LETTER

A mechanistic assessment of the potential ecological risk to seagrass meadows posed by marine echosounders

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Abstract

Motivated by experimental evidence, a mechanistic model is used to investigate the impact of marine echosounder transmissions on seagrass leaves. The interaction of the ultrasonic field with the seagrass is solved within the leaf cross-section. The leaf tissue is assumed to be elastic, homogeneous and isotropic, with embedded cavities representing lacunae. A standard Galerkin finite element method is employed to numerically solve the resulting equations. Natural vibration frequencies are computed for leaves of Halodule wrightii and Syringodium filiforme. Strong perturbations in the leaf structure are expected when natural and echosounder frequencies match. The results reveal that a significant number of natural frequencies are within or near the typical frequency bands of echosounder operations. In addition, stresses in the leaf tissues of seagrass at 20 m depth were computed in a typical scenario for echosounder operations. Leaf-tissue damage in S. filiforme could result under these conditions. Within the framework of the theoretical assumptions, the results highlight the potential and, until now, unnoticed risks to seagrass meadows posed by marine echosounders.

1. Introduction

Seagrasses are a key component of many marine coastal regions worldwide (Orth et al. 2006). Ecologically, they constitute the habitat of diverse species (Duffy 2006, Heck et al. 2008), improve the water quality conditions in coastal regions (Denninson et al. 1993, McGlathery et al. 2007) and represent an important carbon sink (Duarte et al. 2005, Fourquarean et al. 2012) and nitrogen cycletzer (Zarnoch et al. 2017) in marine areas. Seagrass meadows are not exempted of anthropogenic disturbances in coastal environments which have resulted in reductions in their populations (Duarte 2002, Orth et al. 2006, Waycott et al. 2009). Degradation of water quality, increased loading of sediment, contaminants and nutrients from both diffuse and point sources, eutrophication, introduction of nonnative species and dredging and boating effects are some anthropogenic stressors behind seagrass declines (Orth et al. 2006). The identification and quantification of the different anthropogenic pressures on seagrass meadows is required for their present and future preservation. Unfortunately, relevant anthropogenic stressors on seagrass meadows may remain unnoticed.

Seagrass leaves generally present a large number of areal spaces, or lacunae, surrounded by mesophyll tissue (Kuo and den Hartog 2006). Lacunae allow the accumulation and pressure-driven flow of gases resulting from photosynthetic activity. These cavities interconnect all vegetative and reproductive organs in the seagrass, but the cavities are interrupted by septa between organs (Kuo and den Hartog 2006). Lacunae differ in cross-sectional size (hundreds of μm) and shape (circular to elliptical) among species (Kuo and den Hartog 2006, Wilson and Dunton 2009). These areal spaces comprise 4% to 30% of the leaf cross-sectional area (Grice et al. 1996).

Gas bodies in biological tissues can energetically pulsate when insonified under suitable conditions, a phenomenon termed gas-body activation (Miller 1977). Despite the terminology, these oscillations are often associated more with the natural vibration modes and frequencies of the elastic structure where the cavity is
embedded with the pulsation of gas (Miller 1984). Under external periodic excitation at natural frequencies, the structural vibration amplitudes increase significantly (resonance), which, due to the occurrence of stresses with a large absolute magnitude, can lead to a decrease in strength, cracking, or even destruction of the biological tissue near the cavity wall. Specifically, Miller and Thomas (1993) experimentally found that ultrasonic activation of gas channels enclosed by cell walls in *Elodea* leaves resulted in plant-tissue damage. Due to the small size of these gas bodies (approximately 10 μm), the ultrasound frequencies ranged from 0.7 to 15 MHz. The observed thresholds for plant-tissue damage ranged from 50 Pa and 6 kPa for ultrasound durations of 5 min and 30 s, respectively (Miller and Thomas 1993). Similarly, gas-body activation of lacunae in seagrass leaves can occur if the marine environment is sonified with frequencies close to the lacunae natural frequency. The strong acoustic backscatter from seagrass observed at high frequencies (>80 kHz) during seafloor acoustic surveys provides indirect evidence of gas-body activation (Lyons and Abraham 1999, McCarthy, Sabol (2000), Komatsu et al. 2003).

Echosounders are widespread acoustic devices used for hydrography, seafloor mapping, fish-finding and navigation safety. These acoustic systems operate at frequencies with typical values of 12, 24, 30, 38, 50, 80, 100, 120 or 200 kHz. (Lurton and DeRuiter 2011). Low (high) frequencies are usually selected in deep (shallow) water operations. Systems dedicated to very shallow water depths (few metres) can operate at nominal frequencies above 200 kHz (300, 400 or 450 kHz; Lurton 2016). The associated bandwidths are approximately 10 kHz. The transmission geometry is described by a main lobe of acoustic radiation with a small angular aperture (5° to 15°) and spurious sidelobes 20 dB to 30 dB below the intensity of the main lobe. The maximal transmit power may be as high as 230 dB re 1 μPa @1 m. The pulse duration is approximately 0.1% to 1% of the two-way travel time from the source to the seafloor. Duty cycle values also range from 0.1% to 1%. Multibeam echosounders transmit pulses in the vertical plane perpendicular to the ship’s axis and adjacent sectors to widen the along-track angular aperture. These systems can sonify with across-track apertures up to 150°. Interested readers are referred to Lurton and DeRuiter (2011) and Lurton (2016) for a concise review of this subject. Regarding the potential effects of echosounders on ecosystems, Lurton and DeRuiter (2011) conclude that despite the high power transmitted by these acoustic devices, the short duration of their pulses and their high spatial directivity make these systems unlikely to cause physiological injuries to marine fauna. However, field studies suggest that some marine fauna may respond to echosounder signals even though the operating frequency is above their hearing range (Hastie et al. 2014, Cholewiak et al. 2017, Quick et al. 2017).

Whether marine echosounders constitute an anthropogenic stressor to seagrasses remains, to the author’s knowledge, an unexplored issue. This article argues that these popular acoustic systems could have significant bio-effects on seagrass meadows. The high directivity and power levels transmitted by these devices could represent a risk if acoustic beams are radiated in the range of the natural or resonance frequencies of lacunae. In this study, lacunae resonance frequencies are computed for realistic geometries of cross-sections of *Halodule wrightii* and *Syringodium filiforme* leaves. The two species exemplify marine angiosperms with low and high plant-tissue rigidity, respectively (Touchette et al. 2014). The interaction of the ultrasonic field with the leaf is studied in the framework of linear elastodynamics. The theoretical equations are numerically solved using a finite element approach.

### 2. Methods

The leaves of *H. wrightii* are thin, flat and tinsel-like and are typically 10–30 cm in length. The larger lacunae are cylindrical in cross-section, with diameters of approximately 100 μm. These lacunae are symmetrically located with respect to the central axis of the leaf cross-section (figure 1(a)). *H. wrightii* is a marine species with surprisingly elastic tissue. *H. wrightii* elastic modulus, depicting the flexibility of plant tissue, is approximately 1 MPa (Touchette et al. 2014). The leaf blades of *S. filiforme* are cylindrical in cross-section and are up to 50 cm in length. Their larger lacunae have an approximate elliptical cross-section with major and minor axes of approximately 200 μm and 125 μm, respectively (figure 1(b)). Cavities with a major axis aligned with the radial direction surround the centre of the leaf cross-section. The elastic modulus of the *S. filiforme* tissue is approximately 30 MPa and is one of the most rigid tissues among seagrass species (Touchette et al 2014).

Theoretically, the geometry of the leaves of *H. wrightii* and *S. filiforme* can be described as a very slender structure oriented along the vertical axis with a length much greater than the cross-section area. Mathematically, the strains associated with the vertical length are assumed to be small compared to the cross-sectional strains, since they are constrained by the nearby material (plain strain). This assumption reduces the analysis of the ultrasound-leaf interaction to a two-dimensional problem within the leaf cross section. Moreover, it is also assumed that leaf tissues are constituted by a linearly elastic, homogeneous and isotropic material. Under these assumptions, the ultrasound-leaf interaction is mathematically described as follows:
\( \rho \frac{\partial^2 \mathbf{u}}{\partial t^2} = \nabla \cdot \mathbf{\sigma} \) \hspace{1cm} (1)

where \( \rho \) is the tissue density, \( \mathbf{u}(t) = [u_x(x, y, t) \ u_y(x, y, t)] \) is the displacement vector of material points with respect to time \( t \) and \( \mathbf{\sigma} \) is the symmetric stress tensor. Equation (1) is completed with the constitutive equation:

\[ \mathbf{\sigma} = D \mathbf{\varepsilon} \] \hspace{1cm} (2)

With

\[
D = \begin{bmatrix}
\lambda + 2\mu & \lambda & 0 \\
\lambda & \lambda + 2\mu & 0 \\
0 & 0 & \mu
\end{bmatrix}
\]

\[
\sigma = \begin{bmatrix} \sigma_{xx} & \sigma_{xy} & \sigma_{xz} \end{bmatrix}^T; \quad \mathbf{\varepsilon} = \begin{bmatrix} \varepsilon_{xx} & \varepsilon_{xy} & \varepsilon_{xz} \end{bmatrix}^T
\]

\[
\sigma_{xx} = \frac{\lambda}{2(\lambda + \mu)} (\sigma_{xx} + \sigma_{yy})
\]

\[
\varepsilon_{xx} = \frac{\partial u_x}{\partial x}, \quad \varepsilon_{xy} = \frac{\partial u_y}{\partial x}, \quad \varepsilon_{xz} = \frac{\partial u_z}{\partial x}
\]

where \( \lambda \) and \( \mu \) are the Lamé parameters. These are derived from the previously reported bulk elastic modulus and a Poisson ratio of 0.3 (Enenstein et al. 2013). Geometrically, the strain component \( \varepsilon_{ii} (i = x, y) \) is the relative change in length along the \( x_i \)-axis, whereas \( \varepsilon_{xy} \) is proportional to the change in angle between the initially orthogonal coordinate axes \( x \) and \( y \). When strains are small, equation (2) assumes that the relation between the stress and the strain tensors is approximately linear (Hooke’s law). The model described by equations (1) and (2) is supplemented by boundary conditions to obtain a unique solution of the deformation field \( \mathbf{u}(x, y, t) \).

A constraint on the normal stress (Neumann boundary condition) is prescribed at the external boundary of the leaf. The boundary condition takes the form \( \sigma \cdot \mathbf{n} = -P(t) \cdot \mathbf{n} \), where \( \mathbf{n} \) is the outward unit normal on the boundary and \( P(t) \) is the overall pressure generated by the water column and the ultrasound field. At the lacunae wall, boundary conditions are either \( \sigma \cdot \mathbf{n} = 0 \) (where \( \mathbf{n} \) is the outward unit normal on the internal boundary) when there is no internal pressure or \( \left( \sigma + Z_g \frac{\partial u}{\partial n} \right) \cdot \mathbf{n} \bigg|_{\text{internal}} = 0 \) when the lacunae are pressurized. In the latter, \( Z_g \) is the acoustic impedance for the gas at the internal boundary wall (Bird et al. 1960).

Leaves of \( H. wrightii \) and \( S. filiforme \) are assumed to be at a depth of 20 m in the numerical simulations, which is the lower depth limit for both species (Short et al. 2010a, b). Thus, the leaf tissue is subjected to a constant compressional load \( P_w \) of 300 kPa due to the pressure of the water column. A maximal lacunae pressure \( P_l \) of approximately 10 kPa was reported for \( S. isoetifolium \) and \( H. ovalis \) (Brodersen et al. 2018). In the absence of data, this value of the maximal lacunae pressure is also assumed for \( H. wrightii \) and \( S. filiforme \).
An acoustic pressure load $P_E(t) = P_e \sin(\omega t)$ (where $P_e$ and $\omega$ are the amplitude and frequency, respectively) transmitted from a virtual echosounder at the sea surface is added to $P_w$. The source level of the echosounder is assumed to be 230 dB re 1 $\mu$Pa @ 1 m, which implies a pressure amplitude $P_e$ of 16 kPa at 20 m depth. Due to linearity, the problem of the leaf-ultrasound interaction equation (1) can be split into the determination of the tissue deformation $u_o(x, y)$ due to the static pressure field $P_w$:}

$$\nabla \cdot \sigma_o = 0; \quad \sigma_o \cdot n_{\text{external}} = -P_e \cdot n_{\text{external}}; \quad \left\{ \begin{array}{l} \sigma_o \cdot n_{\text{internal}} = 0 \quad \text{or} \quad \sigma_o \cdot n_{\text{internal}} = -P_e \cdot n_{\text{internal}} \end{array} \right.$$ (3)

The determination of the tissue deformation $u_b(x, y, t)$ due to the acoustic load $P_b(t)$ can be expressed as follows:

$$-\rho \omega^2 u_e = \nabla \cdot \sigma_e; \quad \sigma_e \cdot n_{\text{external}} = -P_e \cdot n_{\text{external}}; \quad \left\{ \begin{array}{l} \sigma_e \cdot n_{\text{internal}} = 0 \quad \text{or} \quad \sigma_e \cdot n_{\text{internal}} = -P_e \cdot n_{\text{internal}} \end{array} \right.$$ (4)

where the time harmonic dependence $u_b(x, y, t) = u_b(x, y) \sin(\omega t)$ and $\sigma_e(x, y, t) = \sigma_e(x, y) \sin(\omega t)$ are considered. The time harmonic dependence is justified by the fact that most echosounders transmit pulses defined by continuous wave (CW) signals (sine waves at a nominal frequency and with a time-limited amplitude). Moreover, pulses are about 20–200 cycles long with duty cycles of the order of a few thousandths (Lurton 2016). Miller (1977) reported for Elodea leaves that pulse exposures with 10 cycles long and duty cycles of $10^{-4}$, already have cell death thresholds near those for CW exposures with the same on-time. For a generic $\omega$, equation (4) defines a continuous eigenvalue problem for the pair $(u_b, \omega)$. The eigenvalues correspond to the natural resonance frequencies of the plant cross-section. Strong deformations in the tissue structure are expected when the tissue is insonified with frequencies close to the natural frequencies. Finally, the total deformation field and stress are given by $u(x, y, t) = u_o(x, y) + u_b(x, y) \sin(\omega t)$ and $\sigma(x, y, t) = \sigma_o(x, y) + \sigma_e(x, y) \sin(\omega t)$, respectively.

A standard Galerkin finite element method has been employed to spatially discretize equations (3) and (4). To do so, the leaf geometry is subdivided into a finite number of area elements (triangles). The corners of the elements are called nodes. The discretization of equations (3) and (4) results in an algebraic system of equations for the values of the displacement field at the nodes. Once solved, low-order piecewise polynomials are usually employed to interpolate the solution from the nodes to other locations of the physical domain. The specific mathematical expressions of the procedure are not replicated here, as they can be found in textbooks about finite elements (e.g., Dhatt and Touzot 1984, Zienkiewicz and Taylor 1995).

3. Results

According to the finite element methodology, the domain geometry of the leaf of $H$ wrightii was tessellated into 7526 triangular elements with characteristic sizes ranging from 2.5 $\mu$m near the cavity surface to 9.4 $\mu$m at the external boundary (figure 2(a)). Similarly, a mesh with 13 300 triangular elements and resolutions between 6.7 $\mu$m and 19.6 $\mu$m was employed to discretize the leaf of $S$ filiforme (figure 2(b)). Computational leaf representations capture the main geometrical aspects of the cross sections displayed in figure 1.

Natural frequencies of oscillations are first computed for each leaf and pressurized condition, considering the corresponding elastic parameters previously mentioned. Only the first ten natural frequencies were computed, since they are the frequencies within the spectral range of interest. For $H$. wrightii, natural oscillation frequencies range between 20 kHz and 200 kHz under unpressurized conditions (figure 3(a)). The results reveal that a significant number of natural vibration frequencies are within or near the frequency bands typical of echosounder operations. A similar situation is found under lacunae pressurization (figure 3(a)).

Natural oscillations of $S$. filiforme occur at higher frequencies than the oscillations in the previous case (figure 3(b)). This results from the rigidity of the biological tissue in this seagrass species. Comparisons of natural frequencies under unpressurized conditions with the spectral operation bands of echosounders show that the former are within or near the range of the latter, except for the three last oscillation modes. Moreover, figure 3(b) shows a substantial overlap between natural vibrations and echosounder frequencies for this seagrass species. A significant number of natural frequencies lie within or near the frequency bands of 200 kHz and 400 kHz, whether the lacunae are pressurized or not. The former is the frequency band in which the navigation echosounders normally operate.

Forces and torques have been computed for leaves at 20 m depth excited with ultrasound transmissions at 200 kHz with a power of 230 dB re 1 $\mu$Pa @ 1 m. As previously indicated, this setup corresponds to a typical
configuration for echosounder operations in shallow regions. An equivalent tensile (or von Mises) stress $\sigma_M$ is derived from the resulting forces and torques (Sadd 2014). This magnitude encodes different components of the stress into a scalar tensile stress that generates an equal distortion energy in the material. The equivalent tensile stress facilitates comparison with experimental data.

No significant differences were found between the unpressurized and pressurized cases at the excitation frequency considered here, and for this reason, only results from the former case are shown. Figure 4(a) displays the deformation field resulting from the cross-section of $H. wrightii$ at the most stretched stage. Most of the observed deformation results from the compression of the flexible tissue induced by the water column. The highest amplitudes of $\sigma_M$ are located between lacunae, where the curvature of the distorted lacunae boundary is maximum. Stress amplitudes can exceed 0.7 N mm$^{-2}$ at these locations. This value is below the tensile strength, the maximum stress that a material can withstand while being stretched before tearing, as measured for the leaf tissues of other $Halodule$ species (4.36 ± 1.36 N mm$^{-2}$, De los Santos et al 2012).

Similar computations were performed for the leaf cross-section of $S. filiforme$ (figure 4(b)). Unlike the case of $H. wrightii$, the rigidity of the leaf tissue prevents the appearance of large deformations under compression. The highest amplitudes of the equivalent tensile stress are located in the inner region determined by the lacunae internal vertices around the leaf geometric centre. Points of high stress amplitudes are also found at the external vertices of the lacunae. The maximum stress amplitude of 0.8 N mm$^{-2}$ is in the range of the tensile strength reported for the leaf tissues of other $Syringodium$ species (0.69 ± 0.39 N mm$^{-2}$, De los Santos et al 2012). Thus, plant-tissue damage could result under these conditions.

The variation in the highest amplitudes of $\sigma_M$ is not consistent with depth (figure 5). This is due to the different variations with depth of acoustic and water pressure loads. The former varies inversely as the square of the distance to the transmitter, while the latter increases linearly with depth. The acoustic pressure load

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Figure 2. Finite element grid for the computational geometry of the (a) $H. wrightii$ and (b) $S. filiforme$ leaf cross-sections. The scope of the figure is intended to provide an understanding of the resolution of the mesh.

Figure 3. Natural frequencies under internal unpressurized (triangles) and pressurized (squares) conditions for the (a) $H. wrightii$ and (b) $S. filiforme$ leaf cross-sections. Spectral bands of echosounder operations are displayed in grey.
dominates the stress at very shallow water depths (a few metres). At higher depths, stresses are mostly determined by the pressure load from the water column. A minimum in the highest amplitude value of $\sigma_M$ occurs at the transition between the previously described load regimes. This transition is observed at approximately 10 m depth in the present study (figure 5).

4. Discussion

The potential effects of echosounders on the seagrass population were analysed and quantified in this study. Natural oscillation frequencies of seagrass leaves were obtained based on a mechanistic model, near-real geometries and measured mechanical traits of leaf tissues. Specifically, the theoretical model assumes that leaf tissues are constituted by a linearly elastic, homogeneous and isotropic material. An advantage of this assumption is that its implementation is fully supported by the mechanical parameters reported in the literature (Touchette et al 2014). However, seagrasses show a complex leaf blade anatomy and ultrastructure. Seagrass leaves are generally characterised by the existence of cuticle, epidermis, fibres, mesophyll tissue and phyllospheres (Kuo and den Hartog 2006). These structures have different compositions and mechanical traits, and their
mechanical response could deviate from the assumed leaf elasticity when mechanical excitations exceed a certain threshold. Additional mechanical characterisations of the leaf tissue (e.g., dissipative and non-linear properties or the criteria for the onset of damage) would result in more accurate tissue models, but in the absence of suitable data, these must be presently ignored.

The model geometry, although realistic, simplifies the real geometry of the plant cross-section up to a certain scale. Specifically, small gas cavities and intercellular channels coexist with larger lacunae in seagrass leaves (Miller 1979, Kuo and den Hartog 2006). According to the size of these cavities, their resonance frequencies are well above (>1 MHz; Miller 1979) the range of frequencies of echosounder operations. Thus, their potential effects are negligible in the framework of this study. A model geometry that only includes those leaf structures that strongly interact with the ultrasound field transmitted by echosounders is a reasonable approximation.

Natural oscillation frequencies of the leaf cross-sections of H. wrightii and S. filiforme were computed within the previously discussed theoretical framework. H. wrightii and S. filiforme exemplify seagrass cases with more flexible and rigid leaf tissues, respectively. The size and shape of the lacunae of these species also differ. Despite their differences, computational results show significant overlaps between the natural frequencies and spectral bands of echosounder operations of both species. Overlaps mostly occur at frequency bands lower than 120 kHz for H. wrightii. Conversely, overlaps between natural and operating frequencies are concentrated at 200 kHz and 400 kHz for S. filiforme.

When the echosounder operates at the leaf natural frequency, all locations of the leaf cross-section vibrate at the same frequency, with a constant amplitude pattern and relative phase (natural vibration mode). The energy transfer from the echosounder transmission to the vibration mode is maximum. This resonance mechanism can perturb the tissue structure of the leaf. A plausible scenario was simulated to further investigate this issue. The results suggest two possible scenarios in which acoustic transmissions could result in stresses with a significant impact on tissue integrity. In very shallow conditions, the power levels transmitted by an echosounder at spectral bands near the lacunae natural frequencies induce strong forces and torques in the leaf tissue. At higher depths, the leaf structure is compressed by the dominant pressure of the water column. Despite the decrease in the acoustic pressure due to the distance from the source, this produces a stress field resulting from the pressure at depth, and the tensile strength of the tissue could be exceeded during the stretching phase. Locations of high curvature at the lacunae boundary and inter-lacunae spaces are where perturbations from echosounder transmissions are more prominent. This finding establishes a causal relationship between the stressor and its effect, indicating where to focus to determine the effects of echosounder transmissions in leaves.

Recreational boats are relatively small and powerful crafts that can access shallow and remote coastal areas due to their manoeuvrability and accessibility. Globally, the number of recreational boats has significantly increased with economic growth, and, consequently, their traffic has increased in nearshore areas (Burgin and Hardiman 2011). These nearshore areas are often marine wildlife habitats. As their visiting and anchoring sites are usually far away from other sources of anthropogenic impacts, recreational vessels tend to be a major source of anthropogenic impacts at these sites. For this reason, there has been increasing concern about their interactions with the nearshore marine environment (European Commission DG ENV 2007). A variety of mechanisms, including exhaust and other emissions, propeller contact, turbulence from propulsion systems, waves produced by movement, propeller noise, and anchoring, can mediate these interactions (Murphy and Eaton 1983, Wagner 1994, Mumma et al 1996, Abadie et al 2016). In turn, each of these mechanisms may have multiple effects on the marine ecosystem, including declines in submerged vegetation (Asplund and Cook 1997). Unfortunately, not all of the mechanisms by which recreational boating interacts with ecosystems have been elucidated. This may limit the effectiveness of environmental management for mitigating the harmful effects related to this anthropogenic activity.

For most recreational boats, an echosounder is considered an essential piece of navigation equipment. These devices are particularly helpful when approaching shallow waters and to support activities like fishing. Thus, nearshore regions of heavy recreational boating could be significantly exposed to echosounder ultrasound radiation. Seagrass meadows are among them. A rough estimate of the spatial scales potentially exposed to the ultrasound radiation can be obtained by considering the density of recreational boat traffic and assuming typical navigation parameters. For example, on the busiest day of the high season, Balaguer et al (2011) computed a total of 6082 recreational boats navigating around the Mallorca Island. The latter is the main island in the Balearic archipelago (Spain) where the largest community of Posidonia oceanica in the Mediterranean Sea is located. For an average depth of 20 m, a transmission angular aperture of 5° and transit time of 1 hour at 10 knots (5 m s⁻¹), the total area exposed to echosounder transmissions is about 200 km². In this case, a seagrass leaf would be exposed 0.35 s to ultrasound radiation under the passage of a recreational boat.

The findings of the present study suggest that marine echosounders transmissions could generate harmful effects on exposed seagrass meadows. The identification of this previously unnoticed anthropogenic stressor, results from a theoretical framework limited by the assumptions and idealizations required to make the problem tractable. In this regard, the study is intended to highlight the potential risk to seagrass meadows posed by
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