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# Variability of the low-frequency acoustic response along leaf blades and between species of seagrass (*Posidonia oceanica* and *Cymodocea nodosa*)

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**Abstract:** An acoustic resonator was used to measure the low-frequency (1–5 kHz) effective acoustic properties of the leaf blades of two Mediterranean seagrass species (*Posidonia oceanica* and *Cymodocea nodosa*). Variability along blades was assessed by measuring the effective change in sound speed per gram blade biomass of the basal and apical halves of *P. oceanica* leaves separately ( $-11$  and  $-1.5 \text{ m s}^{-1} \text{ g}^{-1}$ , respectively). Large differences in the effective sound speed per unit biomass between *P. oceanica* and *C. nodosa* ( $43\text{--}52 \text{ m s}^{-1} \text{ g}^{-1}$  larger for *C. nodosa*) are discussed using microscopic imagery of blade cross-sections. © 2021 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).

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## 1. Introduction

Seagrass meadows are one of the most important ecosystems on the planet. They are a significant primary producer in coastal waters, a habitat for economically important fish communities, and constitute a significant portion of blue carbon sequestration.<sup>1</sup> There is a growing body of work, over the last decade, dedicated to creating a forward propagation model for sound through seagrass meadows.<sup>2–5</sup> Such a model could be used to invert for ecological parameters of the seabed<sup>6</sup> or to optimize military applications in littoral environments. Since 2009, a one-dimensional acoustic resonator technique, outlined in Sec. 2.2, has been used to measure the low-frequency acoustic response of seagrass leaf blades<sup>2,4,5,7</sup> and seagrass leaf tissues.<sup>3,8</sup>

The first *ex situ* measurements of seagrasses, using this resonator technique, were performed by Wilson and Dunton<sup>2</sup> on three Texas Gulf coast seagrass species. The acoustic resonator was used to measure the low-frequency effective sound speed  $c_{\text{eff}}$  of mixtures of leaves and artificial seawater. Their data revealed that  $c_{\text{eff}}$  can strongly depend on species, biomass inside the resonator, and the shape of the leaf blades (round vs flat cross-sections). Their measurements were extended to the Mediterranean seagrass species *Posidonia oceanica* in the MEDGRASS15 experiment<sup>4</sup> when a similar one-dimensional resonator was used to measure  $c_{\text{eff}}$  for three separate collections of *P. oceanica*. Each collection exhibited a consistent acoustic response but responses varied between collections, as shown in Fig. 3 of Johnson *et al.* (2017). The average blade length, surface area, mass, and percent covered by epiphytes were quantified and compared to the acoustic responses. Smaller blades with higher epiphytic coverage correlated to a larger decrease in effective sound speed per unit biomass. In this paper, as with previous studies of effective sound speed in seagrass, results are presented in terms of plant biomass, not density  $\rho$ , as is typical of many acoustic propagation problems. This choice is twofold, first, it was shown in Ref. 2 that simple propagation models were insufficient to accurately model the acoustic response of seagrass inside a resonator. And so, direct inferences of seagrass density  $\rho$  or bulk modulus  $B$  could not be made from resonator measurements of intact leaf blades. The complexity of solving the forward modeling problem does not diminish the ability of the resonator to extract useful acoustic information or to assess the relative strength of different acoustic effects, as is done in this paper. Second, many in the remote sensing community prefer to use plant biomass as the preferred metric for reporting as biomass is easy to measure and informative for comparative results.

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This paper presents two measurements from MEDGRASS16 that build directly upon those of MEDGRASS15. First, a method was developed to measure the variability in acoustic response along leaf blades. The previous experiments only considered the acoustic response of leaf blades as a whole and any variation in acoustic behavior along the blades was not resolvable. To investigate how acoustic response may vary along leaf blades a collection of *P. oceanica* leaf blades were cut in half crosswise and  $c_{\text{eff}}$  was measured for the basal halves and apical halves separately, using the same acoustic resonator technique. The effective sound speed of the mixture with the apical halves showed much less dependence on leaf mass than for the basal halves, as shown in Fig. 1(a).

Second,  $c_{\text{eff}}$  was measured for the leaf blades of an additional species of Mediterranean seagrass, *Cymodocea nodosa*. The blades of *C. nodosa* have a very different morphology to *P. oceanica*. Although both blades have flat cross-sections, the blades of *C. nodosa* are typically much shorter and have a less variability in aerenchyma structure along the blade. These measurements are the first measurements of  $c_{\text{eff}}$  for *C. nodosa* shown in Fig. 1(b) and are compared to the 2015 and 2016 measurements of *P. oceanica* leaf blades. Additionally, the average epiphytic coverage on the *C. nodosa* leaves was quantified and no significant effect on the acoustic response was seen.

Microscopic imagery of *P. oceanica* and *C. nodosa* cross-sections are shown in Fig. 2. The cross-sections of each species were taken from the same leaf blade at distances  $y_i$  from the basal end to highlight the differences in aerenchyma structure which can largely explain the variation in  $c_{\text{eff}}$  measurements between the two species and between the basal and apical halves of *P. oceanica* and *C. nodosa*. Additional microscopic images of an entire leaf cross section for both species are shown in Fig. 1 of the supplementary material.<sup>9</sup>

## 2. Materials and methods

### 2.1 Plant details

The collections of *P. oceanica* and *C. nodosa* were freshly picked in the summer of 2016 in Sicily, Italy and in Crete, Greece, respectively. Samples were immediately placed in a refrigerated container at a temperature of 6 °C before being transferred to Brussels’ lab for processing, which began within 48 h. Previous experience by the authors and evidence based on microscopic images of internal plant structure show that the plants remained healthy during the transportation and during the processing at the lab.

Leaf blades were cut from the rhizomes immediately above the sheath. The *P. oceanica* leaf blades were cut again, halfway between the leaf sheath and apex and separated into basal halves (bottom) and apical halves (top). The *C. nodosa* leaf blades were separated into two batches of blades with higher and lower average epiphyte coverage (20.3% ± 9.2 and 10.9% ± 6.0, respectively). All uncertainties reported throughout this manuscript are standard deviations. From these groups, leaf blades were selected randomly for sound speed measurements. The surface water on each blade was removed by gently absorbing with a paper towel before being weighed for plant biomass. Then each blade was photographed for size, shape, and epiphyte coverage before being inserted into the resonator (described below). The specific details of each collection date, location, and the number of leaves processed as well as the average physical characteristics of the leaves in each collection are tabulated in Table 1. A typical *P. oceanica* leaf blade and *C. nodosa* blade were also selected for microscopic imaging, shown in Fig. 2.

### 2.2 Description of the sound speed measurements

A one-dimensional acoustic resonator apparatus was used to measure the low-frequency effective sound speed of mixtures of seagrass leaf blades and artificial seawater. This type of resonator measurement has been used in multiple previous

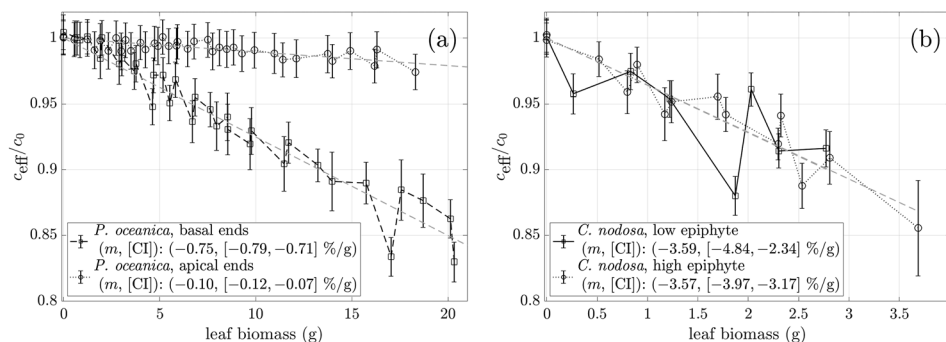


Fig. 1. MEDGRASS16 effective sound speed  $c_{\text{eff}}$  vs biomass measurements for (a) the basal and apical halves of *P. oceanica* processed in June 2016 and for (b) *C. nodosa* blades with low and high average epiphyte coverage by area (11% and 20%, respectively). The slope  $m$  and 95% confidence interval (CI) values of a constrained linear regression for each batch are displayed in the legend in the units of percent change in effective sound speed per gram biomass in the resonator. Both linear fits for the *C. nodosa* collections are shown in (b) but are so similar that they appear to overlap.

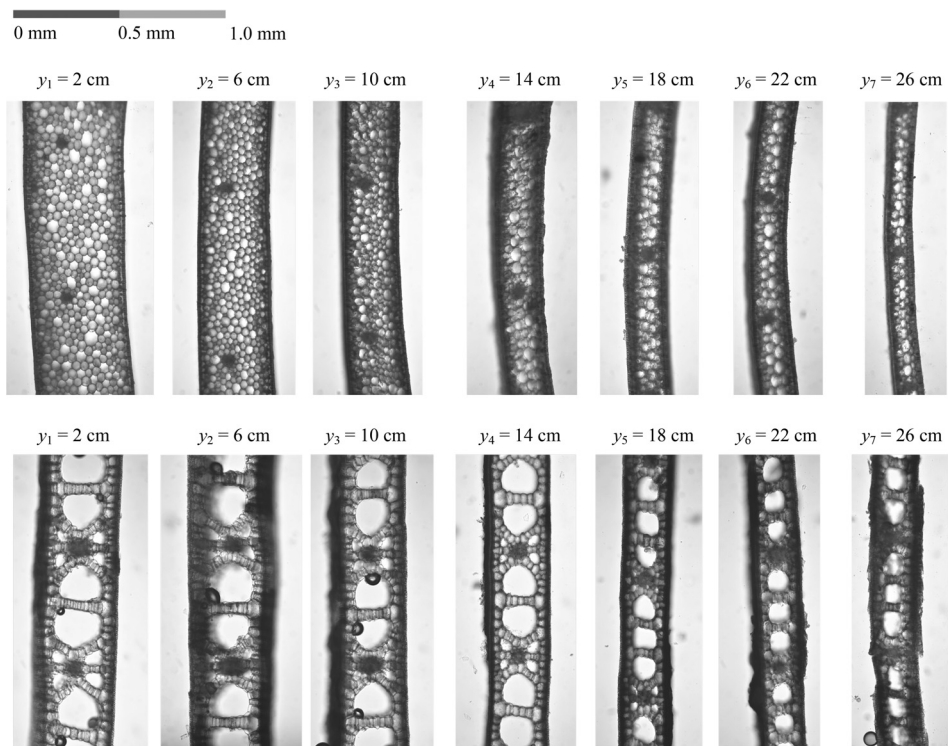


Fig. 2. Cross-sectional microscopy images of a *P. oceanica* (above) and a *C. nodosa* (below) leaf blade at seven different locations. Distance  $y_i$  is measured from the basal end where the blade meets the leaf sheath. All images were taken at the same magnification with the scale bar listed above. The leaf blade was collected in the summer of 2016 during the MEDGRASS16 experiment.

experiments and is only outlined here for brevity. For a more detailed explanation of the apparatus, the interested reader is directed to Refs. 2, 4, 5, and 10. The theory of its operation is unchanged, although, the experimental setup used in the following experiments, including the dimensions of the resonator, was not exactly as those used before.

A cylindrical borosilicate glass tube was sealed on the bottom by a thin rubber sheet and an approximate pressure release boundary condition was achieved by placing the tube on a piece of extruded polystyrene. A 2-cm-diameter aluminum piston, at the top of the tube, was driven by an electromagnetic shaker. The system wasinsonified with a continuously repeated logarithmic chirp excitation from 0.1–10 kHz which was synthesized onboard a PC equipped with a

Table 1. Physical characteristics and collection information for the leaf blades processed from each batch during MEDGRASS15 and MEDGRASS16 experiments. The mean and standard deviation of each quantity is presented for all leaf blades analyzed ( $N$  blades processed per batch). The slope  $m$  and 95% confidence interval of a constrained linear fit of percent change in effective sound speed per gram of biomass added to the mixture are shown in the second to last column. The final column is the change in effective sound speed per gram of biomass  $\Delta c_{\text{eff}}$  normalized to reference water  $c_0 = 1500$  m/s and 95% confidence interval. The 2015 data were adapted from Ref. 4, where the collections were referred to as “Crete,” “Sicily-1,” and “Sicily-2.”

Collection	Location	Date	Leaf Blade					Results	
			$N$	Length (cm)	Area (cm <sup>2</sup> )	Mass (g)	Epiphyte cvge. (%)	$m$ , (95% CI) (% g <sup>-1</sup> )	$\Delta c_{\text{eff}}$ , (95% CI) (m s <sup>-1</sup> g <sup>-1</sup> )
<i>P. oceanica</i>									
Crete	W Crete	26 June 2015	73	31.5 ± 9.7	21.3 ± 8.6	0.64 ± 0.27	4.5 ± 2.3	-0.47, (-0.55, -0.40)	-7.0, (-8.3, -6.0)
Sicily-1	NW Sicily	29 June 2015	55	14.2 ± 4.2	8.7 ± 2.9	0.17 ± 0.06	40.7 ± 25.4	-4.30, (-4.98, -3.66)	-64, (-75, -55)
Sicily-2	NW Sicily	7 July 2015	88	47.0 ± 13.9	27.5 ± 6.6	0.90 ± 0.40	12.0 ± 7.4	-0.66, (-0.73, -0.58)	-10, (-11, -8.7)
Apical half	NW Sicily	21 June 2016	53	30.6 ± 7.7	24.5 ± 5.2	0.60 ± 0.16	44.5 ± 26.0	-0.10, (-0.12, -0.07)	-1.5, (-1.9, -1.1)
Basal half	NW Sicily	21 June 2016	53	33.6 ± 5.3	26.8 ± 4.5	0.82 ± 0.24	1.1 ± 0.6	-0.75, (-0.79, -0.71)	-11, (-12, -10)
<i>C. nodosa</i>									
High epiphyte	W Crete	11 July 2016	45	20.2 ± 4.1	6.2 ± 1.5	0.16 ± 0.05	20.3 ± 9.2	-3.57, (-3.97, -3.17)	-54, (-60, -48)
Low epiphyte	W Crete	11 July 2016	33	21.3 ± 6.6	6.9 ± 2.6	0.16 ± 0.06	10.9 ± 6.0	-3.59, (-4.84, -2.35)	-54, (-73, -35)

data acquisition card and directed to the shaker via a power amplifier. A miniature hydrophone was placed at the top to record the system response. The received signals were bandpass filtered (10 Hz to 10 kHz), amplified with a charge amplifier, and digitized by the same data acquisition card. The broadband excitation chirp signals emitted by the shaker into the tube produced normal mode standing waves at half-wavelength intervals and the resulting acoustic response measured by the hydrophone exhibited strong spectral peaks that correspond to the modal frequencies. The phase speed  $c_{ph}$  inside the tube was inferred from these frequencies of the normal modes by the relationship,  $f_n = (c_{ph}/2L)n$ , where  $n$  is the standing wave mode number inside the tube,  $f_n$  is the frequency of the resonance peak for the  $n$ th mode, and  $L$  is the tube length. As leaf blades are inserted into the resonator there is typically a noticeable shift downward in the resonance frequencies indicating a slower sound speed. In the case of fluid-filled glass cylinders, there is significant coupling between the fluid inside and the elastic walls which results in a decreased sound speed measured inside the resonator relative to that observed in the free field. There is an exact analytical model<sup>11,12</sup> from which a systematic correction can be applied to convert the sound speeds measured inside the resonator  $c_{ph}$  to the intrinsic sound speed of the fluid (or suspension) in a free-field  $c_{eff}$ .

For each batch of plants processed, first, the sound speed in a water-only configuration  $c_0$  was measured inside the resonator and compared to tabulated values for a similar temperature and salinity. Then, leaves were added to the resonator in groups of one to five blades after removing surface moisture and weighing for biomass. After each addition of leaves,  $c_{eff}$  was determined from each of the first three resonance modes and the three values were averaged to give a single value for low-frequency sound speed. The relative sound speeds  $c_{eff}/c_0$  as a function of biomass in the resonator for each species are shown in Figs. 1(a) and 1(b). Biomass was chosen as the independent variable because it is useful in the remote sensing communities and is measured quickly and accurately. The error bars represent the quadrature sum of the standard deviation of  $c_{eff}$  for the three resonance modes and a 1.3% measurement uncertainty calculated from uncertainty in resonator length  $L$  and the finite resolution of the frequency spectra. A linear least squares regression constrained to unity at zero biomass was applied to the data and is plotted as a dashed line and the slope  $m$  and 95% confidence interval (CI) values are printed in the legend as percent change in sound speed per gram of biomass inside the resonator. These slopes allow for efficient comparison in acoustic behavior between collections and species.

### 3. Conclusion

This paper presents new measurements of the low-frequency acoustic response of leaf blades from *P. oceanica* and *C. nodosa* seagrasses. The measurements demonstrate a variability in the acoustic response and tissue structure along leaf blades of *P. oceanica* as well as a variability in acoustic response between *P. oceanica* and *C. nodosa*. The microscopic images of blade cross-sections shown in Fig. 2 and supplementary Fig. 9 support the acoustic results in two ways. First, the difference in  $\Delta c_{eff}$  between the apical and basal halves of *P. oceanica* is likely explained by a decreasing amount of gas present in the aerenchyma towards the apical ends of the blade. As shown in Fig. 2, the blade thickness and aerenchyma diameter decrease toward the apex indicating less gas present. Additionally, Ott<sup>13</sup> showed that, for *P. oceanica*, leaf growth from the base and leaf decay from the apex occur simultaneously but, their relative rates change throughout the life of the blade (see Fig. 3 of Ref. 13). As the tip of the blade decays, there is a lack of photosynthesis from which the aerenchyma is filled with gas. Therefore, there is both a decreasing volume of space for gas towards the apex, as well as decreasing photosynthetic mechanism to produce the gas.

The second acoustic results supported by the microscopic images is the difference in acoustic response between *P. oceanica* and *C. nodosa*. Although the blades of *C. nodosa* are smaller than those of *P. oceanica*, the aerenchyma are much larger which indicate more gas per gram biomass. This is reflected in the acoustic results as a much larger magnitude  $\Delta c_{eff}$  for *C. nodosa* than the *P. oceanica* collections, except “Sicily-1.” As discussed in Ref. 4, it is not clear why Sicily-1 exhibited such a different response than the other collections. The original hypothesis of the authors that the epiphytic coverage would affect the acoustic response was systematically measured between the two batches of *C. nodosa* and no difference was found. Another possibility, suggested by the basal vs apical half results, is that the Sicily-1 blades, which were much smaller than other collections, contained more gas in their aerenchyma when averaged along the entire length of the blade, than longer blades which may have decayed more near the apical ends.<sup>13</sup>

Despite strong variation in acoustic behavior within a single species and across species, each individual collection of plants demonstrated a consistent acoustic behavior. Furthermore, blades of similar visual aspect had consistent behavior between collection. Specifically, the acoustic response of larger blades, like those from the “Crete,” “Sicily-2,” and the basal halves collection were closer to each other than to those of the smaller blades from the Sicily-1 and *C. nodosa* collections, and vice versa. There will always be variation between individual blades but the consistency within collections highlights the potential for low-frequency acoustic measurements to be used in remote sensing applications to discern physical characteristics of leaf blades within seagrass patches and meadows.

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