for their assistance in the field, and helpful comments in review and figures by Christine Addison, Donald Field, Greg Piniak, Patti Marraro and Amy Uhrin. The paper was materially improved by the sagacious comments of the outside reviewers S. Bell and B. Robbins (anonymity waived) and the editor, J. Baxter. This research was supported by grants from NOAA's Damage Assessment Center, NOAA's Office of National Marine Sanctuaries and base support by CCFHR.

REFERENCES

Bell SS, Hicks GRF. 1991. Marine landscapes and faunal recruitment: a field test with seagrasses and copepods. *Marine Ecology Progress Series* **73**: 61–68.

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

Bell SS, Robbins BD, Jensen SL. 1999. Gap dynamics in a seagrass landscape. *Ecosystems* **2**: 493–504.

Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO. 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation* **100**: 115–123.

Bell SS, Hall MO, Soffian S, Madley K. 2002. Assessing the impact of boat propeller scars on fish and shrimp utilizing seagrass beds. *Ecological Applications* **12**: 206–217.

Connell JW, Keough MJ. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrata. In *The Ecology of Natural Disturbance and Patch Dynamics*, Pickett S, White P (eds). Academic Press: Orlando, FL; 125–151.

Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**: 1119–1144.

Dawes CJ, Andorfer J, Rose C, Uranowski C, Ehringer N. 1997. Regrowth of the seagrass *Thalassia testudinum* into propeller scars. *Aquatic Botany* **59**: 139–155.

Durako MJ, Hall MO, Sargent F, Peck S. 1992 . Propeller scars in seagrass beds: an assessment and experimental study of recolonization in Weedon Island State Preserve, Florida. In *Proceedings of the 19th Annual Conference on Wetlands Creation and Restoration*, Webb WJ (ed.). 14–15 May , Hillsborough Community College, Tampa, FL.

Fonseca MS, Thayer GW, Kenworthy WJ. 1987. The use of ecological data in the implementation and management of seagrass restorations. *Florida Marine Research Institute Publication* **42**: 175–188.

Fonseca MS, Kenworthy WJ, Courtney FX, Hall MO. 1994. Seagrass planting in the southeastern United States: methods for accelerating habitat development. *Restoration Ecology* **2**: 198–212.

Fonseca MS, Kenworthy WJ, Courtney FX. 1996. Development of planted seagrass beds in Tampa Bay, Florida, U.S.A.: I. Plant components. *Marine Ecology Progress Series* **132**: 127–139.

Fonseca MS, Kenworthy WJ, Thayer GW. 1998. Guidelines for mitigation and restoration of seagrass in the United States and adjacent waters. NOAA COP/Decision Analysis Series #12. National Oceanic and Atmospheric Administration, Silver Spring, MD.

Fonseca MS, Julius BE, Kenworthy WJ. 2000. Integrating biology and economics in seagrass restoration: how much is enough and why? *Ecological Engineering* **15**: 227–237.

Guichard F, Bourget E, Robert JL. 2001. Scaling the influence of topographic heterogeneity on intertidal benthic communities: alternate trajectories mediated by hydrodynamics and shading. *Marine Ecology Progress Series* **217**: 27–41.

Hovel K, Lipcius R. 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. *Ecology* **82**: 1814–1829.

Irlandi EA. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* **98**: 176–183.

Irlandi EA. 1996. The effects of seagrass patch size and energy regime on growth of a suspension feeding bivalve. *Journal of Marine Research* **54**: 161–185.

Irlandi EA. 1997. Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* **78**: 511–518.

Irlandi EA. Crawford MK. 1997. Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* **110**: 222–230.

Irlandi EA, Ambrose WG, Orlando BA. 1995. Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. *Oikos* **72**: 307–313.

Irlandi EA, Orlando BA, Ambrose WG. 1999. Influence of seagrass habitat patch size on growth and survival of juvenile bay scallops, *Argopecten irradians concentricus* (Say). *Journal of Experimental Marine Biology and Ecology* **235**: 21–43.

Kenworthy WJ, Fonseca MS, Whitfield PE, Hammerstrom K. 2002. Analysis of seagrass recovery in experimental excavations and propeller scar disturbances in the Florida National Marine Sanctuary. *Journal of Coastal Research* **37**: 75–85.

Levin SA. 1978. Pattern formation in ecological communities. In *Spatial Pattern in Phytoplankton Communities*, Steele JH (ed.). Plenum Press: New York; 433–465.

Loucks OL, Plumb-Mentjes ML, Rogers D. 1985. Gap processes and large–scale disturbances in sand prairies. In *The Ecology of Natural Disturbance and Patch Dynamics*, Pickett STA, White PS (eds). Academic Press: Orlando, FL; 72–83.

Marba N, Duarte CM. 1998. Rhizome elongation and seagrass clonal growth. *Marine Ecology Progress Series* **174**: 269–280.

Miller TE. 1982. Community diversity and interactions between the size and frequency of disturbance. *American Naturalist* **120**: 533–536.

Paine RT, Levin SA. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**: 145–178.

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

Pickett STA, White SP (eds). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press: Orlando, FL.

Sargent FJ, Leary TJ, Crewz DW, Kreuer CR. 1995. Scarring of Florida seagrasses, assessment and management options. FMRI Technical Report TR-1. Florida Department of Environmental Protection, St Petersburg, FL.

Sousa WP. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* **49**: 227–254.

Sousa WP. 1985. Disturbance and patchy dynamics on rocky intertidal shores. In *The Ecology of Natural Disturbance and Patch Dynamics*, Pickett STA, White PS (eds). Academic Press: Orlando, FL; 101–124.

Terrados J. 1997. Is light involved in the vertical growth response of seagrasses when buried by sand? *Marine Ecology Progress Series* **152**: 295–299.

Uhrin AV, Holmquist JG. In press. Effects of propeller scarring on macrofaunal use of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series*.

Watt AS. 1947. Pattern and process in the plant community. *Journal of Ecology* **35**: 1–22.

Whitfield PE, Kenworthy WJ, Hammerstrom K, Fonseca MS. 2002. The role of storms in the expansion of disturbances initiated by motor vessels in subtropical seagrass banks. *Journal of Coastal Research* **37**: 86–99.

Whittaker RH, Levin SA. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* **12**: 117–139.

Williams SL. 1987. Competition between seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. *Marine Ecology Progress Series* **35**: 91–98.

Williams SL. 1990. Experimental studies of Caribbean seagrass bed development. *Ecological Monographs* **60**: 449–469.

Zieman JC. 1976. The ecological effects of physical damage from motor boats on turtle grass beds in southern Florida. *Aquatic Botany* **2**: 127–139.

UNCORRECTED PROOF

Copyright © 2004 John Wiley & Sons, Ltd.

John Wiley & Sons Ltd
The Atrium, Southern Gate, Chichester West, Sussex PO19 8S

Author Queries For AQC 610

While preparing this paper/manuscript for typesetting, the following queries have arisen

Query No	Proof Page / line no	Details required	Authors Response
1	3/27	Check changes ,clarify made is sense?	
2	3/27	Pl. update (Uhrin and Holmquis, inpress.)	
3	11/32	From T2 this looks like P/A< or =0.2(not<0.2),Ec<10 and P/A>0.2,Ec > or =10. Clarify.Something wrong anywere it seems,since you have to stateP/A for Ec>10 whatever its value.	
4	15/16	"but" makes no sense here, check change/clarify.	
5	18/9	Pl. update. Ref.(Uhrin AV,)	