

Seagrass meadows provide an acoustic refuge for estuarine fish

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ABSTRACT: It has been widely accepted that fish reside within seagrass meadows because of the visual protection and structure provided by the standing biomass. However, for many larger species of estuarine fish, marine mammals that use echolocation to forage represent a significant threat. We hypothesized that seagrasses may serve as an acoustic refuge to fish from dolphin predators by sufficiently attenuating the high-frequency sounds used in echolocation. To test this hypothesis, we measured the attenuation of a 100 kHz acoustic signal with increasing distance into a seagrass meadow. The transmission loss of low-frequency sound energy relevant to fish calls (300 to 500 Hz) was also investigated to address the hypothesis that marine mammals may use passive acoustic detection to locate fish in vegetated substrates. Our results show that seagrasses attenuate high-frequency sounds during summer months and reduce prey detection thresholds by 58 to 88% relative to bare substrates. Also, based on the low-frequency hearing threshold of bottlenose dolphins, we calculated that dolphins are capable of detecting low-frequency fish calls within vegetation at a distance of roughly 2.3 to 4.2 m, which is within the detection threshold of 2.8 to 9.8 m for dolphins using echolocation. This study demonstrates that acoustically complex features, such as seagrass meadows, can significantly alter bioacoustic signal transmission, possibly providing an important seasonal refuge to fish from marine mammal predators.

KEY WORDS: Seagrass meadows · Acoustics · Echolocation

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INTRODUCTION

Estuaries are highly productive and represent a complex soundscape where marine mammals use high- and low-frequency sounds to communicate and find prey, while many fish species generate low-frequency calls used in communication (Ramcharitar et al. 2006, Rountree et al. 2006, Au & Hastings 2008). Although sound propagation is important in a variety of ecological relationships, very few studies to date have examined the biological significance of acoustic transmission loss within estuaries containing vegetated substrates. One such study, published by Quintana-Rizzo et al. (2006), examined the propagation

distance of low-frequency whistles used by dolphins over multiple substrate types. Quintana-Rizzo et al. (2006) showed that seagrass meadows caused increased attenuation of low-frequency (5 to 19 kHz) whistles, which significantly decreased effective communication distances. Consequently, it is logical to hypothesize that seagrass meadows attenuate the high-frequency clicks used by dolphins for echolocation, serving to provide fish an acoustic refuge from marine mammal predators.

Bottlenose dolphins *Tursiops truncatus* feed predominantly on fish that can be found within seagrass meadows, but the use of these meadows as foraging habitat is still under debate. Barros & Wells (1998)

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related the stomach contents of stranded bottlenose dolphins to shipboard feeding observations of the same species. These authors observed that pinfish *Lagodon rhomboides* dominated the diet of bottlenose dolphins and that foraging activity often occurred in the vicinity of seagrass beds. Later, Allen et al. (2001) documented the behaviors of foraging bottlenose dolphin groups from shipboard surveys, comparing foraging locations with measured abundances of pinfish within bare and vegetated substrates. They reported that dolphins foraged extensively on the edge of seagrass beds but rarely foraged in the middle of the vegetation despite higher concentrations of prey and hypothesized that submerged vegetation was limiting the success of prey capture (Allen et al. 2001).

Nowacek (2005) performed the first acoustic survey of bottlenose dolphin foraging near seagrass meadows, combining video observations with underwater acoustic recordings to document the types of calls used by dolphins in a variety of habitats. The lowest rates of echolocation were observed within vegetated substrates, and a low-frequency call, named a 'pop,' was observed in this dolphin population for the first time. Nowacek (2005) suggested that the cluttered seagrass environment might inhibit echolocation, and the pops, which are much lower in frequency than the echolocation clicks, may scare the fish out from the vegetation.

In addition to using echolocation, dolphins may also use passive acoustic detection to identify potential prey items. After investigating the stomach contents of stranded bottlenose dolphins, Barros & Wells (1998) noted that many of the consumed prey species were soniferous. This led the authors to hypothesize that dolphins are possibly using passive acoustic detection to locate sound-producing fish targets. Gannon et al. (2005) further examined this hypothesis by broadcasting recorded fish sounds underwater in the vicinity of bottlenose dolphins. The authors were able to demonstrate that dolphins traveled towards the sound source and increased their rate of echolocation in response to the acoustic signal. Gannon et al. (2005) concluded that dolphins are likely using passive acoustic detection for prey discovery, while relying on echolocation for prey capture.

Although no study has yet investigated the propagation of soniferous fish calls through submerged vegetation, several investigations have described the limits of acoustic propagation under natural field conditions. For instance, the propagation distance of the oyster toadfish *Opsanus tau* call is inhibited by shallow water depths, and is only audible to con-

specifics located within several meters of the sound source (Fine & Lenhardt 1983). The communication distance of gobies inhabiting freshwater streams is even further restricted (<1 m) by the extremely shallow depth and ambient noise produced by the moving water (Lugli & Fine 2003). On the contrary, damselfish *Dascyllus albisella*, which live in environments more conducive to sound propagation, produce a call that is audible to conspecifics up to 12 m from the sound source (Mann & Lobel 1997). Common sciaenid residents of estuarine waters include the red drum *Sciaenops ocellatus*, spotted seatrout *Cynoscion nebulosus* and Atlantic croaker *Micropogonias undulatus*. These fish also produce vocalizations that are audible to conspecifics at distances ranging from 8 m (Atlantic croaker) to 128 m (spotted seatrout) (Horodysky et al. 2008). The prominent vocalizations of these estuarine sciaenids have allowed investigators to document critical spawning habitats with the use of passive acoustic detection (Luczkovich et al. 2008, Walters et al. 2009).

The free gas contained within the lacunae system of seagrass plants and the bubbles produced during photosynthesis attenuate sound energy within seagrass meadows (Hermand et al. 1998). Field investigations continue to document the unique acoustic signature of seagrass beds relative to bare substrates (Pasqualini et al. 2000, Mulhearn 2001, Komatsu et al. 2003). Acoustic modeling efforts in the laboratory have demonstrated that the interaction of sound energy and seagrass tissue is both species-specific and biomass-dependent (Wilson & Dunton 2009, Wilson et al. 2010).

This study tested the hypotheses that (1) seagrasses attenuate sound energy in the frequency range that is used by dolphins for echolocation and (2) that low-frequency sounds propagate far enough within vegetation to enable passive acoustic detection of fish calls. These hypotheses were tested by measuring transmission loss of high- and low-frequency sound energy within bare and vegetated substrates in a shallow subtropical estuary. Our results suggest that seagrasses may provide an important seasonal refuge to fish where they are protected from the high-frequency echolocation clicks emitted by potential dolphin predators. Furthermore, detection limits of low-frequency sounds relevant to fish communication were within the range of detection thresholds measured for high-frequency echolocation, suggesting that passive acoustic detection of sound-producing fish targets does not represent a viable alternative to echolocation for dolphins foraging within seagrass meadows.

MATERIALS AND METHODS

Study site

Field experiments were conducted within the seagrass meadows of East Flats in Port Aransas, Texas, USA (27° 49' N, 97° 07' W). This location contains pristine populations of both turtle grass *Thalassia testudinum* and shoal grass *Halodule wrightii*, which were the focal species of vegetation examined in this work. Field experiments were conducted between the hours of 09:00 and 13:00 in light winds and calm seas during both February and June 2011. The water depth for all transmission loss measurements varied between 0.5 and 1.0 m (February = 0.85 to 1.0 m; June = 0.52 to 0.63 m). Salinity and temperature ranged from 32.7 to 37.3‰ and 20.1 to 29.8°C, respectively, throughout the entire study period, with little variation over each sampling date.

Transmission loss

High-frequency transmission loss experiments utilized 2 hydrophones (Reson Model TC4033) and a pulser/receiver system (Olympus 5073PR). Both hydrophones were secured to weighted polyvinyl chloride (PVC) stands at a height of 0.34 m above the sediment. These stands allowed for rapid relocation of the hydrophones while ensuring a constant vertical position above the sediment. The source hydrophone emitted a transient sound pulse, of 50 μ s in length, generated at a 200 Hz repetition rate by the pulser/receiver. This signal had a center frequency of 104 kHz and a half-power spectral bandwidth of 23 kHz, which resembles a bottlenose dolphin echolocation signal in open water (center frequency of 93 to 101 kHz and duration of 35 to 45 μ s; Au 1993 listed in Wahlberg et al. 2011). The receiving hydrophone was connected to the receive side of the pulser/receiver, which filtered (1 kHz to 20 MHz) and amplified the signal before reaching a digital storage oscilloscope. The acoustic pressure was obtained from the peak-to-peak amplitude of the average of 64 individual pulses that coincided with the direct path of acoustic transmission. Multiple pulses are received by the hydrophone from each transient acoustic signal, and these additional pulses are the result of an omnidirectional sound source that elicits surface and bottom reflections of acoustic signals on the path to the receiving hydrophone. Because a reflected acoustic pulse travels a

greater distance from the sound source to the receiver than a pulse traveling in a direct path, the reflected pulses arrive later in time. It was, therefore, possible to consistently identify and separate the direct path signal from the reflected signals arriving later in time.

A spherical spreading model provides a reasonable estimation of transmission loss for marine mammal clicks (DeRuiter et al. 2010). We, therefore, modeled acoustic transmission loss (TL) using Eq. (1), where R is the propagation distance and α is a coefficient representing the combined losses attributed to scattering and absorption. The α -value was obtained by using a nonlinear least-squares approach to fit a spherical spreading model (Eq. 2) to the observed data, where p is the observed acoustic pressure and p_0 represents the initial pressure amplitude. For completeness, we also attempted to model the observed transmission loss with a cylindrical spreading model, but the resulting implementation of this model was deemed inappropriate for our data.

$$TL = 20 \log R + \alpha R \quad (1)$$

where

$$p = (p_0/R) \times e^{-\alpha R} \quad (2)$$

Low-frequency transmission loss experiments used a frequency generator and an underwater speaker (Electrovoice UW-30) connected to a power amplifier. The speaker was mounted on a weighted frame at a height of 0.20 m above the sediment, and the receiving hydrophone was secured to a weighted PVC stand at a height of 0.34 m above the bottom. Low-frequency signals consisted of continuous 300, 400 and 500 Hz pure sine tones, which are relevant to the frequencies used by soniferous fish residents of seagrass habitats (Connaughton et al. 1997, Fine et al. 2004, Ramcharitar et al. 2006). Acoustic signals were transmitted in a direction parallel to the ocean bottom. The receiving hydrophone was connected to a charge amplifier, which both band pass filtered (10 Hz to 10 kHz) and amplified the signal before reaching the oscilloscope. The acoustic pressure was obtained from the root-mean-square voltage of the average of 64 individual waveforms.

Field surveys were conducted within both bare and vegetated substrates. High-frequency experiments investigated turtle and shoal grass meadows separately, while low-frequency experiments were conducted in meadows comprised of a mixture of both turtle and shoal grasses. For both winter (February) and summer (June) sampling events, high-frequency transmission loss was measured between 0.25 and 1.75 m in 0.25 m increments within each of

the 3 substrate types. Three replicate transmission paths for each distance and substrate combination were investigated at each sampling event. The low-frequency transmission loss experiments were conducted as part of the June sampling event in both bare and vegetated substrates. Low-frequency transmission loss was measured for each of the 3 frequencies between 1.0 and 6.0 m in 1.0 m increments. Due to a loss in battery power, we were unable to measure the 5 m distance for the vegetated bottom treatment.

Seagrass biomass

For both sampling events, a variety of morphological measurements were obtained for both turtle and shoal grass. At the conclusion of the acoustic experiments, seagrass biomass was collected from 3 replicate cores of diameter 0.10 m (*Halodule wrightii*) or 0.15 m (*Thalassia testudinum*). The core locations were randomly chosen within the path of acoustic transmission. The seagrass material was then rinsed with filtered seawater at the laboratory and stored for no more than 72 h prior to analysis. For each seagrass core, the total number of shoots and the lengths of 30 randomly chosen leaves were recorded. The above-ground and below-ground biomass was then separated and dried to a constant weight in a 60°C oven. Finally, for each sampling date, 3 replicate shoots from each of the 2 species were used to measure epiphytic abundance. To quantify epiphyte cover, a known leaf area was scraped with a razor blade. The epiphytes were transferred from the blade to a pre-weighed filter and dried to a constant weight in a 60°C oven. The epiphyte abundance was then expressed as the dry weight of epiphytic material scaled to the leaf area.

Canopy height and sound transmission

A separate laboratory experiment was used to investigate the importance of the vertical position of sound transmission relative to the seagrass canopy. For this experiment, freshly collected turtle grass was placed in an outdoor cylindrical tank (depth = 0.5 m, radius = 0.5 m) filled with seawater from the Gulf of Mexico. One hydrophone was placed on each of 2 sides of the seagrass plot, and the same transmission characteristics used in the high-frequency field experiments were implemented here (Fig. 1). The peak-to-peak amplitude from the

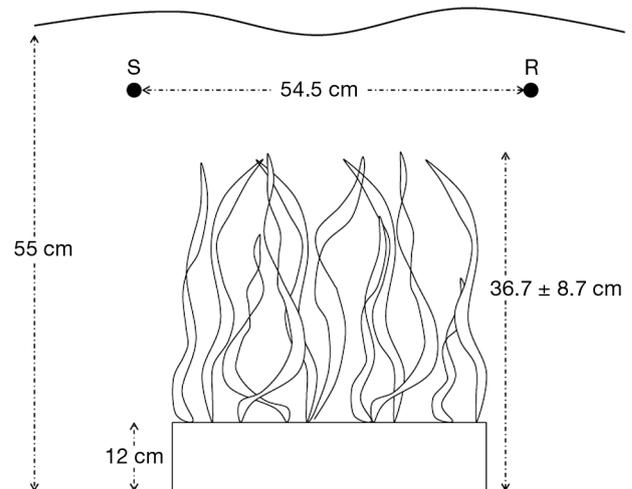


Fig. 1. Configuration of the laboratory experiment measuring the importance of vertical positioning and sound transmission. The separation distance of the sound source (S) and receiver (R) remained constant for each of the 5 vertical positions (30, 35, 40, 45 and 50 cm above the bottom). Vegetation height above the bottom represents the average \pm SD obtained from the leaf length ($n = 30$) and sediment box height

direct path of sound transmission was obtained for a total of 5 vertical positions (0.30, 0.35, 0.40, 0.45 and 0.50 m above the bottom). Shoot length from a random selection of 30 plants was measured following the acoustic experiment.

Statistical analyses

Differences in the means of the seagrass morphological measurements, derived attenuation coefficients (α) and prey detection threshold calculations for the high-frequency transmission loss experiments were examined using a 2-way analysis of variance (ANOVA). For each of the parameters, the 2-way ANOVA was used to test for significant differences ($p < 0.05$) in the means of the observations for the main effects of substrate type, season and the interaction of substrate and season. For the low-frequency transmission loss experiments, a linear regression model was used to quantify the empirical relationship between transmission distances and received acoustic energy. A source level of 150 dB re 1 μ Pa at 1 m was used for all low-frequency experiments and the linear regression model applied this source level as the y -intercept. Regression slopes for the bare and vegetated substrate treatments for each frequency were compared using a Student's t -test ($p < 0.05$).

RESULTS

High-frequency transmission loss

High-frequency transmission loss varied between both season and substrate type (Fig. 2). Significant differences in α were observed for the main effects of substrate type, season and their interaction (Table 1) ($p < 0.01$). Transmission loss varied more in summer ($\alpha = 1.2$ to 16.5 dB m^{-1}) than in winter ($\alpha = 0.2$ to 0.5 dB m^{-1}), and increased transmission loss was observed in the summer for all substrate types (Table 2). *Thalassia testudinum* consistently attenuated more high-frequency sound energy than *Halodule wrightii* regardless of season. Differences in the derived α -values are clearly evident in calculations of the target detection thresholds for a potential prey item, as thresholds significantly ($p < 0.01$) decreased from winter to summer (Table 1). Sound transmission was also influenced by the vertical position within the seagrass canopy as laboratory measurements demonstrated that sound transmission increased linearly with increasing distance above the substrate (Fig. 3).

Low-frequency transmission loss

Low-frequency transmission loss varied by substrate type for each of the 3 frequency treatments (Table 3). However, only the 300 Hz treatments exhibited a significant difference in attenuation rates between substrate types ($p < 0.01$), as evident in the statistical comparison of the regression slopes. Specifically for the 300 Hz treatments, sound was attenuated at a significantly greater rate over bare substrate compared to vegetated substrate. Although there was no significant difference observed in attenuation rates between substrate types for the 400 Hz ($p = 0.07$) and 500 Hz ($p =$

0.08) treatments, sound was attenuated at a slightly lower rate in vegetated substrate for the 400 Hz tone and a slightly higher rate in vegetated substrate for the 500 Hz tone.

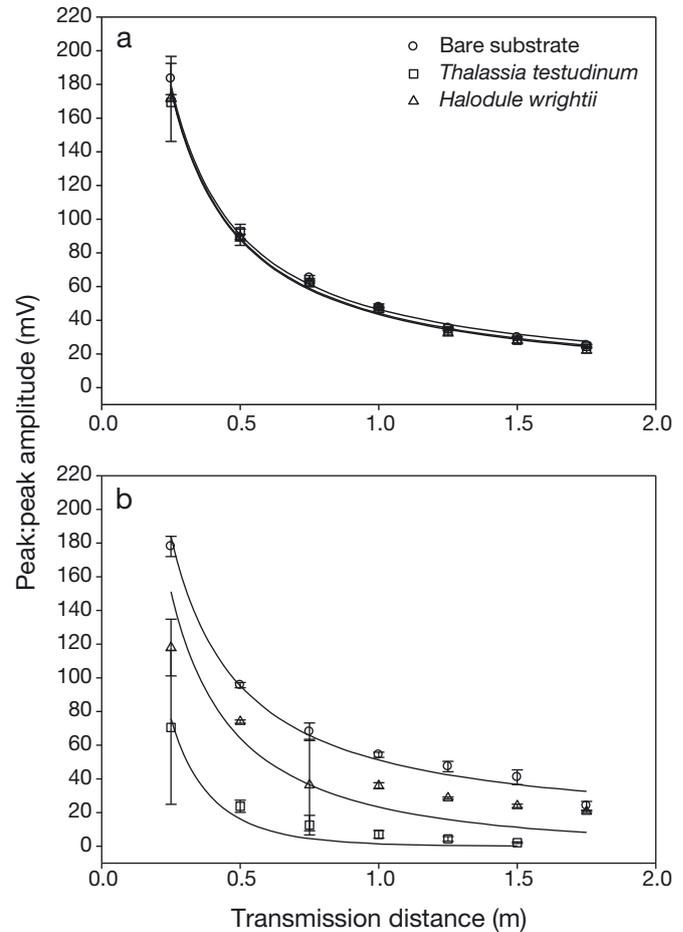


Fig. 2. Observed peak-to-peak acoustic pressure as a function of transmission distance for the (a) February and (b) June high-frequency transmission loss experiments. Values of acoustic pressure represent the mean \pm SD of 3 replicate transmission paths. The data for each treatment were fitted with a spherical attenuation model (Eq. 2)

Table 1. Results of the 2-way ANOVA for the derived attenuation coefficients (α), calculated prey detection thresholds and seagrass morphological measurements from the high-frequency transmission loss experiments. For each of the parameters, the 2-way ANOVA was used to test for significant differences ($p < 0.05$) in the means of the observations for the main effects of substrate type (bare substrate, *Thalassia testudinum* and *Halodule wrightii*), season (February and June) and the interaction of substrate and season. ns: not significant

	α (dB m^{-1})	Detection threshold (m)	Leaf length (cm)	Epiphyte cover (mg DW m^{-2})	Shoot density (shoots m^{-2})	Above-ground biomass (g DW m^{-2})	Below-ground biomass (mg DW m^{-2})
Species	<0.01	ns	<0.01	ns	<0.01	<0.05	<0.05
Season	<0.01	<0.01	<0.01	<0.05	<0.01	ns	<0.05
Species \times Season	<0.01	ns	<0.01	ns	<0.01	ns	ns

Table 2. Measurements of seagrass morphology and sound attenuation for *Halodule wrightii*, *Thalassia testudinum* and bare sediment treatments. Values represent mean \pm SD ($n = 3$ for the derived attenuation coefficient [α], detection threshold, epiphyte cover, shoot density, above- and below-ground biomass; $n = 30$ for leaf length). Values of α were obtained by fitting a spherical spreading model ($TL = 20 \log R + \alpha R$) to the observed attenuation data using nonlinear regression analysis. The detection threshold was calculated using the equation $EE = SE - 2TL + TS_E$, where EE is the energy flux detection threshold, SE is the source energy flux density, TL is the transmission loss and TS_E is the target strength (derived from Au et al. 2007). Previously obtained values for EE (33.1 dB; Au et al. 2002), SE (167 dB; Au & Snyder 1980) and TS_E (-24 dB for a 17 cm mullet; Au et al. 2007) were all used in the detection threshold calculation

	α (dB m ⁻¹)	Detection threshold (m)	Leaf length (cm)	Epiphyte cover (mg DW m ⁻²)	Shoot density (shoots m ⁻²)	Above-ground biomass (g DW m ⁻²)	Below-ground biomass (mg DW m ⁻²)
<i>Halodule wrightii</i>							
February	0.2 \pm 0.2	161 \pm 115	12.5 \pm 3.8	7.15 \pm 7.37	7179 \pm 117	77.40 \pm 3.73	270.5 \pm 11.77
June	3.8 \pm 1.2	9.81 \pm 2.26	13.4 \pm 4.9	1.15 \pm 0.36	12729 \pm 304	169.9 \pm 38.89	666.5 \pm 96.20
<i>Thalassia testudinum</i>							
February	0.3 \pm 0.1	61.1 \pm 17.1	15.0 \pm 5.3	7.59 \pm 0.68	849.0 \pm 86.5	244.0 \pm 20.82	563.7 \pm 127.1
June	16.5 \pm 2.6	2.82 \pm 0.34	30.7 \pm 12.2	1.45 \pm 0.70	1038 \pm 218.0	417.4 \pm 129.9	1021.6 \pm 224.9
Bare substrate							
February	0.3 \pm 0.1	60.4 \pm 50.1					
June	16.5 \pm 2.6	23.45 \pm 5.49					

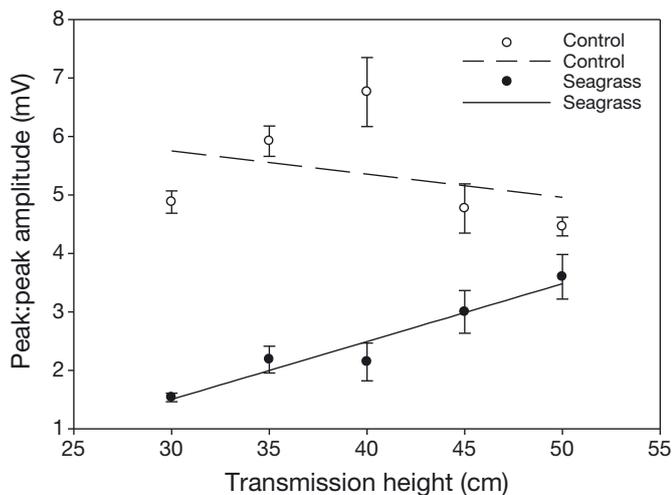


Fig. 3. Measured peak-to-peak acoustic pressure as a function of transmission height above the tank bottom for the high-frequency laboratory experiment. Points represent the mean and SD of 10 replicate acoustic measurements taken at each height for the control ($r^2 = 0.11$; slope = -0.04 ; $p = 0.59$) and seagrass ($r^2 = 0.93$; slope = 0.10 ; $p < 0.01$) treatments

Seagrass biomass

Morphological characteristics of the seagrass meadows differed markedly between sample dates (Table 2). Leaf length, shoot density, and below-ground biomass all increased significantly from February to June in both *Halodule wrightii* and *Thalassia testudinum* meadows ($p < 0.05$). The increase in leaf length was greater in *T. testudinum*, while *H. wrightii* exhibited a greater increase in shoot density. Overall,

Table 3. Results of the linear regression models for the low-frequency transmission loss experiments. Results of the t -test represent statistical comparisons of the slopes of the regression lines between the bare and vegetated substrate combinations for each individual frequency

	Slope	r^2	t -test
300 Hz			
Bare	-43.68	0.78	$t_7 = 6.95$, $p < 0.01$
Vegetated	-21	0.97	
400 Hz			
Bare	-38.65	0.97	$t_7 = 2.14$, $p = 0.07$
Vegetated	-31.46	0.79	
500 Hz			
Bare	-39.97	0.8	$t_7 = 2.01$, $p = 0.08$
Vegetated	-54.25	0.78	

shoot density was an order of magnitude greater in *H. wrightii* beds ($p < 0.01$), but this species contained half as much above- ($p < 0.05$) and below- ($p < 0.05$) ground biomass when compared to *T. testudinum*. Epiphyte cover increased significantly ($p < 0.05$) from summer to winter, but did not differ significantly between species.

DISCUSSION

High-frequency transmission loss and echolocation

Seasonal differences in high-frequency sound propagation were clearly evident during this study. This is not surprising given the significant changes in morphology of the seagrass meadows between sam-

pling dates. In the *Thalassia testudinum* meadow, seagrass leaves doubled in length from February to June. Since the vertical position of the source and receiver remained constant between sampling dates, we believe that leaf length alone describes the seasonal differences observed in sound transmission in the *T. testudinum* meadow. During the February sampling, the leaf canopy height, as determined from leaf length measurements, was below the path of acoustic transmission. However, in the June sampling event, the leaf canopy height was taller than the height of the hydrophones, which placed leaf tissue directly in the transmission path. The laboratory experiment corroborated the importance of transmission height relative to the height of the seagrass canopy, as sound propagation readily declined with increasing depth into the seagrass canopy.

Although leaf length increased in *Halodule wrightii* meadows from winter to summer, the height of the canopy was below the path of acoustic transmission during both sampling events. The lack of leaf tissue between the source and receiver is a likely explanation for why *Thalassia testudinum* attenuated more sound energy than *H. wrightii* during the summer sampling event. Since the leaf canopy was always contained below the path of acoustic transmission, seagrass morphological measurements provide no obvious explanation for the observed seasonal differences in acoustic propagation in the *H. wrightii* meadow. Since transmission loss in the *H. wrightii* meadow was significantly greater than the bare substrate, there must be a feature of the meadow, other than leaf morphology, that is serving to attenuate sound energy. Bubbles produced by seagrass meadows during photosynthesis have been shown to scatter and absorb acoustic energy (Hermund et al. 1998, Hermund 2006). It is, therefore, logical to hypothesize that photosynthetically derived bubbles produced during the summer sampling event served to attenuate more sound energy in the *H. wrightii* meadow compared to the bare substrate.

Transmission loss measurements clearly demonstrate the potential for seagrass meadows to serve as an acoustic refuge from echolocation (Table 2). In this study, the quality of the refuge was highly seasonal with seagrass beds providing very little protection (via acoustic transmission loss) during the winter. However, these seasonal and species-specific differences in refuge quality are likely to differ by location. In tropical regions, seasonal differences are likely reduced due to the continuous growth and replacement of the seagrass canopy. Similarly, it is possible that species-specific differences observed

here could change depending on regional characteristics of the health and condition of individual meadows (Creed 1997, May-Ku et al. 2010).

Acoustic modeling studies have consistently demonstrated that the sound propagation characteristics of a seagrass and seawater medium are highly dependent on total biomass (Wilson & Dunton 2009, Wilson et al. 2010). Biomass-dependent sound propagation is also evident in the high-frequency surveys conducted here, as an increase in biomass consistently decreased acoustic propagation across comparisons of both species and season. Numerous studies have demonstrated that climax species of seagrass, such as *Thalassia testudinum*, generally contain more standing biomass than pioneer species like *Halodule wrightii* or *Syringodium filiforme* (Iverson & Bittaker 1986, Zieman et al. 1989, Onuf 1996). Therefore, it appears that seagrass meadows consisting of climax plant populations provide a better acoustic refuge than meadows of pioneer seagrass species. As a result, natural or anthropogenic disturbances that replace climax species with colonizing species could also serve to decrease the potential refuge quality of seagrass meadows.

Acoustic detection of fish targets by marine mammals is influenced by the morphology of the individual fish. As one would expect, larger fish display a greater acoustic target strength than smaller fish (Boswell et al. 2008). The structure and size of a fish's swim bladder also dictates the acoustic target strength for different fish species (Au et al. 2009). These differing acoustic signatures would, therefore, promote differential exploitation of an acoustic refuge. For instance, smaller fish and species with an inconspicuous swim bladder could remain hidden within smaller expanses of vegetation. It is also likely that some fish would reach a size threshold when they are no longer acoustically obscured by the seagrass canopy. As a result, the possible benefits of acoustic protection are more likely for small individuals.

It is highly unlikely that fish actively choose to live within seagrass meadows because of any acoustic protection provided by the vegetation. Seagrass meadows provide both a food source and visual protection (Heck & Thoman 1981, Kirsch et al. 2002). Since these traits are perceivable by fish, they are undoubtedly the primary qualities influencing habitat choice. It is not yet known if estuarine fish actively seek submerged vegetation because of the reduced noise. It is widely accepted, however, that most fish are unable to hear the high-frequencies of sound used in echolocation (Astrup 1999, Ramcharitar et al. 2006). It is, therefore, entirely possible that fish are

completely unaware of the acoustic protection provided by the vegetation. Thus, although the size distributions of fish in seagrass patches may be influenced by the acoustic protection provided by the structure, this is strictly a top-down control mechanism. Nevertheless, acoustic detection and subsequent predation of large fish in small seagrass patches may provide an important ecological control on the distribution of estuarine species.

Low-frequency transmission loss and passive acoustic detection

The unique propagation characteristics of low-frequency energy have important ecological implications. In this study, 300 and 400 Hz tones propagated farther in the presence of vegetation than over a bare substrate (Fig. 4). For the 300 Hz tone, it initially appears as if the vegetation layer functioned as a resonant structure transmitting these frequencies of energy. In contrast, the 500 Hz tone was slightly inhibited by the presence of the vegetation. For this frequency of energy, it is likely that air contained within the seagrass tissue scattered and absorbed sound energy similar to the observed attenuation of higher frequencies. For fish with lower frequency calls (300 to 400 Hz), such as red drum *Sciaenops ocellatus* and Atlantic croaker *Micropogonias undulatus*, the presence of seagrass may promote the transmission of vocalizations. Conversely, for fish such as spotted seatrout *Cynoscion nebulosus*, higher frequency components of vocalizations (400 to 500 Hz) are possibly inhibited by submerged vegetation. Recent acoustic surveys have documented the abundance of fish vocalizations in nearshore environments (Holt 2008, Luczkovitch et al. 2008). However, fine-scale acoustic investigations have yet to reveal whether these fish are actively choosing specific habitats based on their ability to convey acoustic information.

Since the low-frequency sounds generated by soniferous fish are clearly audible to marine mammals, one might conclude that passive acoustic detection is a viable hunting strategy for marine mammals without the use of echolocation. However, a closer look into the sound pressure level of vocalizations and the low-frequency hearing threshold of marine mammals provides little evidence that passive acoustic detection is an advantageous strategy. For instance, a call generated by Atlantic croaker has an initial sound pressure level of 114 dB re 1 μ Pa (Barimo & Fine 1998). This sound pressure level is

below the detection threshold for low-frequencies of roughly 120 dB re 1 μ Pa exhibited by bottlenose dolphins (Finneran et al. 2002). Spotted seatrout has a

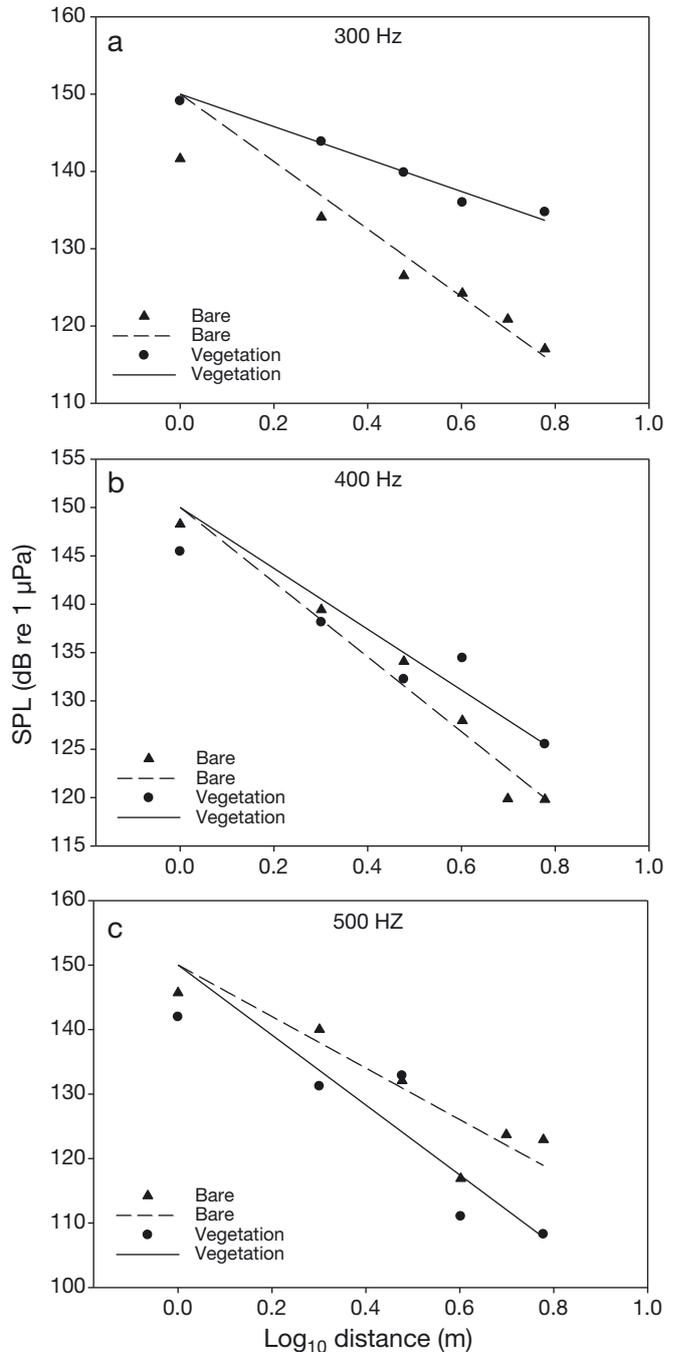


Fig. 4. Sound pressure levels (SPL) obtained for the low-frequency transmission loss experiments for (a) 300, (b) 400 and (c) 500 Hz tones. SPL for the vegetated (\bullet) and bare (\blacktriangle) substrates represent the root-mean-square average of 64 recorded waveforms. Data for each substrate type was fit to a linear regression model forced through the y-intercept of 150 dB re 1 μ Pa at 1 m, which represents the source level of the underwater speaker

vocalization sound pressure level of 139.6 dB re 1 μ Pa and spans a frequency range of 400 to 500 Hz (Baltz 2002, Ramcharitar et al. 2006). Based on our transmission loss measurements, this call should be audible to dolphins hunting in vegetation at a distance of 2.3 to 4.2 m. This range is well within the detection threshold of 2.8 to 9.8 m for dolphins using echolocation in vegetated substrates, and, therefore, demonstrates no measureable advantage associated with the use of passive acoustic detection (Table 1).

Seagrass condition and refuge quality

It is important to note that in this study, seagrass meadows did not attenuate more sound energy than bare substrates during the winter sampling event. Specifically for the *Halodule wrightii* meadow, the height of the canopy was below the transmission path during both sampling events, but there was a large seasonal difference in sound attenuation. Leaf length and shoot density were both lower in the winter sampling event, but a conspicuous seagrass canopy was still present. This suggests that the condition of the seagrass tissue, and not simply the presence of standing biomass, is an important determinant in acoustic refuge quality. Sound is attenuated in seagrass meadows by the air contained within the lacunae system of the tissue and the bubbles produced during photosynthesis. During winter months, photosynthesis, growth and subsequently bubble formation, decrease (Roberts & Caperon 1986, Kaldy & Dunton 2000, Kowalski et al. 2009). As a result, lack of bubble formation and the inability to repair damaged leaf tissue, likely serve to decrease acoustic scattering and absorption characteristics of seagrass meadows.

Seagrass meadows also undergo significant daily transformations as a result of photosynthesis and respiration. Using the same high-frequency acoustic procedure utilized in the current study, Wilson et al. (2012) examined sound transmission through the seagrass canopies of *Halodule wrightii*, *Thalassia testudinum* and *Syringodium filiforme* over a 24 h period. Temporal patterns in acoustic transmission were highly species-dependent, and the amount of energy transmitted throughout the seagrass canopy varied as much as 4.7 dB over the course of a single day. Furthermore, sound transmission increased during the overnight hours for *S. filiforme*, but decreased during this same time period for *H. wrightii* (Wilson et al. 2012). It is important to note, however, that despite the observed temporal variations in acoustic

transmission, the received acoustic energy was still greatly reduced by the presence of any vegetation. As a result, the quality of an acoustic refuge is likely affected by the interaction of species and time period, but it is unlikely that the refuge disappears entirely due to the continued presence of air-filled seagrass leaves.

Although the acoustic significance of seagrass epiphytes is currently unknown, increased epiphyte loading during the winter sampling event corresponded to a decrease in transmission loss. Epiphytes may increase sound transmission through the seagrass canopy in several ways. First, it is possible that high epiphyte loads result in reduced light availability for seagrass plants, which serves to decrease photosynthetic production and the creation of gas bubbles. Second, epiphytes increase the volumetric proportion of the solid phase within the seagrass canopy, which would result in a decrease in acoustic compressibility and a subsequent increase in acoustic transmission. Since epiphytes are commonly associated with many different seagrass species, the acoustic contribution of epiphyte loading deserves further investigation.

The functional quality of an acoustic refuge is likely more sensitive to environmental stressors than a structural refuge. Coastal eutrophication has been implicated in macroalgal growth and phytoplankton blooms, which decrease light availability for seagrasses (Duarte 1995). If light conditions are limited such that seagrasses can persist at a lower growth rate, then the functional quality of a visual refuge is largely unaffected. Conversely, reduced light availability decreases the rate of primary production, which results in reduced bubble production and tissue regeneration (Roberts & Caperon 1986, Lee & Dunton 1997, Neely 2000). The ultimate consequence of eutrophication and subsequent light reduction is a decline in the functional quality of the acoustic refuge. This example reiterates the idea that the presence of a seagrass canopy does not ensure the function of an acoustic refuge, even during the growing season.

The relative importance of a visual refuge vs. an acoustic refuge warrants further investigation. Field studies using artificial seagrass units (ASUs) report lower species richness and abundance of resident fauna in artificial meadows than in natural meadows under the same environmental conditions (Bell et al. 1987, Lee et al. 2001). ASUs mimic natural seagrasses in leaf shape, shoot density and color, and, therefore, provide the same visual refuge as natural meadows. However, ASUs are made from buoyant plastic or

nylon strips and do not produce bubbles (Bell et al. 1987, Lee et al. 2001). These artificial substrates are likely acoustically similar to the water column and may not provide acoustic protection to seagrass residents. It is possible that the reported differences in resident fauna between natural and artificial meadows are attributable to the lack of noise reduction in ASUs and subsequent protection from echolocation. As a result, future investigations should examine levels of noise reduction within ASUs to determine the relative importance of an acoustic refuge to a visual refuge.

CONCLUSIONS

Marine organisms are known to utilize acoustic information for reproduction, settlement and feeding (Simpson et al. 2004, Rountree et al. 2006). Estuaries have inherently high rates of primary and secondary production, but these shallow waters are also considered acoustically complex systems. This study demonstrated how the presence of vegetation alters the transmission of biologically relevant segments of the acoustic spectrum. Our results suggest that both echolocation and fish communication are influenced by the presence of vegetation, which has important ecological implications. Future research should continue to investigate how complex acoustic environments alter the dissemination of bioacoustic information and how these features impact ecosystem function.

Acknowledgements. The authors thank G. C. Shank, J. McClelland and L. Fuiman for their helpful reviews of this manuscript. The authors are also grateful for the field support provided by K. Lee, N. McTigue and K. Jackson. The University of Texas Applied Research Laboratories provided partial financial support for this project.

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