

**Dear Editor,**

We would like to submit our manuscript entitled “ **Hydrodynamics in Short Indo-Pacific Seagrasses**” for consideration for publication in *Botanica Marina*. This study is first to describe the relationship between five tropical seagrass species from Indonesia and their effect on hydrodynamic regimes, which is important information for seagrass restoration, particularly in Indonesia, a center of seagrass biodiversity. This manuscript has not been submitted for publication elsewhere.

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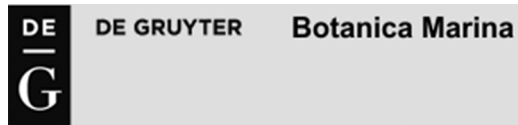
The authors have been worked together from designing and conducting the experiment, analyzing the data, writing and editing the manuscript.

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**Kind Regards,**

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## Hydrodynamics in Short Indo-Pacific Seagrasses

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**Hydrodynamics in Short Indo-Pacific Seagrasses**

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**Running title:** Seagrass hydrodynamics

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## Abstract

We provide data on the relationship between Indonesia seagrass species and hydrodynamics. Seagrass hydrodynamic regimes are important to understand in general and also to guide seagrass restoration, which is of great interest in Indonesia because of environmental threats to the exceptionally high seagrass species richness. In a flume, we determined the effect of canopies of *Cymodocea rotundata* Ascherson & Schweinfurth, *Enhalus acoroides* (Linnaeus f.) Royle, *Halodule uninervis* (Forsskål) Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii* (Ehrenberg) Ascherson *Cymodocea rotundata* Ascherson & Schweinfurth, *Enhalus acoroides* (Linnaeus f.) Royle, *Halodule uninervis* (Forsskål) Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii* (Ehrenberg) Ascherson at natural densities on water velocity, turbulence, turbulence intensity, and shear velocity. The taller canopies of *Enhalus* and *Cymodocea* slowed water flow, but the shorter canopies (<5 cm) had little effect. Seagrasses did not influence turbulence and turbulence intensity (turbulence normalized to mean velocity) but they reduced shear velocity  $U^*$ . Our results indicate that *Enhalus* is a good candidate for transplantation in terms of reducing mean water flow and shear velocities, but that *Halodule* should also be considered as it also reduced shear velocities and it spreads quickly after transplantation. Our results extend the understanding of seagrass-hydrodynamic relationships to include very short canopies, unlike the taller canopies studied to date.

Keywords: *Cymodocea*, *Enhalus*, hydrodynamics, Indonesia, seagrass

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68

69 **Introduction**

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72 Seagrass leaf canopies profoundly influence water flow dynamics. In turn, water

73 flow dynamics influence both the physical marine environment by affecting sediment

74 deposition and resuspension and the associated biological communities through effects

75 on physiological processes, food availability, larval recruitment and dispersal (Eckman

76 1987, Thomas et al. 2000, Williams and Heck 2001, Koch et al. 2006, González-Ortiz et

77 al. 2014). Understanding the seagrass-hydrodynamic relationship is also important for

78 successful restoration efforts (Fonseca and Fisher 1986, van Katwijk et al. 2009).

79 In general, seagrass canopies modify the hydrodynamic environment within and

80 around them by: 1) attenuating of water flow and dissipating wave energy, promoting

81 the retention of sediments and biological particles, 2) changing the velocity profile close

82 to the bottom and thus, the boundary layer of more viscous, slower flow, 3) increasing

83 or decreasing the turbulence and thus advection (the transport of materials), and 4)

84 propagating monamis, or leaf waving, which enhances advection (reviewed in Madsen

85 et al. 2001 and Koch et al. 2006). These influences in turn govern the ecological

86 processes mentioned above. These reviews and other references highlight that seagrass-

87 hydrodynamic studies differ widely in their approach and results and more research is

88 required to build a comprehensive understanding of the specific ways that seagrasses

89 influence water flow. Of note for our study is that most seagrass-hydrodynamic studies

90 have been devoted to temperate species and to canopies that are relatively tall (&gt; 5 cm,

91 see Discussion).

92 The influence of a seagrass canopy on water flow depends on its physical

93 structure. Most simply, in the case of a continuous monospecific canopy, structure is

dictated by leaf morphology (including stiffness and length relative to water depth),

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3 94 density, and arrangement, while patchiness in the meadow influences water flow at the  
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5 95 larger landscape scale (references above; Nepf and Vivoni 2000, Bouma et al. 2005,  
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7 96 Fonseca et al. 2007, Peralta et al. 2008). Leaf morphology varies widely in size and  
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9 97 shape across seagrass genera and species (Duarte 1991), ranging from straps (*Enhalus*,  
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11 98 *Posidonia*, *Thalassia*, *Zostera*, *Cymodocea*, *Halodule*), small ovals (*Halophila*),  
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13 99 cylinders (*Syringodium*), to more complex shapes (*Thalassadendron*, *Amphibolis*).  
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16 100 Seagrass morphology itself adjusts plastically to hydrodynamic regimes (Peralta et al.  
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18 101 2006).

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20 102 The objective of our study was to generate some basic understanding of the  
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22 103 effect of common Indonesian seagrass species on water flow dynamics. Although  
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24 104 Indonesia is a center of seagrass species richness (Green and Short 2003, Short et al.  
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26 105 2007), its seagrasses have been studied relatively little compared to coral reefs and  
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28 106 mangroves (Orth et al. 2006), despite the fact that Indonesian seagrasses are threatened  
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30 107 by many factors (Nadiarti et al. 2012). To generate baseline information, we measured  
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32 108 basic hydrodynamic descriptors of the canopies of five species under controlled  
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34 109 conditions in a laboratory flume. *Cymodocea rotundata* Ascherson & Schweinfurth,  
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36 110 *Enhalus acoroides* (Linnaeus f.) Royle, *Halodule uninervis* (Forsskål) Ascherson,  
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38 111 *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii* (Ehrenberg)  
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40 112 Ascherson *Cymodocea rotundata* Ascherson & Schweinfurth, *Enhalus acoroides*  
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42 113 (Linnaeus f.) Royle, *Halodule uninervis* (Forsskål) Ascherson, *Syringodium isoetifolium*  
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44 114 (Ascherson) Dandy, and *Thalassia hemprichii* (Ehrenberg) Ascherson (hereafter  
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46 115 referred to by genus) differ widely in their leaf morphology and thus canopy structure.  
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48 116 They are common throughout the Indo-Pacific region where they form monospecific  
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50 117 and mixed-species canopies, including some very short ones (see Results and  
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52 118 Discussion).

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5 120 **Material and methods**

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7 121 Our field seagrass bed was located at Barranglompo Island (5°03'S, 119°20'E)  
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9 122 in the Spermonde Archipelago, south Sulawesi, Indonesia. We measured freestream  
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11 123 water flow speed and direction every minute for 48 hours (19-21 October 2013) using  
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13 124 an Infinity Series ver. 0.10 current meter (JFE Advantech Co., Ltd. 3-48 Takahata-cho,  
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15 125 Nishinomiya, Hyogo, Japan 63-8202), deployed at 1.5 m above the substratum (water  
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17 126 depth = 4 m). We estimated the leaf shoot densities of *Enhalus*, *Cymocodea*, *Thalassia*,  
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19 127 *Syringodium*, and *Halodule* in 1 m<sup>2</sup> quadrats (n = 4 per species) in monospecific stands  
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21 128 before collecting intact rhizomes with attached leaf shoots. Seagrasses were cleaned of  
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23 129 sediments and epiphytes, cushioned by plastic fiber batting, and placed in coolers for air  
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25 130 shipment to the Bodega Marine Laboratory, University of California at Davis, USA,  
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27 131 where flume studies were conducted in September 2014.

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29 132 A straight flume (Model 504, Engineering Design Laboratory, Lake City,  
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31 133 Minnesota 55041-0278, USA, working section 45 x 45 x 250 cm) was used to  
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33 134 characterize the effect of the leaf canopy on water flow dynamics. The flume was filled  
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35 135 with seawater to a depth of 44 cm above the bottom and was not changed during the  
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37 136 experiment. Measurements were made at a flume speeds of 0.60 - 0.65 m/s.

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39 137 We created a seagrass bed (45 cm wide x 100 cm long) of each species using a  
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41 138 plastic-coated wire mesh (0.5 cm x 0.5 cm mesh size) fitted across the width of working  
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43 139 section and centered in the middle of the working section's length. To secure the  
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45 140 buoyant seagrass in the flume, we placed the rhizomes between two pieces of mesh,  
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47 141 spacing them irregularly to mimic their natural arrangement, added small lead fishing  
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49 142 sinkers, and threaded the leaf shoots through the top mesh layer. The edges of the mesh  
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51 143 were smoothed with duct tape. The mesh was placed as close to the flume bottom as  
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3 144 possible (average height above bottom:  $1.8 \text{ cm} \pm 0.43 \text{ SD}$ ,  $n = 275$  measurements). The  
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5 145 mesh created a rough bottom generally analogous to the rough bottoms created by small  
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7 146 pieces of coral rubble and animal tubes in Indo-Pacific seagrass beds. To compare the  
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9 147 experimental seagrass bed to the field and other studies, we counted the leaf shoots in  
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11 148 the mesh and measured the leaf canopy height as the distance between the mesh surface  
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13 149 and the longest leaf of 55 shoots of each species. We then clipped the leaves flush with  
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15 150 the mesh and measured leaf area (Li-Cor meter, Model Li-3100, Lincoln, Nebraska,  
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17 151 USA) to calculate the leaf area index (LAI) as the one-sided leaf area ( $\text{m}^2$ ) per  $\text{m}^2$  of  
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19 152 mesh. *Syringodium*'s cylindrical leaf area was calculated as the lateral area (leaf area  
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21 153 multiplied by  $\pi$ ). Leaves were oven-dried at  $60^\circ\text{C}$  until constant mass and weighed.  
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24 154 LAI, leaf biomass, and density theoretically relate to the canopy's influence on  
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26 155 hydrodynamics (Gambi et al. 1990, Koch et al. 2006, Peterson et al. 2004).

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29 156 The water flow velocity in the flume was determined using an Acoustic Doppler  
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31 157 Velocimeter (ADV, Field Vetrino serial #VNO0224, Nortek AS, Vangkroken 2, NO-  
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33 158 1351 RUD, Norway) with Vetrino Plus software, a baud of 57600, and sampling rate  
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35 159 of 200 Hz. The ADV was centered in the width of the working section. The flume was  
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37 160 calibrated by averaging velocity measurements without seagrass at 3, 5.5, 10, 15, and  
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39 161 25.5 cm above the bottom at 38 and 116 cm from the beginning of the working section.  
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41 162 Seagrass measurements were made at 5.5, 10, 15, and 25.5 cm heights; 5.5 cm was the  
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43 163 closest ADV measurements could be made next to the flume bottom due to the mesh.  
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45 164 After velocity stabilized upon repositioning the ADV, it was recorded over two minutes.  
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47 165 The mesh itself without attached seagrasses slowed the flow minimally by 0.049 m/s at  
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49 166  $\geq 5.5$  cm above the bottom.

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52 167 We calculated the mean velocity as the square root of the sum of squares of the  
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54 168 ADV's three velocity components averaged across instantaneous recordings made  
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3 169 during the measurement period. Turbulence, the measure of the variation in the average  
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5 170 flow, was calculated as the root mean square of the standard deviation of each velocity  
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7 171 component (Denny, 1988, Gambi et al. 1990). Turbulence intensity (%) was calculated  
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9 172 as the turbulence divided by the mean velocity. The depth ratio (water depth/canopy  
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11 173 height) was calculated to compare hydrodynamic environments due to differences in  
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13 174 canopy heights in the flume (Nepf and Vivoni 2000).

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16 175 The shear velocity  $U^*$  was determined from the von Karman-Prandtl velocity-  
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18 176 depth profile relationship (Denny 1988, Gambi et al. 1990):

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20 177  $U(z) = U^*/K (\ln(z_2/z_1))$ , where:

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22 178  $K$  = von Karman's constant (0.41),  $U$  is the difference in velocity between two heights  
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24 179 above the substratum ( $z_1$  and  $z_2$ ). Depth  $z_1$  was 5.5 cm and  $z_2$  was 25.5 cm for *Enhalus*  
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26 180 and *Cymodocea*, 5.5 and 15 for *Syringodium* and *Halodule*, and 3 and 25.5 upstream,  
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28 181 respectively, to conform to the log relationship between velocity and height above the  
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30 182 bottom. We performed linear regressions of  $U^*$  versus LAI, canopy height, and density,  
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32 183 which can be predictors of the canopy's influence on hydrodynamics (Gambi et al. 1990,  
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34 184 Koch et al. 2006, Peterson et al. 2004).

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39 186 **Results**

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41 188 The average water flow speed at the seagrass collection site was 0.160 m/s,  
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43 189 ranging from 0.002 to 0.430 m/s (Fig. 1), which corresponded to freestream flow at 18  
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45 190 cm above the flume bottom (Fig. 2, Table 1). Conditions were calm during the  
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47 191 measurements, which were taken during spring tides.

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49 192 In the flume, the average velocities differed depending on the species (Fig. 2).  
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51 193 The two short species (*Syringodium*, *Halodule*, < 5 cm tall, Table 1) had no observable  
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53 194 effect on average velocities compared to upstream (no seagrass, 0.600 - 0.650 m/s  
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3 195 freestream flow above 3 cm). Water flow was slowed by *Enhalus* and *Cymodocea* (and  
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5 196 less so by *Thalassia*) even at velocities faster than at the collection site.

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7 197 The depth ratios (Table 1) for all species except *Enhalus* was  $>2$ , indicating they  
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9 198 experienced similar hydrodynamic environments unconfined by water depth in the  
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11 199 flume (Nepf and Vivoni 2000) and that some cross comparisons can be made. The ratio  
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13 200 for *Enhalus* indicated its canopy was at the transition between a depth-limited and  
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15 201 emergent canopy. At this ratio, which is analogous to low tide in a shallow bed, a  
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17 202 vertical exchange zone develops at the top of the canopy and density and morphology  
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19 203 influence the hydrodynamics within the canopy, unlike in the unconfined condition of  
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21 204 very short canopies.

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24 205 Seagrass canopies had minimal effects on turbulence and turbulence intensity  
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26 206 (Table 1). The taller canopies (*Enhalus*, *Cymodocea*, *Thalassia*) increased values only  
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28 207 2-3% compared to upstream (no seagrass) values.

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31 208 All species reduced the shear velocity  $U^*$  ( $\leq 0.091$  m/s) compared to the no  
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33 209 seagrass value (0.104 m/s) (Table 1). There was no relationship between  $U^*$  versus  
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35 210 canopy height or LAI (Fig. 3), which was highly correlated to leaf biomass (Pearson  
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37 211 correlation coefficient = 0.988). These potential predictors of shear velocity explained  
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39 212 only 25-36% of  $U^*$  variation (height  $p = 0.210$ ,  $r^2 = 0.357$ ;  $df = 1, 4$ ; LAI  $p = 0.318$ ,  $r^2 =$   
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41 213 0.245). Shoot densities, which were within the low range of natural canopies (Table 1),  
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43 214 explained  $<0.1\%$  of  $U^*$  variation ( $p = 0.976$ ).

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## 47 48 216 **Discussion**

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50 217 Our data are limited to qualitative comparisons across species because there was  
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52 218 no replication within a species due to the logistical limitations inherent in bringing  
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54 219 seagrasses from Indonesia to the flume facility in California and keeping them in good

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3 220 condition. Nevertheless, there are some general patterns worth noting. First, water flow  
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5 221 speeds were lower within taller canopies such as *Enhalus* and *Cymodocea*, which is the  
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7 222 expected hydrodynamic result. Second, seagrasses had minimal influence on turbulence,  
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9 223 the variation in the time-averaged mean velocity, which is important for the advection  
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11 224 of essential elements, pollutants, and biological and non-biological particles (Denny  
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13 225 1988, Koch et al. 2006).

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15 226 Another important finding is that even the shorter canopies (< 5 cm) reduced the  
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17 227 shear velocity ( $U^*$ ).  $U^*$  scales with shear stress, the force resulting from the vertical  
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19 228 velocity gradient, which is responsible for initiating movements of sediment and other  
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21 229 particles at and near the bottom (Denny 1988, Koch et al. 2006). Thus, smaller  $U^*$   
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23 230 values indicate that very short canopies can reduce shear stress, providing increased  
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25 231 sediment stabilization, such as found for short *Halodule uninervis* in the field  
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27 232 (Christianen 2013). Sediment stabilization is an important coastal ecosystem function  
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29 233 in itself but it also helps set the rate of seagrass community development and thus is  
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31 234 important in seagrass restoration (Fonseca and Fisher 1986, Williams 1990, van der  
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33 235 Heide et al. 2007, van Katwijk et al. 2009, Lanuru 2011). Although the focus on much  
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35 236 of the Indo-Pacific seagrass restoration has been on taller 'climax' seagrass such as  
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37 237 *Enhalus* (Ambo-Rappe and Yasir, 2015, Lanuru, 2011), short but fast-growing species  
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39 238 such as *Halodule* would not only cover the sediments more quickly but also provide  
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41 239 some measure of sediment stabilization, based on our result and that of Christianen et al.  
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43 240 (2013).

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45 241 Submerged vegetation canopies are understood to strongly influence water flow,  
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47 242 typically by slowing water flow and, under specific conditions including fast flow,  
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49 243 creating skimming flow above the canopies and a vertical velocity maximum close to  
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51 244 the substratum (Gambi et al. 1990, Nepf and Vivoni 2000, Madsen et al. 2001, Peterson  
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3 245 et al. 2004, Hendriks et al. 2008). This understanding has been based on empirical and  
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5 246 theoretical studies of seagrasses and mimics with generally much taller canopies than  
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7 247 the seagrasses we studied. For example, studies of 'short' species reported canopy  
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9 248 heights  $\geq 5$  cm (Fonseca and Fisher 1986, Heis et al. 2000, Peterson et al. 2004, Bouma  
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11 249 et al. 2005, Widdows et al. 2008, Paul and Gillis 2015). Thus, our study expands the  
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13 250 understanding of seagrass-hydrodynamic relationships by demonstrating that in very  
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15 251 short seagrass canopies, such as commonly occur in intertidal to shallow waters in the  
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17 252 Indo-Pacific region, seagrasses do not necessarily exert a strong influence on  
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19 253 hydrodynamics, yet nevertheless they can decrease shear velocity and thus provide  
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21 254 increased sediment stabilization.  
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24 255 Several predictions can be made about short seagrass canopies, to be tested  
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26 256 empirically. For example, very short canopies do not necessarily enhance the retention  
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28 257 of organic matter or larvae. On the other hand, the supply of resources, e.g., nutrients  
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30 258 for primary producers and phytoplankton for filter feeders (Thomas et al. 2000,  
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32 259 González-Ortiz et al. 2014), could be less limiting in shorter canopies. When waves are  
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34 260 present along with currents, a canopy of short seagrass will oscillate and open and close  
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36 261 more than taller seagrass under the same current speed, which theoretically enhances the  
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38 262 supply of resources (Paul and Gillis 2015).  
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41 263 Our results provide some basic information to guide future studies, in addition to  
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43 264 highlighting the dearth of information on short seagrass canopies, which are common  
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45 265 close to shore or where herbivory is intense (Christeanen et al. 2013). This basic lack of  
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47 266 understanding of seagrass-hydrodynamic relationships constrains the creation of  
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49 267 guidelines for seagrass restoration efforts (Bos and Katwijk 2007, van Katwijk et al.  
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51 268 2009), yet restoration is critical to combat the global seagrass decline. There is great  
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53 269 interest in Indonesia in establishing guidelines for seagrass restoration to combat loss  
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3 270 and conserve its high seagrass diversity, dependent organisms, and ecosystem functions.  
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5 271 To this end, there are many next steps in seagrass-hydrodynamic research, for example,  
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7 272 manipulations of seagrass density, measurements of hydrodynamic conditions *in situ*  
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9 273 and the shear strengths of different sediment types found in Indonesia's coastal habitats.  
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11 274 In our study, the predictive relationship typically reported between seagrass density,  
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13 275 biomass, and leaf area and hydrodynamic parameters (Gambi et al. 1990, Peterson et al.  
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15 276 2004, Koch et al. 2006, Widdows et al. 2008, Paul and Gillis 2015) seemed to break  
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17 277 down in the short canopies, as Christianen et al. (2013) also reported. If this is the  
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19 278 general case for very short canopies, then an easy-to-measure canopy metric that  
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21 279 predicts seagrass-hydrodynamic relations would be especially valuable in regions such  
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23 280 as Indonesia where state-of-the-art facilities for hydrodynamic studies are lacking.  
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38  
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43 289 and supplemented the housing for the Indonesian researchers. Seagrasses were imported  
44  
45 290 for research under Permit #P588-140711-003 from the US Animal and Plant Inspection  
46  
47 291 Service. We dedicate this study to the memory of our dear colleague Evamaria Koch.  
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387 Table 1. Mean (SD) seagrass and hydrodynamic variables. 'No seagrass' is the average of two flume calibrations without seagrass  
 388 (N/A: Not applicable). Canopy height in flume (n = 55 leaves). Depth ratio: flume water depth/canopy height. Turbulence and  
 389 turbulence intensity: average of heights  $\geq 5.5$  cm above the bottom (n = 4). LAI: one-sided leaf area/m<sup>2</sup> in flume. Leaf shoots/m<sup>2</sup> of  
 390 mesh in flume. Natural bed leaf shoot density from 1 m x 1 m quadrats (n = 4).

Canopy Type	Canopy height (cm)	Depth ratio	Turbulence (m/s)	Turbulence intensity (%)	Shear velocity U* (m/s)	LAI (m <sup>2</sup> /m <sup>2</sup> )	Leaf biomass (g dry)	Leaf shoots/m <sup>2</sup>	Natural bed leaf shoots/ m <sup>2</sup>
<i>Enhalus</i>	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
<i>Cymodocea</i>	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
<i>Thalassia</i>	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
<i>Syringodium</i>	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
<i>Halodule</i>	4.3 (0.2)	10.3	0.400 (0.014)	63 (1)	0.016	0.050	0.8	522	1583 (540)
No seagrass	N/A	N/A	0.398 (0.011)	65 (1)	0.104 (0.018)	N/A	N/A	N/A	N/A

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3 394 **Figure Legends**  
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8 396 Fig. 1. Current speed and direction at the seagrass collection site, Barranglombo,  
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10 397 Spermonde, south Sulawesi, Indonesia.  
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14 399 Fig. 2. Water flow velocity profiles for a 1-m long seagrass bed  
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17 400 of each of five seagrass species measured in a flume (44 cm water depth) at 0.60 -  
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19 401 0.65 m/s freestream flow speeds. Dashed line indicates the mean height of the leaf  
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21 402 canopy by species. Two velocity profiles were averaged for the flume calibration  
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23 403 without seagrass. The error bars indicate standard errors.  
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28 405 Fig. 3. Shear velocity  $U^*$  (m/s) versus Leaf Area Index ( $m^2/m^2$ ).  
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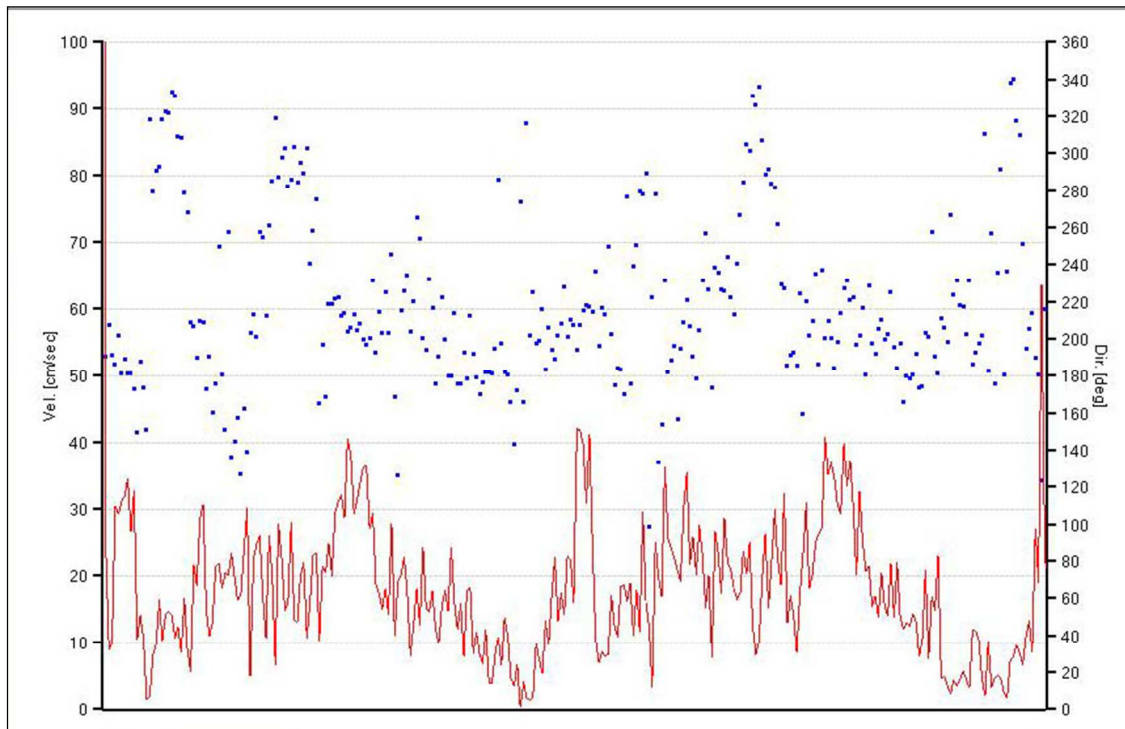
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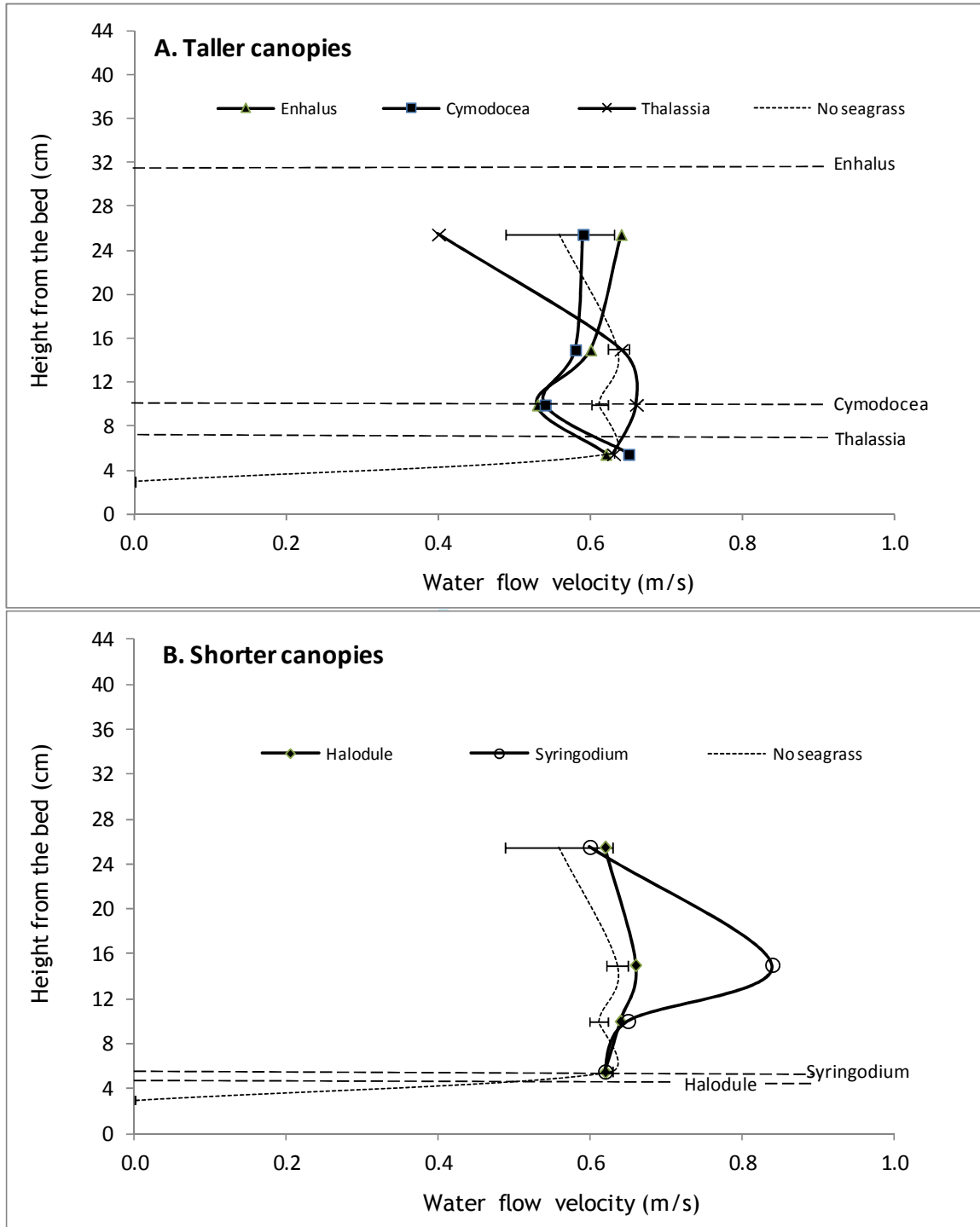
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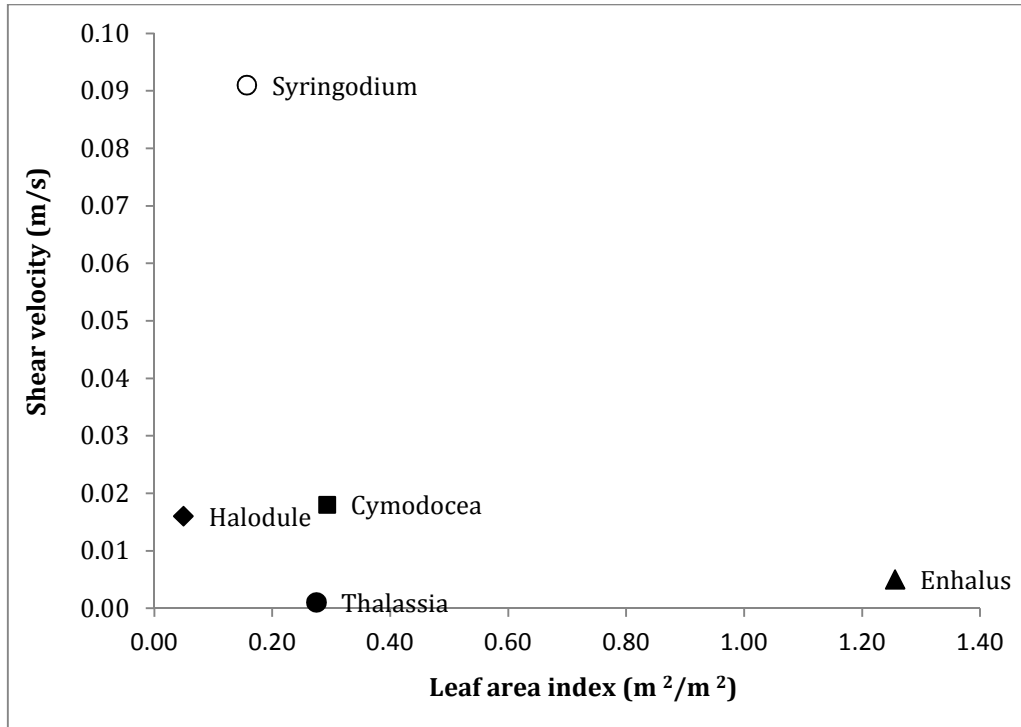


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9 **Figure 3**



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For Review Only

**Decision Letter (BOTMAR.2017.0037)****From:** bot.mar.editorial@degruyter.com**To:** mahat70@gmail.com**CC:****Subject:** Hydrodynamics in Short Indo-Pacific Seagrasses: Decision Major revision**Body:** Dear Dr. Lanuru:

Thank you again for submitting your manuscript BOTMAR.2017.0037 entitled: "Hydrodynamics in Short Indo-Pacific Seagrasses" to our journal Botanica Marina (BOTMAR).

Your manuscript has been reviewed and requires some major modifications before it can be accepted. The very detailed and constructive comments of the reviewers are included at the bottom of this letter, and in an attachment from Reviewer 2 (Review - Hydrodynamics\_in\_short\_indo\_pacific\_seagrasses.pdf). Please follow the advice that the reviewers offer. I have also read through most of your manuscript carefully, and my suggestions and comments are tracked in the attached file (Lanuru+al2017BotMar0037-Text+EditorComments.docx). I have identified some examples of the "incidences of informal writing" (primarily the overuse of first person) and "some obvious grammatical errors" mentioned by Reviewer 2, as well as the need to adjust some aspects of the formatting to conform to the style of the journal (see attached 'Instructions for Authors'). It is also important to submit your figures as files in graphics format (jpg or tiff). In addition, please note the paragraph below about the material that will be needed for a 'Graphical abstract' and 'Author biographies'.

I invite you to respond to these comments and to revise your manuscript. The revised paper needs to be submitted within 60 days from now but, if you can complete the revisions more quickly than this, we should be able to publish your article online within about one month of acceptance.

To revise your manuscript, log into <https://mc.manuscriptcentral.com/botmar> and enter your Author Center, where you will find your manuscript title listed under "Manuscripts Awaiting Revision". Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

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When submitting your revised manuscript, there is no need to respond to all the comments, but it will be helpful if you can indicate what significant changes you have made.

You will be able to respond to the comments made by the reviewers under File Upload - File Designation - Author's Response to Reviewer/Editor Critique.

You will be unable to make your revision on the originally submitted version of the manuscript. Instead, revise your manuscript and save it on your computer. There is no need to highlight the changes to your manuscript within the document by using underlined or coloured text, but it will be helpful if you can indicate where significant passages of new text have been added. Once the revised manuscript is prepared, you can upload and submit it through your Author Center. Your original files are available to you when you upload your revised manuscript. You may delete these files or keep them.

Please pay attention to the order of your uploaded files: the first one is the reply to the reviewers' comments, followed by the revised manuscript, and, if applicable, Tables and Figures, and Supplementary Material.

If you decide to keep the original files, these must be the last ones in the order of your uploaded files.

When submitting your revised script, please include - at the end of the main text file - the text and illustrations that will be needed for the 'Graphical abstract' and 'Author biographies' that are being published for all articles in Botanica Marina from the start of 2015. You will find details of what is required in the section headed 'Manuscripts accepted for publication' on p.2 of the 'Instructions for Authors' (copy attached). You can find examples of both Graphical abstracts and Author biographies in any issue of Botanica Marina published since February 2015. You may find these helpful in designing and writing these 'extras' for your own manuscript. Please also submit all the illustrations for these 'extras' in graphics (jpg or tiff) format with your revised manuscript.

Once again, thank you for submitting your manuscript to Botanica Marina. I look forward to receiving your revision.

Best wishes,  
Matt Dring

Prof. Matthew J. Dring  
Editor in Chief, Botanica Marina

**Reviewers' Comments to Author:****Reviewer: 1**

The submitted manuscript Bot Mar 2017 37 "Hydrodynamics in Short Indo-Pacific Seagrasses" by Lanuru et al. describes how Indo-Pacific seagrass canopies affect the hydrodynamics in their surrounding micro-habitats. One set of measurements is done in the field and most of the work was conducted in a flume. The ms covers a highly interesting aspect of seagrass biology and ecology and is relatively unique in the attempt to study Indo-Pacific species. The topic is suitable for the journal. However, several aspects of the study/manuscript need reconsideration. There are unclear sections in the methodology that need clarification. For example, I wonder why the water velocity in the flume was set at relatively high 0.6 m/s instead of using a range of more realistic velocities. The presentation of the results needs attention. Instead of discussing their own results (looking at the figures I see the need of that), most of the Discussion covers a literature review. I provide detailed comments and suggestions for improving the manuscript below. I suggest that the ms is reconsidered after a major revision.

**Detailed suggestions and comments:****Title**

You refer to short seagrasses, but you studied *Enhalus*, a species with relatively long blades. Change the title accordingly.

**Abstract**

P3 L39 Avoid using first person throughout the ms. Moreover, never start the abstract with "We provide...". I suggest removing the first sentence.

P3 L43-48 Why do you repeat the names of the seagrass species? There must be a more elegant solution to explain that you studied mixed-species canopies, if that is what you did.

P3 L50 I am surprised that you studied *Enhalus* as your title refers to short seagrasses.

P3 L54 When you refer to *Halodule* in your conclusions, you should also provide brief results about this species.

**Keyword**

No comments.

**Introduction**

P5 L112 Here happens the same as in the abstract; all species names are repeated. I do not understand why. Explain or remove one set.

P5 L117 "including some very short ones". I do not understand what this refers to; the length of the blades? Rephrase.

P5 L117 Also, there is no reason to refer to your Results and Discussion in your introduction. Remove.

**Materials and methods**

P6 L121 Avoid using "our seagrass bed". It is not yours, is it?; you just visited it to conduct your research.

P6 L122 Again. Avoid first person throughout the ms.

P6 L129 How did you remove epiphytes without damaging the shoots? Provide more detail.

P6 L131 Does that mean that the plants survived one year in the lab before using them in the flume?

P6 L135 You had only 1 cm of sediment? (So, there was some variation See L144).

P7 L153 Not completely clear how you calculated the 'lateral' leaf area for *Syringodium*. Did you measure the width (like you did for the other seagrasses [= diameter]) and multiply that by the length and pi? If so, you will have to redo it and use the radius. Please clarify.

P7 L153 Why 60 degrees C? I am familiar with 105 degrees C for dry weight.

P7 L163 Was the mesh layer thicker than 1.8 cm or did the probe have an extension that did not allow to measure closer to the bottom? Without seagrass you were able to measure at 3 cm. The mesh should have been used when you measured without seagrass to actually determine the effect of the seagrass and avoid the impact of your methodology. Now, your results are based on a combined effect of the mesh and the seagrass.

P7 L164 How often did you measure 'every two minutes'?

P7 L165 This refers to the above. So, did you deduct this value from your results?

P8 L178 Present the proxies in order of appearance in the formula.

**Results**

P8 L188 Which central tendency (average) did you use? Refer to 'mean', which I think you used.

P8 L191 "Conditions were calm .... during spring tides". This seems contradictory. Then you must have measured during high tide, I guess (the is no information on the X-axis in Figure 1). Rephrase. Moreover, this sentence should go to the methodology, because it is your basis for deciding to work with 0.6 m/s. How do you know that 0.6 m/s is a reasonable value?

P8 L192 Same as above. Change throughout the ms.

P9 L196 How can *Thalassia* significantly reduce velocity at 25 cm when its canopy is only 7 cm high? In this sentence you state that *Thalassia* has 'less so' impact than the other grasses. Explain.

P9 L212 Provide information about the statistical analyses in the methodology. Also, present your test results in a commonly used format.

**Discussion**

P10 L220 So they were in poor condition? That is the first time I read about that. Does this have to do with the experiment being conducted one year after the collection of the plants?

P10 L221 I do not see this in figure 2.

**Acknowledgements**

L286 Provide surnames to each person.

**References**

No comments.

Table 1 Provide the scientific names for the species; the table must provide all information as a stand-alone unit. What do the values in parentheses represent? Standard error?

Figure 1 What does the X-axis represent? Label.

It would be very interesting to know which species (and at what ratio) appeared at this site.

Figure 2 Reduce the range of the X-axis to better show the variation between the several measurements/lines. Information about standard error must be provided in the methodology.

How can flow increase up to almost 9 m/s above the canopy? And this is a mean value... (where is the error bar?) Standard errors are missing at several points in both graphs. Why?

**Reviewer: 2**

I've put all of my comments in the attached file (Review - Hydrodynamics\_in\_short\_indo\_pacific\_seagrasses.pdf).

**Date Sent:** 14-Jun-2017**File 1:** [BotanicaMarina-InstructionsForAuthors.pdf](#)**File 2:** [Lanuru-al2017BotMar0037-Text-EditorComments.docx](#)**File 3:** [- Review - Hydrodynamics in short indo pacific seagrasses.pdf](#)**Files attached**

[Review - Hydrodynamics in short indo pacific seagrasses.pdf](#)

 Close Window

*August 13, 2017*

Professor Matthew Dring  
Editor-in-Chief, *Botanica Marina*

Dear Professor Dring,

We are submitting a major revision of the manuscript BOTMAR.2017.0037, with a revised title of "Hydrodynamics in Indo-Pacific Seagrasses with a Focus on Short Canopies". We thank you for your comments and the reviewers for their detailed comments and appreciated their interest in the subject and results.

The Response to Reviewers, in which every comment was addressed, was uploaded. The major changes include more detailed explanations of the flume measurements, explanations for two outlier points, revisions of each figure, and an expanded discussion. The formats of the figures and the references were standardized according to the Instructions for Authors.

We thank you for your attention and look forward to hearing your response.

Kind Regards,  
Dr Mahatma Lanuru  
Lecturer and Head of Marine Science Department,  
Hasanuddin University, Indonesia

BOTMAR.2017.0037

Lanuru et al. "Hydrodynamics in Short Indo-Pacific Seagrasses"

Response to Professor Dring, Editor

'Monami' is the term coined to describe waving of seagrasses and the description and details are found in the reference we cited.

'Batting' is correct. Its definition is "cotton wadding prepared in sheets"

## Response to Reviewers

Reviewers' Comments to Author:

Reviewer: 1

The submitted manuscript Bot Mar 2017 37 "Hydrodynamics in Short Indo-Pacific Seagrasses" by Lanuru et al. describes how Indo-Pacific seagrass canopies affect the hydrodynamics in their surrounding micro-habitats. One set of measurements is done in the field and most of the work was conducted in a flume.

The ms covers a highly interesting aspect of seagrass biology and ecology and is relatively unique in the attempt to study Indo-Pacific species. The topic is suitable for the journal. However, several aspects of the study/manuscript need reconsideration. There are unclear sections in the methodology that need clarification. For example, I wonder why the water velocity in the flume was set at relatively high 0.6 m/s instead of using a range of more realistic velocities. The presentation of the results needs attention. Instead of discussing their own results (looking at the figures I see the need of that), most of the Discussion covers a literature review. I provide detailed comments and suggestions for improving the manuscript below. I suggest that the ms is reconsidered after a major revision.

**Response:** We thank the reviewer for his/her comments and high interest in the subject.

Below, we explain the selection of the flume flow speed in more detail.

Detailed suggestions and comments:

Title

You refer to short seagrasses, but you studied *Enhalus*, a species with relatively long blades. Change the title accordingly.

**Response:** Title was changed to "Hydrodynamics in Indo-Pacific Seagrasses with a Focus on Short Canopies"

Abstract

P3 L39 Avoid using first person throughout the ms. Moreover, never start the abstract with "We provide...". I suggest removing the first sentence.

**Response:** First sentence was deleted. The authors note that there has been a shift in biological and ecological publications to using first person. That said, the number of times first person is used in the manuscript has been reduced.

P3 L43-48 Why do you repeat the names of the seagrass species? There must be a more elegant solution to explain that you studied mixed-species canopies, if that is what you did.

**Response:** Single species were measured in the study, so each species was listed.

P3 L50 I am surprised that you studied *Enhalus* as your title refers to short

seagrasses.

**Response:** The title was changed. While conducting the study we realized that the hydrodynamics of short canopies have not been addressed much in the literature, which then we emphasized as a novel aspect of our study, despite its limitations.

P3 L54 When you refer to *Halodule* in your conclusions, you should also provide brief results about this species.

**Response:** We combined *Halodule* in the results for short species and reported that they had no observable effect on mean velocities.

Keyword

No comments.

Introduction

P5 L112 Here happens the same as in the abstract; all species names are repeated. I do not understand why. Explain or remove one set.

**Response:** We deleted the species from the Introduction and added them and their taxonomic authorities to the Materials and Methods.

P5 L117 "including some very short ones". I do not understand what this refers to; the length of the blades? Rephrase.

**Response:** The wording was changed to "...including some with very short leaves.."

P5 L117 Also, there is no reason to refer to your Results and Discussion in your introduction. Remove.

**Response:** The reference was deleted.

Materials and methods

P6 L121 Avoid using "our seagrass bed". It is not yours, is it?; you just visited it to conduct your research.

**Response:** "Our" was changed the "The".

P6 L122 Again. Avoid first person throughout the ms.

**Response:** Third person was used more in the revision, including this line.

P6 L129 How did you remove epiphytes without damaging the shoots? Provide more detail.

**Response:** The revised manuscript states that the epiphytes were removed by gently wiping the leaves with a soft towel.

P6 L131 Does that mean that the plants survived one year in the lab before using them in the flume?

**Response:** The wording was changed to "In September 2014, the leaf shoot densities of .... were measured...before collecting intact rhizomes...". The measurements were made as soon as the air shipment arrived at Bodega Marine Laboratory.

P6 L135 You had only 1 cm of sediment? (So, there was some variation See L144).

**Response:** The flume floor was not filled with sediment, which could not be removed from the research flume. The flume was used for many other research applications, all of which were not in soft sediments. The seagrasses were attached to the mesh to anchor them. The variation in the mesh height above the bottom was very small and caused by differences in the rhizome thickness, but the mesh had a limited effect on the flow speed.

P7 L153 Not completely clear how you calculated the 'lateral' leaf area for

Syringodium. Did you measure the width (like you did for the other seagrasses [= diameter]) and multiply that by the length and pi? If so, you will have to redo it and use the radius. Please clarify.

**Response:** Leaf area was measured in a leaf area meter (l. 150). The lateral surface area of a cylinder is the circumference ( $= \pi \times \text{diameter}$ ) multiplied by the height. The leaf area meter measurement is equal to the diameter x the height. We believe the lateral leaf area as calculated is correct. [Lateral surface area definitions and equations can be found in trigonometry textbooks or online.]

P7 L153 Why 60 degrees C? I am familiar with 105 degrees C for dry weight.

**Response:** The biomass was dried to constant mass and thus the temperature makes little difference. A temperature below 90 degrees C preserves nitrogenous compounds and thus allows dried samples to be retained for other purposes, if desired.

P7 L163 Was the mesh layer thicker than 1.8 cm or did the probe have an extension that did not allow to measure closer to the bottom? Without seagrass you were able to measure at 3 cm. The mesh should have been used when you measured without seagrass to actually determine the effect of the seagrass and avoid the impact of your methodology. Now, your results are based on a combined effect of the mesh and the seagrass.

**Response:** We measured the flume velocity with only the mesh in the flume and it had a minimal effect on the velocity in the flume (l. 166). The average height of the mesh above the bottom was 1.8 cm. With the mesh in place, the probe could only be positioned 5.5 cm above the flume bottom. All seagrass measurements were made with the mesh in place, so the effect of the mesh was comparable across the species.

P7 L164 How often did you measure 'every two minutes'?

**Response:** We are not certain we understand this question. At each position (height) above the bottom, velocity was sampled for 2 minutes once the velocity stabilized after repositioning the ADV. The sampling rate was 200 measurements per second over the 2 minutes.

P7 L165 This refers to the above. So, did you deduct this value from your results?

**Response:** Again, we are sorry that we do not understand this and the above question. The ADV provides a continuous readout and running graph to visualize extreme measurements as the sensor is repositioned. As typical in these types of measurements, one can see the trace on the plot "settling down" and becoming "steady", which became the time point we selected for the digital data processing. The aberrations in the flow caused by moving the probe to a new position were also easily discernable on the digital record (which obviously was used for the software-produced readout).

P8 L178 Present the proxies in order of appearance in the formula.

**Response:** The order was changed.

Results

P8 L188 Which central tendency (average) did you use? Refer to 'mean', which I think you used.

**Response:** "Average" was changed to "mean".

P8 L191 "Conditions were calm .... during spring tides". This seems contradictory. Then you must have measured during high tide, I guess (there is no information on the X-axis in Figure 1). Rephrase. Moreover, this sentence should go to the methodology,

because it is your basis for deciding to work with 0.6 m/s. How do you know that 0.6 m/s is a reasonable value?

**Response:** The sentence was moved to Methods. The field measurements were made over 3 days and thus over both low and high tides.

The flume speed is close to the maximum velocity in the 3-day field record (Fig. 1). Measurements covering a longer time period would likely include days with stronger wind and wave action and thus higher velocities than measured during the calm period.

P8 L192 Same as above. Change throughout the ms.

**Response:** Measurement conditions were moved to Methods.

P9 L196 How can *Thalassia* significantly reduce velocity at 25 cm when its canopy is only 7 cm high? In this sentence you state that *Thalassia* has 'less so' impact than the other grasses. Explain.

**Response:** We removed the reference to *Thalassia*. In the revision we discuss that reason why this point might be an outlier.

P9 L212 Provide information about the statistical analyses in the methodology. Also, present your test results in a commonly used format.

**Response:** The statistical method (linear regression) was described on p. 7, l. 182 of the original manuscript. **We searched Botania Marina for a 'commonly used format' but did not find one.** We provided the p and  $r^2$  values from the regressions.

#### Discussion

P10 L220 So they were in poor condition? That is the first time I read about that. Does this have to do with the experiment being conducted one year after the collection of the plants?

**Response:** We did not say the plants were in poor condition but rather we needed to take measurements *before* the plants began to degrade. As mentioned in a comment above, the phrasing was changed to reflect the fact that the seagrasses were collected, air-shipped to the flume facility where measurements were made.

P10 L221 I do not see this in figure 2.

**Response:** This sentence was rewritten to state "First, water flow speeds in *Enhalus* and *Cymodocea* canopies were reduced between 4 - 16 cm height above the bottom."

#### Acknowledgements

L286 Provide surnames to each person.

**Response:** Steven *Limpong* was added.

#### References

No comments.

Table 1 Provide the scientific names for the species; the table must provide all information as a stand-alone unit.

**Response:** The scientific names were added.

What do the values in parentheses represent? Standard error?

**Response:** The legend was clarified as "Mean and standard deviation (in parenthesis) seagrass and hydrodynamic variables." The original manuscript stated Mean (SD).

Figure 1 What does the X-axis represent? Label.

It would be very interesting to know which species (and at what ratio) appeared at this site.

**Response:** The seagrasses used in the flume were collected from monospecific stands.

Figure 2 Reduce the range of the X-axis to better show the variation between the several measurements/lines. Information about standard error must be provided in the methodology.

How can flow increase up to almost 9 m/s above the canopy? And this is a mean value... (where is the error bar?)

**Response:** We cannot explain this outlier point. However, outliers in a velocity profiles in flumes is not unusual, probably due to variation a wobble in the ADV or a transient difference in flume conditions (e.g., as caused by a power surge). For example, published velocity profiles also show outlier points (please see Fig. 2 in Gambi et al., 1990 and Fig. 1 in Fonseca and Koehl, 2006).

Standard errors are missing at several points in both graphs. Why?

**Response:** As explained in the first part of the discussion, we were not able to replicate any measurements except the flume calibration due to logistics limitations (time allotted for Indonesian coauthors for visit to US).

## Response to Reviewer #2

### Introduction

This study examines how the canopies of 5 seagrass species (both long and short) influence the hydrodynamics flowing through and over the canopy. There is only one replicate, so the data is qualitative, but indicates that water flow is attenuated within taller canopies but not short canopies. While both long and short seagrass species reduce the shear velocity, however, there was no correlation between LAI, biomass or canopy height to this reduction in shear velocity. This paper shows that even short seagrass species can be used to help stabilize sediment and aid restoration efforts, however, the authors identify a need for further research.

### Merits

This study looks at 5 varying seagrass species, and considering there is no replication, does not overstate the conclusions. The authors make clear the intended practical application of using this information to aid restoration efforts, and as a beginning point for future work. The effect of short canopies on reducing shear velocity is an interesting result.

### Critique

In general, the writing requires some work (although the discussion is quite well written), there are a few incidences of informal writing, statements that require more explanation, and some obvious grammatical errors.

The methods require further explanation. The *in-situ* flow measurements were made 1.5 m above the substratum, this is quite some distance from where the seagrass would inhabit, and flow conditions may be different, so this depth needs to be justified in the text. The shoot density used for the patches in the flume work is also significantly lower than what is measured *in-situ*, and should be explained. In the flume work, it is stated that the ADV measurements were centered in the width, but not where in the length of the seagrass patch, which is critical considering the seagrass patches were one meter long, and therefore, the velocity is likely to vary along the patch if attenuation is occurring.

**Response:** The meter was deployed in freestream flow conditions, that is, away from the bottom and over 1 m above the seagrass canopy. The height was chosen to avoid boundary layer effects created by the bottom and the canopy.

The ADV was positioned halfway along the length of the seagrass bed (50 cm) from the edge.

The above information was added to the Methods. Lower-than-natural seagrass density occurs in a restoration, which is a point that was added to the revised discussion on  $U^*$  and sediment stabilization.

Considering replication was not possible, but a lot of work went into creating the patches of seagrasses in the flume, the research would have benefited from more water flow measurements in the flume. Such as, measuring the effect of the seagrass patches at varying water speeds, and/or measuring water flow in more areas of the patch (e.g. start, middle, and end). More water flow measurements in seagrass patches *in situ* could also be used to strengthen the study.

**Response:** We also wanted to expand the study but it was not possible given the resources and the distance the seagrasses and Indonesian coauthors had to travel to conduct the study. Their time was limited both by their grant and obligations at their home university.

Given this limitation, these types of desirable studies were added to the Discussion where we present future research needs.

Fig. 2 shows an obvious increase in water speed at 15 cm height for the *Syringodium* canopy, yet nothing is mentioned of this peak. An increase in water flow by a skimming effect is described in the discussion, which could be related back to this result along with the smaller turbulence intensity. There is also no mention or reasoning for the drop-in water flow at the top height for *Thalassia*.

**Response:** In the first part of the revised discussion we state that because there was unfortunately no replication, we cannot differentiate whether these points were outliers or seagrass effects. We suspect they are outliers for the reasons provided in the discussion (transient wobble in the ADV, power surge). Outliers are not unusual in published velocity profiles taken in flumes (references provided in revision). Because of these uncertainties, we are uncomfortable suggesting the skimming flow was occurring.

#### **Additional comments for authors:**

39-40: The beginning of the abstract doesn't flow very nicely when reading. I would recommend moving the first sentence nearer to the end of the abstract. And elaborate more on why seagrass hydrodynamic regimes are important to understand (coastal protection services, nursery refugia etc.), please don't just say "in general".

**Response:** The first sentence and "in general" were deleted. "Hydrodynamics influence the physical stability of seagrass beds, sedimentation rates, and the advection of nutrients and food to seagrasses and associated organisms" was added.

43-48: Species list has been repeated twice.

**Response:** The repetition was deleted.

73: Need to explain how water flow affects physiological processes, food availability etc.

**Response:** In the following paragraph in which we summarize the major possible effects of seagrass on hydrodynamics, we added specific examples.

77: Why is seagrass-hydrodynamic relationship important for successful restoration efforts, need to elaborate on this point more.

**Response:** The rationale was added: "Understanding the seagrass-hydrodynamic relationship is also important for successful restoration efforts *because currents or wave action can uproot fragile seagrass transplants* (Fonseca and Fisher 1986, van Katwijk et al. 2009)."

In the discussion we added that hydrodynamics can affect leaf loss from a seagrass transplant or even the entire transplantation.

79: "attenuating of water flow" should be "attenuating the water flow"

**Response:** The wording was corrected.

81: Sentence doesn't make sense (and thus, the boundary layer of more viscous, slower flow)

**Response:** The sentence was revised to "...changing the velocity profile close to the bottom and affecting the boundary layer of more viscous, slower flow"

85: Informal to say "mentioned above", and "these reviews and other references". Need to be more specific.

**Response:** We changed the wording to "The reviews by Madsen et al. (2001) and Koch et al. (2006) highlight that seagrass-hydrodynamic studies differ widely....".

109-114: the seagrass names are repeated twice (again)

**Response:** The repetition was removed.

201-203: This statement is more of a discussion statement, and should be said in the discussion to explain the results of *Enhalus*.

**Response:** This explanation was moved into the first paragraph of the revised Discussion.

In the future, a false bottom in the flume could be used to remove the effect of the mesh that the seagrass was attached to.

**Response:** We understand this point but a false bottom cannot be added to the model of flume available at the Bodega Marine Laboratory.

Need to be consistent when using shear velocity or  $U^*$ . First mention of shear velocity, ' $U^*$ ' should be put in brackets, and then after can just use  $U^*$  instead of saying shear velocity (or just continue saying shear velocity but don't use  $U^*$  in the text, otherwise it gets confusing).

**Response:**  $U^*$  is consistent throughout the revised manuscript except where it is first mentioned in the Discussion, where 'shear velocity' is added parenthetically to remind readers who might not be familiar with  $U^*$ .



## Hydrodynamics in Indo-Pacific Seagrasses with a Focus on Short Canopies

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Manuscripts

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3 **1 Hydrodynamics in Indo-Pacific Seagrasses with a Focus on Short Canopies**  
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33 **24 Running title:** Seagrass hydrodynamics  
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36 **Abstract**

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38 Seagrass hydrodynamic regimes are important to understand and also to guide seagrass  
39 restoration, which is of great interest in Indonesia because of environmental threats to  
40 the exceptionally high seagrass species richness. Hydrodynamic regimes influence the  
41 physical stability of seagrass beds, sedimentation rates, and the advection of nutrients  
42 and food to seagrasses and associated organisms. In a flume, we determined the effect  
43 of canopies of *Cymodocea rotundata*, *Enhalus acoroides*, *Halodule uninervis*,  
44 *Syringodium isoetifolium*, and *Thalassia hemprichii* at natural densities on water  
45 velocity, turbulence, turbulence intensity, and shear velocity. The taller canopies of  
46 *Enhalus* and *Cymodocea* slowed water flow, but the shorter canopies (<5 cm) had little  
47 effect. Seagrasses did not influence turbulence and turbulence intensity (turbulence  
48 normalized to mean velocity) but they reduced shear velocity  $U^*$ . Our results indicate  
49 that *Enhalus* is a good candidate for transplantation in terms of reducing mean water  
50 flow and shear velocities, but that *Halodule* should also be considered as it also reduced  
51 shear velocities and it spreads quickly after transplantation. Our results extend the  
52 understanding of seagrass-hydrodynamic relationships to include very short canopies,  
53 unlike the taller canopies studied to date.

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55 **Keywords:** *Cymodocea*, *Enhalus*, hydrodynamics, Indonesia, seagrass

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3 **56 Introduction**  
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5 Seagrass leaf canopies profoundly influence water flow dynamics. In turn, water  
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7 flow dynamics influence both the physical marine environment by affecting sediment  
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9 deposition and resuspension and the associated biological communities through effects  
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11 on physiological processes, food availability, larval recruitment and dispersal (Eckman  
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13 1987, Thomas et al. 2000, Williams and Heck 2001, Koch et al. 2006, González-Ortiz et  
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15 al. 2014). Understanding the seagrass-hydrodynamic relationship is also important for  
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17 successful restoration efforts because currents or wave action can uproot fragile  
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19 seagrass transplants (Fonseca and Fisher 1986, van Katwijk et al. 2009).  
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23 In general, seagrass canopies modify the hydrodynamic environment within and  
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25 around them by: 1) attenuating the water flow and dissipating wave energy, promoting  
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27 the retention of sediments and biological particles, 2) changing the velocity profile close  
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29 to the bottom and affecting the boundary layer of more viscous, slower flow, 3)  
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31 increasing or decreasing the turbulence and thus advection (the transport of materials),  
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33 and 4) propagating monamis, or leaf waving, which enhances advection (reviewed in  
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35 Madsen et al. 2001 and Koch et al. 2006). These influences in turn govern the  
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37 ecological processes mentioned above. For example, very slow water flow, decreased  
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39 turbulence and advection can create mass transfer limitation of critical substrates  
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41 including carbon dioxide and dissolved nutrients to seagrass and associated primary  
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43 producers (Thomas et al. 2000, Koch et al. 2006). Reduced advective fluxes of food  
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45 particles and larvae can limit the recruitment, survival, and growth of animals living  
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47 within the seagrass bed. High flow speeds can rip seagrasses from the substratum. The  
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49 reviews by Madsen et al. (2001) and Koch et al. (2006) highlight that seagrass-  
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51 hydrodynamic studies differ widely in their approach and results and that more research  
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60 is required to build a comprehensive understanding of the specific ways in which

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3 81 seagrasses influence water flow. Of note for our study is that most seagrass-  
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5 82 hydrodynamic studies have been devoted to temperate species and to canopies that are  
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7 83 relatively tall (> 5 cm, see Discussion).  
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10 84 The influence of a seagrass canopy on water flow depends on its physical  
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12 85 structure. Most simply, in the case of a continuous monospecific canopy, structure is  
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14 86 dictated by leaf morphology (including stiffness and length relative to water depth),  
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16 87 density, and arrangement, while patchiness in the meadow influences water flow at the  
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18 88 larger landscape scale (references above; Nepf and Vivoni 2000, Bouma et al. 2005,  
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20 89 Fonseca et al. 2007, Peralta et al. 2008). Leaf morphology varies widely in size and  
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22 90 shape across seagrass genera and species (Duarte 1991), ranging from straps (*Enhalus*,  
23  
24 91 *Posidonia*, *Thalassia*, *Zostera*, *Cymodocea*, *Halodule*), small ovals (*Halophila*),  
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26 92 cylinders (*Syringodium*), to more complex shapes (*Thalassodendron*, *Amphibolis*).  
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28 93 Seagrass morphology itself adjusts plastically to hydrodynamic regimes (Peralta et al.  
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30 94 2006).  
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34 95 The objective of our study was to generate some basic understanding of the  
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36 96 effect of common Indonesian seagrass species on water flow dynamics. Although  
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38 97 Indonesia is a centre of seagrass species richness (Green and Short 2003, Short et al.  
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40 98 2007), its seagrasses have been studied relatively little compared to coral reefs and  
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42 99 mangroves (Orth et al. 2006), despite the fact that Indonesian seagrasses are threatened  
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44 100 by many factors (Nadiarti et al. 2012). To generate baseline information, we measured  
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46 101 basic hydrodynamic descriptors of the canopies of five species, which differ widely in  
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48 102 leaf morphology and thus canopy structure, under controlled conditions in a laboratory  
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50 103 flume. The species are common throughout the Indo-Pacific region where they form  
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52 104 monospecific and mixed-species canopies, including ones with very short leaves.  
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3 106 **Material and methods**  
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5 107 The field seagrass bed was located at Barranglompo Island (5°03'S, 119°20'E)  
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7 108 in the Spermonde Archipelago, south Sulawesi, Indonesia. We measured freestream  
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9 109 water flow speed and direction every minute for 48 hours (19-21 October 2013) using  
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11 110 an Infinity Series ver. 0.10 current meter (JFE Advantech Co., Ltd. 3-48 Takahata-cho,  
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13 111 Nishinomiya, Hyogo, Japan 63-8202). The current meter was deployed in freestream  
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15 112 flow at 1.5 m above the substratum (water depth = 4 m) and over a meter above the  
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17 113 seagrass canopy. Freestream flow, i.e., where there are no boundary layer influences  
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19 114 caused by friction with the bottom and the seagrass, was measured to estimate flow  
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21 115 speeds to be used in the flume study described below. Measurements were recorded  
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23 116 during a spring tide cycle and under calm wind and wave conditions.  
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27 117 In September 2014, the leaf shoots of *Cymodocea rotundata* Ascherson &  
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29 118 Schweinfurth, *Enhalus acoroides* (Linnaeus f.) Royle, *Halodule uninervis* (Forsskål)  
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31 119 Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii*  
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33 120 (Ehrenberg) Ascherson were counted in 1-m<sup>2</sup> quadrats (n = 4 per species) in  
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35 121 monospecific stands before collecting intact rhizomes with attached leaf shoots.  
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37 122 Seagrasses were rinsed of sediments and epiphytes removed by gently wiping the leaves  
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39 123 with a soft towel, cushioned by plastic fibre batting, and placed in coolers for air  
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41 124 shipment to the Bodega Marine Laboratory, University of California at Davis, USA,  
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43 125 where flume studies were conducted.  
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47 126 A straight flume (Model 504, Engineering Design Laboratory, Lake City,  
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49 127 Minnesota 55041-0278, USA, working section 45 x 45 x 250 cm) was used to  
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51 128 characterize the effect of the leaf canopy on water flow dynamics. The flume was filled  
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53 129 with seawater to a depth of 44 cm above the bottom and the seawater was not changed  
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55 130 during the experiment. Measurements were made at a flume speeds of 0.60 - 0.65 m/s.  
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3 131 The velocity was chosen to be at the high end of the field conditions recorded over 48  
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5 132 hours because undoubtedly the velocity would reach higher levels under less calm field  
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7 133 conditions.

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10 134 We created a seagrass bed (45 cm wide x 100 cm long) of each species using a  
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12 135 plastic-coated wire mesh (0.5 cm x 0.5 cm mesh size) fitted across the width of working  
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14 136 section and centred in the middle of the working section's length. To secure the buoyant  
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16 137 seagrass in the flume, we placed the rhizomes between two pieces of mesh, spacing  
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18 138 them irregularly to mimic their natural arrangement, added small lead fishing sinkers,  
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20 139 and threaded the leaf shoots through the top mesh layer. The edges of the mesh were  
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22 140 smoothed with duct tape. The mesh was placed as close to the flume bottom as possible  
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24 141 (average height above bottom:  $1.8 \text{ cm} \pm 0.43 \text{ SD}$ ,  $n = 275$  measurements). The mesh  
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26 142 created a rough bottom generally analogous to the rough bottoms created by small  
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28 143 pieces of coral rubble and animal tubes in Indo-Pacific seagrass beds. To compare the  
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30 144 experimental seagrass bed to the field and other studies, we counted the leaf shoots in  
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32 145 the mesh and measured the leaf canopy height as the distance between the mesh surface  
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34 146 and the longest leaf of 55 shoots of each species. We then clipped the leaves flush with  
35  
36 147 the mesh and measured leaf area (Li-Cor meter, Model Li-3100, Lincoln, Nebraska,  
37  
38 148 USA) to calculate the leaf area index (LAI) as the one-sided leaf area ( $\text{m}^2$ ) per  $\text{m}^2$  of  
39  
40 149 mesh. *Syringodium*'s cylindrical leaf area was calculated as the lateral area (leaf area  
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42 150 multiplied by  $\pi$ ). Leaves were oven-dried at  $60^\circ\text{C}$  until constant mass and weighed.  
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47 151 LAI, leaf biomass, and density theoretically relate to the canopy's influence on  
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49 152 hydrodynamics (Gambi et al. 1990, Koch et al. 2006, Peterson et al. 2004).

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51  
52 153 The water flow velocity in the flume was determined using an Acoustic Doppler  
53  
54 154 Velocimeter (ADV, Field Vetrino serial #VNO0224, Nortek AS, Vangkroken 2, NO-  
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56 155 1351 RUD, Norway) with Vetrino Plus software, a baud of 57600, and sampling rate  
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3 156 of 200 Hz. The ADV was centred in the width of the working section for all  
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5 157 measurements. The flume was calibrated by averaging velocity measurements without  
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7 158 seagrass at 3, 5.5, 10, 15, and 25.5 cm above the bottom at 38 and 116 cm from the  
8  
9 159 beginning of the working section. Seagrass measurements were made at midway along  
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11 160 the length of the mesh (50 cm downstream from the edge of the seagrass bed) at 5.5, 10,  
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13 161 15, and 25.5 cm heights and in the middle of the seagrass bed. Due to the mesh, the  
14  
15 162 closest the ADV could be positioned above the flume bottom was 5.5 cm. After velocity  
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17 163 stabilized upon repositioning the ADV, it was recorded over two minutes. The mesh  
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19 164 itself without attached seagrasses slowed the flow minimally by 0.049 m/s at  $\geq 5.5$  cm  
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21 165 above the bottom.  
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25 166 We calculated the mean velocity as the square root of the sum of squares of the  
26  
27 167 ADV's three velocity components averaged across instantaneous recordings made  
28  
29 168 during the measurement period. Turbulence, the measure of the variation in the average  
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31 169 flow, was calculated as the root mean square of the standard deviation of each velocity  
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33 170 component (Denny 1988, Gambi et al. 1990). Turbulence intensity (%) was calculated  
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35 171 as the turbulence divided by the mean velocity. The depth ratio (water depth/canopy  
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37 172 height) was calculated to compare hydrodynamic environments due to differences in  
38  
39 173 canopy heights in the flume (Nepf and Vivoni 2000).  
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43 174 The shear velocity  $U^*$  was determined from the von Karman-Prandtl velocity-  
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45 175 depth profile relationship (Denny 1988, Gambi et al. 1990):  
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47 176  $U(z) = U^*/K (\ln(z_2/z_1))$ , where:

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49 177  $U$  is the difference in velocity between two heights above the substratum ( $z_1$  and  $z_2$ ) and  
50  
51 178  $K$  = von Karman's constant (0.41). Depth  $z_1$  was 5.5 cm and  $z_2$  was 25.5 cm for *Enhalus*  
52  
53 179 and *Cymodocea*, 5.5 and 15 for *Syringodium* and *Halodule*, and 3 and 25.5 upstream,  
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55 180 respectively, to conform to the log relationship between velocity and height above the  
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3 181 bottom. We performed linear regressions of  $U^*$  versus LAI, canopy height, and density,  
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5 182 which can be predictors of the canopy's influence on hydrodynamics (Gambi et al. 1990,  
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7 183 Koch et al. 2006, Peterson et al. 2004).  
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10 184  
11 **Results**  
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13 186  
14 187 The mean water flow speed at the seagrass collection site was 0.160 m/s,  
15  
16 188 ranging from 0.002 to 0.430 m/s (Fig. 1), which corresponded to freestream flow at 18  
17  
18 189 cm above the flume bottom (Fig. 2, Table 1).  
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20 190 In the flume, mean velocities differed depending on the species (Fig. 2). The two  
21  
22 191 short species (*Syringodium*, *Halodule*, < 5 cm tall, Table 1) had no observable effect on  
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24 192 mean velocities compared to upstream (no seagrass, 0.600 - 0.650 m/s freestream flow  
25  
26 193 above 3 cm). Water flow decreased between 10 and 16 cm height above the bottom in  
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28 194 the *Enhalus* and *Cymodocea* experimental beds. At 24 cm, which was well above the  
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30 195 *Cymodocea* canopy's mean maximum height (Table 1) and approaching *Enhalus*'s mean  
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32 196 maximum canopy height, flow was equivalent to freestream conditions. Due to lack of  
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34 197 replication, the outliers at 24 cm in the *Thalassia* and at 16 cm in the *Syringodium*  
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36 198 profiles cannot be explained.  
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39 199 The depth ratio (Table 1) for all species except *Enhalus* was >2, indicating they  
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41 200 experienced similar hydrodynamic environments unconfined by water depth in the  
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43 201 flume (Nepf and Vivoni 2000) and that some cross comparisons can be made. The ratio  
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45 202 for *Enhalus* indicated that its canopy was at the transition between a depth-limited and  
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47 203 emergent canopy.  
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49 204 Seagrass canopies had minimal effects on turbulence and turbulence intensity  
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51 205 (Table 1). The taller canopies (*Enhalus*, *Cymodocea*, *Thalassia*) increased values only  
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53 206 2-3% compared to upstream (no seagrass) values.  
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3 207 All species reduced  $U^*$  ( $\leq 0.091$  m/s) compared to the no seagrass value (0.104  
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5 208 m/s) (Table 1). There was no relationship between  $U^*$  versus canopy height or LAI  
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7 209 (Fig. 3), which was highly correlated to leaf biomass (Pearson correlation coefficient =  
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9 210 0.988). These potential predictors of  $U^*$  explained only 25-36% of  $U^*$  variation (height  
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12 211  $p = 0.210$ ,  $r^2 = 0.357$ ;  $df = 1, 4$ ; LAI  $p = 0.318$ ,  $r^2 = 0.245$ ). Shoot densities, which were  
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14 212 within the low range of natural canopies (Table 1), explained  $<0.1\%$  of  $U^*$  variation ( $p$   
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16 213 = 0.976).  
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## 21 **Discussion**

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23 216 The data are limited to qualitative comparisons across species because there was  
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25 217 no replication within a species due to the logistical limitations inherent in bringing  
26  
27 218 seagrasses from Indonesia to the flume facility in California and keeping them in good  
28  
29 219 condition. We therefore cannot explain whether extreme points in the velocity profiles  
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31 220 are outliers or represent a seagrass effect. Outliers in flume velocity profiles are not  
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33 221 unusual and can result from a transient wobble in the ADV or a transient difference in  
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35 222 flume conditions, such as could result from a power surge. For example, published  
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37 223 velocity profiles also show outlier points (Fig. 2 in Gambi et al. 1990; Fig.1 in Fonseca  
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39 224 and Koehl 2006). Despite the lack of replication, there are some general patterns worth  
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41 225 noting that can be addressed in future studies. First, water flow speeds in *Enhalus* and  
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43 226 *Cymodocea* canopies were reduced between 4 - 16 cm height above the bottom. The  
44  
45 227 depth ratio for *Enhalus* (Table1), which in this study was measured in a situation  
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47 228 analogous to low tide in a shallow bed, a vertical exchange zone is predicted to develop  
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49 229 at the top of the canopy wherein the density and morphology influence the  
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51 230 hydrodynamics within the canopy, unlike in the 'unconfined' condition of very short  
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53 231 canopies (Nepf and Vivoni 2000). Second, seagrasses had minimal influence on  
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3 232 turbulence, the variation in the time-averaged mean velocity, which is important for the  
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5 233 advection of essential elements, pollutants, and biological and non-biological particles  
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7 234 (Denny 1988, Koch et al. 2006).  
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9  
10 235 Another important finding is that even the shorter canopies (< 5 cm) and at the  
11  
12 236 low end of natural densities (*Enhalus*) or even lower reduced the  $U^*$  (shear velocity).  
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14 237  $U^*$  scales with shear stress, the force resulting from the vertical velocity gradient, which  
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16 238 is responsible for initiating movements of sediment and other particles at and near the  
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18 239 bottom (Denny 1988, Koch et al. 2006). Thus, smaller  $U^*$  values indicate that very short  
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20 240 canopies at relatively low densities, can reduce shear stress, providing increased  
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22 241 sediment stabilization, such as found for short *Halodule uninervis* in the field  
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24 242 (Christianen et al. 2013). Sediment stabilization is an important coastal ecosystem  
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26 243 function in itself but it also helps set the rate of seagrass community development and  
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28 244 thus is important in seagrass restoration (Fonseca and Fisher 1986, Williams 1990, van  
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30 245 der Heide et al. 2007, van Katwijk et al. 2009, Lanuru 2011). Although the focus on  
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32 246 much of the Indo-Pacific seagrass restoration has been on taller 'climax' species such as  
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34 247 *Enhalus* (Ambo-Rappe and Yasir 2015, Lanuru 2011), short but fast-growing species  
35  
36 248 such as *Halodule* would not only cover the sediments more quickly but also provide  
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38 249 some measure of sediment stabilization even early in restoration when densities are low,  
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40 250 based on our result and that of Christianen et al. (2013).  
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45 251 Submerged vegetation canopies are understood to strongly influence water flow,  
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47 252 typically by slowing water flow and, under specific conditions including fast flow,  
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49 253 creating skimming flow above the canopies and a vertical velocity maximum close to  
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51 254 the substratum (Gambi et al. 1990, Nepf and Vivoni 2000, Madsen et al. 2001, Peterson  
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53 255 et al. 2004, Hendriks et al. 2008). This understanding has been based on empirical and  
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55 256 theoretical studies of seagrasses and mimics with generally much taller canopies than  
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3 257 the seagrasses we studied. For example, studies of 'short' species reported canopy  
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5 258 heights  $\geq 5$  cm (Fonseca and Fisher 1986, Heis et al. 2000, Peterson et al. 2004, Bouma  
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7 259 et al. 2005, Widdows et al. 2008, Paul and Gillis 2015). Thus, our study expands the  
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9 260 understanding of seagrass-hydrodynamic relationships by demonstrating that in very  
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11 261 short seagrass canopies, such as commonly occur in intertidal to shallow waters in the  
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13 262 Indo-Pacific region, seagrasses do not necessarily exert a strong influence on  
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15 263 hydrodynamics, yet nevertheless they can decrease shear velocity and thus provide  
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17 264 increased sediment stabilization.  
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21 265 Several predictions can be made about short seagrass canopies, to be tested  
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23 266 empirically. For example, very short canopies do not necessarily enhance the retention  
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25 267 of organic matter or larvae by reducing velocity. On the other hand, the supply of  
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27 268 resources, e.g., nutrients for primary producers and phytoplankton for filter feeders  
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29 269 (Thomas et al. 2000, González-Ortiz et al. 2014), could be less limiting in shorter  
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31 270 canopies. When waves are present along with currents, a canopy of short seagrass will  
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33 271 oscillate and open and close more than taller seagrass under the same current speed,  
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35 272 which theoretically enhances the supply of resources (Paul and Gillis 2015).  
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38 273 Our results provide some basic information to guide future studies, in addition to  
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40 274 highlighting the dearth of information on short seagrass canopies, which are common  
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42 275 close to shore or where herbivory is intense (Christeanen et al. 2013). There are many  
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44 276 avenues for future hydrodynamic research on Indo-Pacific seagrasses. Examples of  
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46 277 important future studies include seagrass effects at varying water speeds and under  
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48 278 oscillating conditions when waves are the dominant hydrodynamic driver. There is also  
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50 279 a need to study the effect of different patch sizes and mixtures of species. This basic  
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52 280 lack of understanding of seagrass-hydrodynamic relationships constrains the creation of  
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54 281 guidelines for seagrass restoration efforts (Bos and Katwijk 2007, van Katwijk et al.  
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3 282 2009), yet restoration is critical to combat the global seagrass decline. Hydrodynamics  
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5 283 can influence loss of leaves in transplanted seagrass or even the transplantation itself  
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7 284 (van Katwijk et al. 2009). There is great interest in Indonesia in establishing guidelines  
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9 285 for seagrass restoration to combat loss and conserve its high seagrass diversity,  
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11 286 dependent organisms, and ecosystem functions. To this end, measurements of  
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13 287 hydrodynamic conditions *in situ* and the shear strengths of different sediment types  
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15 288 found in Indonesia's coastal habitats are also needed to expand laboratory studies to  
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17 289 field applications. In our study, the predictive relationship typically reported between  
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19 290 seagrass density, biomass, and leaf area and hydrodynamic parameters (Gambi et al.  
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21 291 1990, Peterson et al. 2004, Koch et al. 2006, Widdows et al. 2008, Paul and Gillis 2015)  
22  
23 292 seemed to break down in the short canopies, as Christianen et al. (2013) also reported. If  
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25 293 this is the general case for very short canopies, then an easy-to-measure canopy metric  
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27 294 that predicts seagrass-hydrodynamic relations would be especially valuable in regions  
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29 295 such as Indonesia where state-of-the-art facilities for hydrodynamic studies are lacking.  
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34 296  
35  
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51  
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3 306 Plant Inspection Service. We dedicate this study to the memory of our dear colleague  
4  
5 307 Evamaria Koch.  
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5 403 Table 1. Mean and standard deviation (in parenthesis) seagrass and hydrodynamic variables. 'No seagrass' is the average of two flume  
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7 404 calibrations without seagrass (N/A: Not applicable). Canopy height in flume (n = 55 leaves). Depth ratio: flume water depth/canopy  
8  
9 405 height. Turbulence and turbulence intensity: average of heights  $\geq 5.5$  cm above the bottom (n = 4). LAI: one-sided leaf area/m<sup>2</sup> in  
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11 406 flume. Leaf shoots/m<sup>2</sup> of mesh in flume. Natural bed leaf shoot density from 1 m x 1 m quadrats (n = 4).  
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Canopy Type	Canopy height (cm)	Depth ratio	Turbulence (m/s)	Turbulence intensity (%)	Shear velocity U* (m/s)	LAI (m <sup>2</sup> /m <sup>2</sup> )	Leaf biomass (g dry)	Leaf shoots/m <sup>2</sup>	Natural bed leaf shoots/ m <sup>2</sup>
<i>Enhalus aceroides</i>	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
<i>Cymodocea rotundata</i>	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
<i>Thalassia hemprichii</i>	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
<i>Syringodium isoetifolium</i>	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
<i>Halodule uninervis</i>	4.3 (0.2)	10.3	0.400 (0.014)	63 (1)	0.016	0.050	0.8	522	1583 (540)
No seagrass	N/A	N/A	0.398 (0.011)	65 (1)	0.104 (0.018)	N/A	N/A	N/A	N/A

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3 410 **Figure Legends**  
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8 412 Fig. 1. Current speed and direction over 48 hours (19-21 October 2013) at the seagrass  
9 collection site, Barranglompo, Spermonde Islands, south Sulawesi, Indonesia.  
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15 415 Fig. 2. Water flow velocity profiles for a 1-m long seagrass bed of each of five seagrass  
16 species measured in a flume (44 cm water depth) at 0.60 - 0.65 m/s freestream flow  
17 speeds. Dashed line indicates the mean height of the leaf canopy by species. Two velocity  
18 profiles were averaged for the flume calibration without seagrass. The error bars indicate  
19 standard errors of two replicate profiles.  
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29 421 Fig. 3. Shear velocity  $U^*$  (m/s) versus Leaf Area Index ( $m^2/m^2$ ).  $U^*$  scales with shear  
30 stress, the force resulting from the vertical velocity gradient. The Leaf Area Index, a  
31 common predictor of  $U^*$ , is the one-sided area of leaves per  $m^2$  of substratum.  
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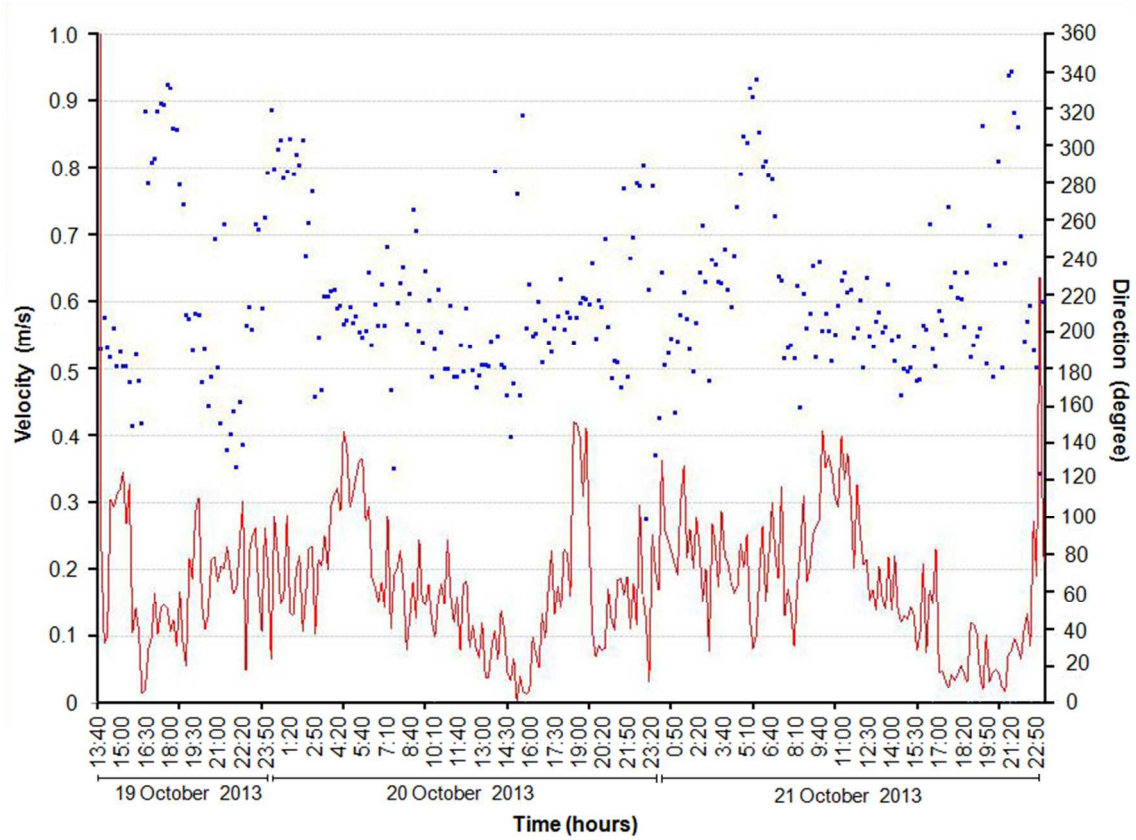
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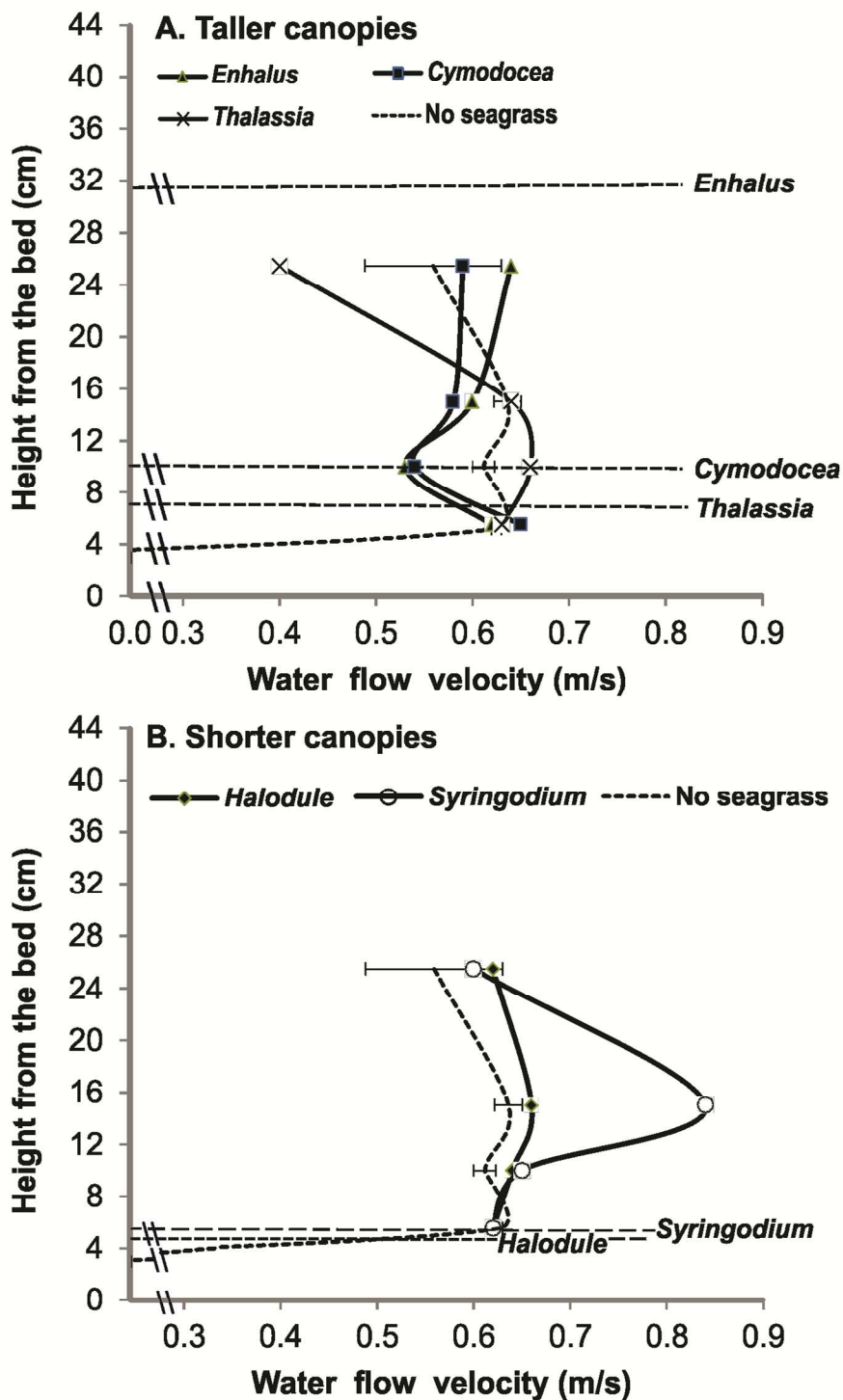
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431 **Figure 1**  
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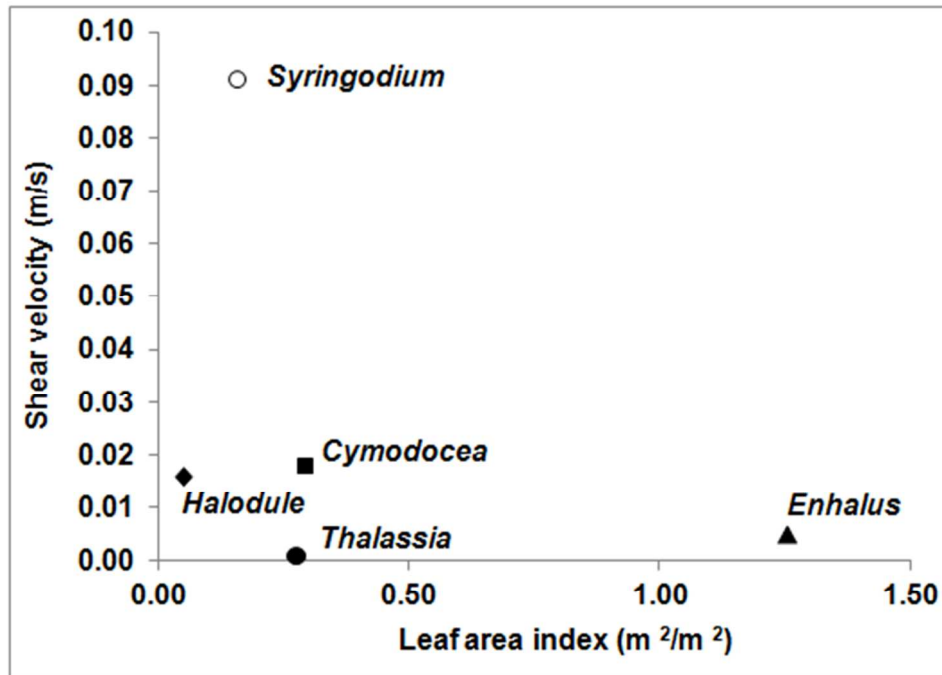
435 Figure 2  
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Figure 3



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## Bionotes

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**Mahatma Lanuru**

Department of Marine Science, Faculty of Marine Science and Fisheries, Hasanuddin University, Tamalanrea Km.10 Makassar, 90245, INDONESIA, mahat70@gmail.com

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Mahatma Lanuru is an associate professor in Marine Science at the Department of Marine Science. He completed his PhD at the University of Kiel (Germany) in 2004. His main

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3 469 research interests are coastal oceanography, sediment dynamic (erosion/deposition) in the  
4 470 estuarine and coastal area, and habitat (seagrass) restoration. He has been recently  
5 471 conducted research on (i) Transplantation experiment for assessing the feasibility of using  
6 472 seagrass for coastal protection in Small Island, and (ii) small island coastal protection  
7 473 using 'Hybrid' (combination of seagrass vegetation and submerged submerged wave  
8 474 breaker).

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30 **481 Rohani Ambo-Rappe**

31 482 Department of Marine Science, Faculty of Marine Science and Fisheries,  
32 483 Hasanuddin University, Jl. Perintis Kemerdekaan, Makassar 90245, INDONESIA.

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36 486 Rohani Ambo-Rappe is a Professor in Marine Ecology at the Faculty of Marine Science  
37 487 and Fisheries. She earned a PhD in Marine Science from The University of Newcastle,  
38 488 Australia. She was the head of Marine Ecology Laboratory (2008 – 2014) and served as  
39 489 Secretary of Marine Science Department (2010 – 2014). Her main research interests are  
40 490 seagrass ecology, ecosystem services, and ecosystem restoration. She is the recipient of  
41 491 national and international research grants and conducted some research collaboration on  
42 492 various topics related to seagrass ecosystem services and restoration.

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**Khairul Amri**

Department of Marine Science, Faculty of Marine Science and Fisheries, Hasanuddin University, Jl. Perintis Kemerdekaan, Makassar 90245, INDONESIA.

Khairul Amri is a lecturer in Marine Botany at the Faculty of Marine Science and Fisheries, Hasanuddin University, Makassar. He was awarded a PhD in Plant Biology by Bogor Agricultural University, Indonesia. Currently, he serves as Secretary of Marine Science Department. His main research interests are marine plant biology and ecology, plant physiology, and plant bioindicator.

**Susan L. Williams**

Bodega Marine Laboratory and the Department of Evolution and Ecology, University of California at Davis, Bodega Bay, California 94923, USA.

Susan L. Williams is a Professor at the Bodega Marine Laboratory, which she directed from 2000-2009. She is a marine ecologist whose research focuses on seagrasses and seaweeds and their conservation and management. Her previous research on hydrodynamics focused on coral reef algal turfs.

**Decision Letter (BOTMAR.2017.0037.R1)****From:** bot.mar.editorial@degruyter.com**To:** mahat70@gmail.com**CC:****Subject:** BOTMAR.2017.0037.R1: Decision Minor revision**Body:** Dear Dr. Lanuru,

Thank you again for submitting your revised manuscript BOTMAR.2017.0037.R1 entitled: "Hydrodynamics in Indo-Pacific Seagrasses with a Focus on Short Canopies" to our journal Botanica Marina (BOTMAR).

Your revised manuscript has been assessed again by one of the reviewers (Rev. 2) who saw the original version. The comments of this reviewer are included at the bottom of this letter and, as you will see, the reviewer is pleased with the many changes and improvements that you have made in response to the comments on the original manuscript, but has added a few points for your consideration. I have also read through your revised manuscript carefully, and was also impressed with the improvements in the language of the text. I have made a few suggestions and comments about possible further improvements, which are tracked in the attached file (Lanuru+al2017BotMar0037.R1-Text+EditorComments.docx). Although the images that you have submitted for the Graphical abstract and Author biographies are satisfactory, and the author bionotes are OK, you do not seem to have submitted any text for the Graphical abstract. This should be a one-sentence (up to 40 words) summary of your work, and it can be included in the main text file alongside the author bionotes.

I invite you to respond to these comments and to revise your manuscript. The revised paper needs to be submitted within 30 days from now but, if you can complete and submit the minor changes requested within the next week (before 18 October), we may be able to include your article in the last printed issue (December) of 2017.

To revise your manuscript, log into <https://mc.manuscriptcentral.com/botmar> and enter your Author Center, where you will find your manuscript title listed under "Manuscripts Awaiting Revision". Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

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When submitting your revised manuscript, there is no need to respond to all the comments, but it will be helpful if you can indicate and justify the significant changes that you have made.

You will be able to respond to the comments under File Upload - File Designation - Author's Response to Reviewer/Editor Critique.

You will be unable to make your revision on the originally submitted version of the manuscript. Instead, revise your manuscript and save it on your computer. There is no need to highlight the changes to your manuscript within the document by using underlined or coloured text, but it will be helpful if you can indicate where significant passages of new text have been added. Once the revised manuscript is prepared, you can upload and submit it through your Author Center. Your original files are available to you when you upload your revised manuscript. You may delete these files or keep them.

Please pay attention to the order of your uploaded files: the first one is the reply to the reviewers' comments, followed by the revised manuscript, and, if applicable, Tables and Figures, and Supplementary Material.

If you decide to keep the original files, these must be the last ones in the order of your uploaded files.

Once again, thank you for submitting your manuscript to Botanica Marina. I look forward to receiving your revision.

Best wishes,  
Matt Dring

Prof. Matthew J. Dring  
Editor in Chief, Botanica Marina

Reviewer's Comments to Author:

Reviewer: 1

Comments to the Corresponding author

The general writing has improved within the revised manuscript and the results are interesting and I believe would stimulate further research on this topic. It is made clear that this is qualitative work due to the lack of replication, but because there are outliers there is a concern that the low number of measurements might not be enough evidence. Further justification is also required for the density and velocity choices for the flume work.

1. The seagrass density used in the flume is a lot lower than what was measured in the field, but on P10 L44 it is stated that flume measurements were conducted on "natural densities of seagrass". In the authors reply the justification was that lower densities were analogous to restoration projects, but this still needs to be clarified in the manuscript.

2. Flow velocity of 0.6m/s is very high, especially considering the field measurements that were made were 0.002-0.43. There is a slight justification for this, but I believe more is required due to the large difference in the field measurements. Are there any references to back up this choice in velocity?

3. L143 - Move the section about measuring LAI and canopy height etc. to after the ADV measurements (around L181 before the statistics), otherwise it sounds like the seagrass was clipped before any measurements were made.

**Date Sent:** 10-Oct-2017**File 1:** [Lanuru-al2017BotMar0037.R1-Text-EditorComments.docx](#) Close Window

October 17, 2017

Professor Matthew Dring  
Editor in Chief, *Botanica Marina*

Dear Professor Dring:

My coauthors and I thank you and Reviewer #2 for your helpful and careful editing and also your patience with our revisions.

We have incorporated all of the suggestions from you and below, we address Rev. #1's comments point by point. At the end of the Bionotes in the revision, we include text for Graphical Abstract.

Thank you very much for your kind consideration.

With my best regards,

Dr Mahatma Lanuru

Lecturer and Head of Marine Science Department,  
Hasanuddin University, Indonesia

October 17, 2017

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Editor in Chief, *Botanica Marina*

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Lecturer and Head of Marine Science Department,  
Hasanuddin University, Indonesia

#### **Responses to Reviewer's Comments to Author:**

##### **Reviewer: 1**

Comments to the Corresponding author

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##### **We thank this Reviewer for all his/her comments.**

1. The seagrass density used in the flume is a lot lower than what was measured in the field, but on P10 L44 it is stated that flume measurements were conducted on "natural densities of seagrass". In the authors reply the justification was that lower densities were analogous to restoration projects, but this still needs to be clarified in the manuscript.

**Response: We removed the reference to density in the Abstract. In the revised Results (l. 191-193) we explained: The seagrass densities in the field were higher than in the flume for all species except *Enhalus*, for which the flume density was within the low end of the range of natural densities (Table 1). The revised Discussion states: The finding that short canopies can reduce  $U^*$  is conservative because measurements were made at the low seagrass densities (Table 1), such as occur early in seagrass restoration projects (l.249-251).**

2. Flow velocity of 0.6m/s is very high, especially considering the field measurements that were made were 0.002-0.43. There is a slight justification for this, but I believe more is required due to the large difference in the field measurements. Are there any references to back up this choice in velocity?

**Response: We added more explanation to the revised Discussion (l. 162-169): Another important finding is that even the shorter canopies (< 5 cm) reduced the  $U^*$  (shear velocity).  $U^*$  scales with shear stress, the force resulting from the vertical velocity gradient, which is responsible for initiating movements of sediment and other particles at and near the bottom (Denny1988, Koch et al. 2006). The finding that short canopies can reduce  $U^*$  is conservative because measurements were made at low seagrass densities (Table 1), such as would occur early in seagrass restoration projects. The velocities in the flume were also higher than measured under calm conditions. The flume velocities created a steeper vertical gradient that better represents the conditions on less calm days at the study site, which was a small island exposed to the open ocean. The flow speed in the flume was similar to high flow speeds in other studies (Fonseca and Kenworthy 1987, Hizon-Fradejas et al.2009).**

3. L143 - Move the section about measuring LAI and canopy height etc. to after the ADV measurements

(around L181 before the statistics), otherwise it sounds like the seagrass was clipped before any measurements were made.

**Response: The move was made.**

1 **Hydrodynamics in Indo-Pacific Seagrasses with a Focus on Short Canopies**

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5 Mahatma Lanuru<sup>1</sup>, Rohani Ambo-Rappe<sup>1</sup>, Khairul Amri<sup>1</sup>, Susan L. Williams<sup>2</sup>

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24 **Running title:** Seagrass hydrodynamics

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36 **Abstract**

37

38 Seagrass hydrodynamic regimes are important to understand and also to guide seagrass  
39 restoration, which is of great interest in Indonesia because of environmental threats to  
40 the exceptionally high seagrass species richness. Hydrodynamic regimes influence the  
41 physical stability of seagrass beds, sedimentation rates, and the advection of nutrients  
42 and food to seagrasses and associated organisms. In a flume, we determined the effect  
43 of canopies of *Cymodocea rotundata*, *Enhalus acoroides*, *Halodule uninervis*,  
44 *Syringodium isoetifolium*, and *Thalassia hemprichii* on water velocity, turbulence,  
45 turbulence intensity, and shear velocity. The taller canopies of *Enhalus* and *Cymodocea*  
46 slowed water flow, but the shorter canopies (<5 cm) had little effect. Seagrasses did not  
47 influence turbulence and turbulence intensity (turbulence normalized to mean velocity)  
48 but they reduced shear velocity  $U^*$ . Our results indicate that *Enhalus* is a good  
49 candidate for transplantation in terms of reducing mean water flow and shear velocities,  
50 but that *Halodule* should also be considered as it also reduced shear velocities and it  
51 spreads quickly after transplantation. Our results extend the understanding of seagrass-  
52 hydrodynamic relationships to include very short canopies, unlike the taller canopies  
53 studied to date.

54

55 Keywords: *Cymodocea*, *Enhalus*, hydrodynamics, Indonesia, seagrass

56 **Introduction**

57           Seagrass leaf canopies profoundly influence water flow dynamics. In turn, water  
58 flow dynamics influence both the physical marine environment by affecting sediment  
59 deposition and resuspension and the associated biological communities through effects  
60 on physiological processes, food availability, larval recruitment and dispersal (Eckman  
61 1987, Thomas et al. 2000, Williams and Heck 2001, Koch et al. 2006, González-Ortiz et  
62 al. 2014). Understanding the seagrass-hydrodynamic relationship is also important for  
63 successful restoration efforts because currents or wave action can uproot fragile  
64 seagrass transplants (Fonseca and Fisher 1986, van Katwijk et al. 2009).

65           In general, seagrass canopies modify the hydrodynamic environment within and  
66 around them by: 1) attenuating the water flow and dissipating wave energy, promoting  
67 the retention of sediments and biological particles, 2) changing the velocity profile close  
68 to the bottom and affecting the boundary layer of more viscous, slower flow, 3)  
69 increasing or decreasing the turbulence and thus advection (the transport of materials),  
70 and 4) propagating monamis, or leaf waving, which enhances advection (reviewed in  
71 Madsen et al. 2001 and Koch et al. 2006). These influences in turn govern the  
72 ecological processes mentioned above. For example, very slow water flow, decreased  
73 turbulence and advection can create mass transfer limitation of critical substrates  
74 including carbon dioxide and dissolved nutrients to seagrass and associated primary  
75 producers (Thomas et al. 2000, Koch et al. 2006). Reduced advective fluxes of food  
76 particles and larvae can limit the recruitment, survival, and growth of animals living  
77 within the seagrass bed. High flow speeds can rip seagrasses from the substratum. The  
78 reviews by Madsen et al. (2001) and Koch et al. (2006) highlight that seagrass-  
79 hydrodynamic studies differ widely in their approach and results, and that more research  
80 is required to build a comprehensive understanding of the specific ways in which

81 seagrasses influence water flow. Of note for our study is that most seagrass-  
82 hydrodynamic studies have been devoted to temperate species and to canopies that are  
83 relatively tall (> 5 cm, see Discussion).

84         The influence of a seagrass canopy on water flow depends on its physical  
85 structure. Most simply, in the case of a continuous monospecific canopy, structure is  
86 dictated by leaf morphology (including stiffness and length relative to water depth),  
87 density, and arrangement, while patchiness in the meadow influences water flow at the  
88 larger landscape scale (references above; Nepf and Vivoni 2000, Bouma et al. 2005,  
89 Fonseca et al. 2007, Peralta et al. 2008). Leaf morphology varies widely in size and  
90 shape across seagrass genera and species (Duarte 1991), ranging from straps (*Enhalus*,  
91 *Posidonia*, *Thalassia*, *Zostera*, *Cymodocea*, *Halodule*), small ovals (*Halophila*),  
92 cylinders (*Syringodium*), to more complex shapes (*Thalassodendron*, *Amphibolis*).  
93 Seagrass morphology itself adjusts plastically to hydrodynamic regimes (Peralta et al.  
94 2006).

95         The objective of our study was to generate some basic understanding of the  
96 effect of common Indonesian seagrass species on water flow dynamics. Although  
97 Indonesia is a centre of seagrass species richness (Green and Short 2003, Short et al.  
98 2007), its seagrasses have been studied relatively little compared to coral reefs and  
99 mangroves (Orth et al. 2006), despite the fact that Indonesian seagrasses are threatened  
100 by many factors (Nadiarti et al. 2012). To generate baseline information, we measured  
101 basic hydrodynamic descriptors of the canopies of five species, which differ widely in  
102 leaf morphology and thus canopy structure, under controlled conditions in a laboratory  
103 flume. The species are common throughout the Indo-Pacific region where they form  
104 monospecific and mixed-species canopies, including ones with very short leaves.

105

106 **Material and methods**

107           The field seagrass bed was located at Barranglompo Island (5°03'S, 119°20'E)  
108 in the Spermonde Archipelago, south Sulawesi, Indonesia. We measured freestream  
109 water flow speed and direction every minute for 48 h (19-21 October 2013) using an  
110 Infinity Series ver. 0.10 current meter (JFE Advantech Co., Ltd. 3-48 Takahata-cho,  
111 Nishinomiya, Hyogo, Japan 63-8202). The current meter was deployed in freestream  
112 flow at 1.5 m above the substratum (water depth = 4 m) and over a metre above the  
113 seagrass canopy. Freestream flow, i.e., where there are no boundary layer influences  
114 caused by friction with the bottom and the seagrass, was measured to estimate flow  
115 speeds to be used in the flume study described below. Measurements were recorded  
116 during a spring tide cycle and under calm wind and wave conditions.

117           In September 2014, the leaf shoots of *Cymodocea rotundata* Ascherson *et*  
118 Schweinfurth, *Enhalus acoroides* (Linnaeus f.) Royle, *Halodule uninervis* (Forsskål)  
119 Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii*  
120 (Ehrenberg) Ascherson were counted in 1-m<sup>2</sup> quadrats (n = 4 per species) in  
121 monospecific stands before collecting intact rhizomes with attached leaf shoots.  
122 Seagrasses were rinsed of sediments, and epiphytes were removed by gently wiping the  
123 leaves with a soft towel, cushioned by plastic fibre batting, and placed in coolers for air  
124 shipment to the Bodega Marine Laboratory, University of California at Davis, USA,  
125 where flume studies were conducted.

126           A straight flume (Model 504, Engineering Design Laboratory, Lake City,  
127 Minnesota 55041-0278, USA, working section 45 x 45 x 250 cm) was used to  
128 characterize the effect of the leaf canopy on water flow dynamics. The flume was filled  
129 with seawater to a depth of 44 cm above the bottom and the seawater was not changed  
130 during the experiment. Measurements were made at a flume speed of 0.60 - 0.65 m s<sup>-1</sup>.

131 The velocity was chosen to be at the high end of the field conditions recorded over 48 h  
132 because undoubtedly the velocity would reach higher levels under less calm field  
133 conditions.

134 We created a seagrass bed (45 cm wide x 100 cm long) of each species using a  
135 plastic-coated wire mesh (0.5 x 0.5 cm mesh size) fitted across the width of working  
136 section and centred in the middle of the working section's length. To secure the buoyant  
137 seagrass in the flume, we placed the rhizomes between two pieces of mesh, spacing  
138 them irregularly to mimic their natural arrangement, added small lead fishing sinkers,  
139 and threaded the leaf shoots through the top mesh layer. The edges of the mesh were  
140 smoothed with duct tape. The mesh was placed as close to the flume bottom as possible  
141 (average height above bottom:  $1.8 \text{ cm} \pm 0.43 \text{ SD}$ ,  $n = 275$  measurements). The mesh  
142 created a rough bottom generally analogous to the rough bottoms created by small  
143 pieces of coral rubble and animal tubes in Indo-Pacific seagrass beds.

144 The water flow velocity in the flume was determined using an Acoustic Doppler  
145 Velocimeter (ADV, Field Vetrino serial #VNO0224, Nortek AS, Vangkroken 2, NO-  
146 1351 RUD, Norway) with Vetrino Plus software, a baud of 57600, and sampling rate  
147 of 200 Hz. The ADV was centred in the width of the working section for all  
148 measurements. The flume was calibrated by averaging velocity measurements without  
149 seagrass at 3, 5.5, 10, 15 and 25.5 cm above the bottom at 38 and 116 cm from the  
150 beginning of the working section. Seagrass measurements were made at midway along  
151 the length of the mesh (50 cm downstream from the edge of the seagrass bed) at 5.5, 10,  
152 15 and 25.5 cm heights and in the middle of the seagrass bed. Due to the mesh, the  
153 closest the ADV could be positioned above the flume bottom was 5.5 cm. After velocity  
154 stabilized upon repositioning the ADV, it was recorded over 2 min. The mesh itself

155 without attached seagrasses slowed the flow minimally by  $0.049 \text{ m s}^{-1}$  at  $\geq 5.5 \text{ cm}$  above  
156 the bottom.

157 To compare the experimental seagrass bed to the field and other studies, we  
158 counted the leaf shoots in the mesh and measured the leaf canopy height as the distance  
159 between the mesh surface and the longest leaf of 55 shoots of each species. We then  
160 clipped the leaves flush with the mesh and measured leaf area (Li-Cor meter, Model Li-  
161 3100, Lincoln, Nebraska, USA) to calculate the leaf area index (LAI) as the one-sided  
162 leaf area ( $\text{m}^2$ ) per  $\text{m}^2$  of mesh. *Syringodium*'s cylindrical leaf area was calculated as the  
163 lateral area (leaf area multiplied by  $\pi$ ). Leaves were oven-dried at  $60^\circ\text{C}$  until constant  
164 mass and weighed. LAI, leaf biomass, and density theoretically relate to the canopy's  
165 influence on hydrodynamics (Gambi et al. 1990, Peterson et al. 2004, Koch et al. 2006).

166 We calculated the mean velocity as the square root of the sum of squares of the  
167 ADV's three velocity components averaged across instantaneous recordings made  
168 during the measurement period. Turbulence, the measure of the variation in the average  
169 flow, was calculated as the root mean square of the standard deviation of each velocity  
170 component (Denny 1988, Gambi et al. 1990). Turbulence intensity (%) was calculated  
171 as the turbulence divided by the mean velocity. The depth ratio (water depth divided by  
172 the canopy height) was calculated to compare hydrodynamic environments due to  
173 differences in canopy heights in the flume (Nepf and Vivoni 2000).

174 The shear velocity  $U^*$  was determined from the von Karman-Prandtl velocity-  
175 depth profile relationship (Denny 1988, Gambi et al. 1990):

176  $U(z) = U^*/K (\ln(z_2/z_1))$ , where:

177  $U$  is the difference in velocity between two heights above the substratum ( $z_1$  and  $z_2$ ) and  
178  $K$  = von Karman's constant (0.41). Depth  $z_1$  was 5.5 cm and  $z_2$  was 25.5 cm for *Enhalus*  
179 and *Cymodocea*, 5.5 and 15 for *Syringodium* and *Halodule*, and 3 and 25.5 upstream,

180 respectively, to conform to the log relationship between velocity and height above the  
181 bottom. We performed linear regressions of  $U^*$  versus LAI, canopy height, and density,  
182 which can be predictors of the canopy's influence on hydrodynamics (Gambi et al. 1990,  
183 Peterson et al. 2004, Koch et al. 2006).

## 184 185 **Results**

186  
187 The mean water flow speed at the seagrass collection site was  $0.160 \text{ m s}^{-1}$ ,  
188 ranging from  $0.002$  to  $0.430 \text{ m s}^{-1}$  (Fig. 1). The seagrass densities in the field were  
189 higher than in the flume for all species except *Enhalus*, for which the flume density was  
190 within the low end of the range of natural densities (Table 1).

191 In the flume, mean velocities differed depending on the species (Fig. 2). The two  
192 short species (*Syringodium*, *Halodule*,  $< 5 \text{ cm}$  tall, Table 1) had no observable effect on  
193 mean velocities compared to upstream (no seagrass,  $0.600 - 0.650 \text{ m s}^{-1}$  freestream flow  
194 above  $3 \text{ cm}$ ). Water flow decreased between  $10$  and  $16 \text{ cm}$  height above the bottom in  
195 the *Enhalus* and *Cymodocea* experimental beds. At  $24 \text{ cm}$ , which was well above the  
196 *Cymodocea* canopy's mean maximum height (Table 1) and approaching *Enhalus*'s mean  
197 maximum canopy height, flow was equivalent to freestream conditions. Due to lack of  
198 replication, the outliers at  $24 \text{ cm}$  in the *Thalassia* and at  $16 \text{ cm}$  in the *Syringodium*  
199 profiles cannot be explained.

200 The depth ratio (Table 1) for all species except *Enhalus* was  $>2$ , indicating they  
201 experienced similar hydrodynamic environments unconfined by water depth in the  
202 flume (Nepf and Vivoni 2000) and that some cross comparisons can be made. The ratio  
203 for *Enhalus* indicated that its canopy was at the transition between a depth-limited and  
204 emergent canopy.

205 Seagrass canopies had minimal effects on turbulence and turbulence intensity  
206 (Table 1). The taller canopies (*Enhalus*, *Cymodocea*, *Thalassia*) increased values only  
207 2-3% compared to upstream (no seagrass) values.

208 All species reduced  $U^*$  ( $\leq 0.091 \text{ m s}^{-1}$ ) compared to the no-seagrass value ( $0.104$   
209  $\text{m s}^{-1}$ ; Table 1). There was no relationship between  $U^*$  versus canopy height or LAI  
210 (Fig. 3), which was highly correlated to leaf biomass (Pearson correlation coefficient =  
211 0.988). These potential predictors of  $U^*$  explained only 25-36% of  $U^*$  variation (height  
212  $p = 0.210$ ,  $r^2 = 0.357$ ;  $df = 1, 4$ ; LAI  $p = 0.318$ ,  $r^2 = 0.245$ ). Shoot densities explained  
213  $<0.1\%$  of  $U^*$  variation ( $p = 0.976$ ).

214

## 215 **Discussion**

216 The data are limited to qualitative comparisons across species because there was  
217 no replication within a species due to the logistical limitations inherent in bringing  
218 seagrasses from Indonesia to the flume facility in California and keeping them in good  
219 condition. We therefore cannot explain whether extreme points in the velocity profiles  
220 are outliers or represent a seagrass effect. Outliers in flume velocity profiles are not  
221 unusual and can result from a transient wobble in the ADV or a transient difference in  
222 flume conditions, such as could result from a power surge. For example, published  
223 velocity profiles also show outlier points (Fig. 2 in Gambi et al. 1990; Fig.1 in Fonseca  
224 and Koehl 2006). Despite the lack of replication, there are some general patterns worth  
225 noting that can be addressed in future studies. First, water flow speeds in *Enhalus* and  
226 *Cymodocea* canopies were reduced between 4 and 16 cm height above the bottom. The  
227 depth ratio for *Enhalus* (Table 1) was measured in a situation analogous to low tide in a  
228 shallow bed. Under this condition, the depth ratio suggests that a vertical exchange zone  
229 could develop at the top of the canopy wherein the density and morphology influence

230 the hydrodynamics within the canopy, in contrast to the 'unconfined' condition of very  
231 short canopies (Nepf and Vivoni 2000). Second, seagrasses had minimal influence on  
232 turbulence, the variation in the time-averaged mean velocity, which is important for the  
233 advection of essential elements, pollutants, and biological and non-biological particles  
234 (Denny 1988, Koch et al. 2006).

235 Another important finding is that even the shorter canopies (< 5 cm) reduced the  
236  $U^*$  (shear velocity).  $U^*$  scales with shear stress, the force resulting from the vertical  
237 velocity gradient, which is responsible for initiating movements of sediment and other  
238 particles at and near the bottom (Denny 1988, Koch et al. 2006). The finding that short  
239 canopies can reduce  $U^*$  is conservative because measurements were made at low  
240 seagrass densities (Table 1), such as would occur early in seagrass restoration projects.  
241 The velocities in the flume were also higher than measured under calm conditions. The  
242 flume velocities created a steeper vertical gradient that better represents the conditions  
243 on less calm days at the study site, which was a small island exposed to the open ocean.  
244 The flow speed in the flume was similar to high flow speeds in other studies (Fonseca  
245 and Kenworthy 1987, Hizon-Fradejas et al. 2009). Thus, smaller  $U^*$  values indicate that  
246 very short canopies at relatively low densities and high freestream velocities can reduce  
247 shear stress, providing increased sediment stabilization, such as found for short  
248 *Halodule uninervis* in the field (Christianen et al. 2013). Sediment stabilization is an  
249 important coastal ecosystem function in itself but it also helps to set the rate of seagrass  
250 community development and thus is important in seagrass restoration (Fonseca and  
251 Fisher 1986, Williams 1990, van der Heide et al. 2007, van Katwijk et al. 2009, Lanuru  
252 2011). Although the focus on much of the Indo-Pacific seagrass restoration has been on  
253 taller 'climax' species such as *Enhalus* (Ambo-Rappe and Yasir 2015, Lanuru 2011),  
254 short but fast-growing species such as *Halodule* would not only cover the sediments

255 more quickly but also provide some measure of sediment stabilization, even early in  
256 restoration when densities are low, based on our result and that of Christianen et al.  
257 (2013).

258           Submerged vegetation canopies are understood to strongly influence water flow,  
259 typically by slowing water flow and, under specific conditions including fast flow,  
260 creating skimming flow above the canopies and a vertical velocity maximum close to  
261 the substratum (Gambi et al.1990, Nepf and Vivoni 2000, Madsen et al. 2001, Peterson  
262 et al. 2004, Hendriks et al. 2008). This understanding has been based on empirical and  
263 theoretical studies of seagrasses and mimics with generally much taller canopies than  
264 the seagrasses we studied. For example, studies of 'short' species reported canopy  
265 heights  $\geq 5$  cm (Fonseca and Fisher 1986, Heis et al. 2000, Peterson et al. 2004, Bouma  
266 et al. 2005, Widdows et al. 2008, Paul and Gillis 2015). Thus, our study expands the  
267 understanding of seagrass-hydrodynamic relationships by demonstrating that in very  
268 short seagrass canopies, such as commonly occur in intertidal to shallow waters in the  
269 Indo-Pacific region, seagrasses do not necessarily exert a strong influence on  
270 hydrodynamics, yet nevertheless they can decrease shear velocity and thus provide  
271 increased sediment stabilization.

272           Several predictions can be made about short seagrass canopies, to be tested  
273 empirically. For example, very short canopies do not necessarily enhance the retention  
274 of organic matter or larvae by reducing velocity. On the other hand, the supply of  
275 resources, e.g., nutrients for primary producers and phytoplankton for filter feeders  
276 (Thomas et al. 2000, González-Ortiz et al. 2014), could be less limiting in shorter  
277 canopies. When waves are present along with currents, a canopy of short seagrass will  
278 oscillate and open and close more than taller seagrass under the same current speed,  
279 which theoretically enhances the supply of resources (Paul and Gillis 2015).

280           Our results provide some basic information to guide future studies, in addition to  
281 highlighting the dearth of information on short seagrass canopies, which are common  
282 close to shore or where herbivory is intense (Christeanen et al. 2013). There are many  
283 avenues for future hydrodynamic research on Indo-Pacific seagrasses. Examples of  
284 important future studies include seagrass effects at varying water speeds and under  
285 oscillating conditions when waves are the dominant hydrodynamic driver. There is also  
286 a need to study the effect of different patch sizes and mixtures of species. This basic  
287 lack of understanding of seagrass-hydrodynamic relationships constrains the creation of  
288 guidelines for seagrass restoration efforts (Bos and Katwijk 2007, van Katwijk et al.  
289 2009), yet restoration is critical to combat the global seagrass decline. Hydrodynamics  
290 can influence loss of leaves in transplanted seagrass or even the transplantation itself  
291 (van Katwijk et al. 2009). There is great interest in Indonesia in establishing guidelines  
292 for seagrass restoration to combat loss and conserve its high seagrass diversity,  
293 dependent organisms, and ecosystem functions. To this end, measurements of  
294 hydrodynamic conditions *in situ* and the shear strengths of different sediment types  
295 found in Indonesia's coastal habitats are also needed to expand laboratory studies to  
296 field applications. In our study, the predictive relationship typically reported between  
297 seagrass density, biomass, and leaf area and hydrodynamic parameters (Gambi et al.  
298 1990, Peterson et al. 2004, Koch et al. 2006, Widdows et al. 2008, Paul and Gillis 2015)  
299 seemed to break down in the short canopies, as Christianen et al. (2013) also reported. If  
300 this is the general case for very short canopies, then an easy-to-measure canopy metric  
301 that predicts seagrass-hydrodynamic relations would be especially valuable in regions  
302 such as Indonesia where state-of-the-art facilities for hydrodynamic studies are lacking.  
303

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315

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414

415 Table 1. Mean and standard deviation (in parenthesis) for seagrass and hydrodynamic variables. 'No seagrass' is the average of two  
 416 flume calibrations without seagrass (N/A: Not applicable). Canopy height in flume (n = 55 leaves). Depth ratio: flume water  
 417 depth/canopy height. Turbulence and turbulence intensity: average of heights  $\geq 5.5$  cm above the bottom (n = 4). LAI: one-sided leaf  
 418 area m<sup>-2</sup> in flume. Leaf shoots m<sup>-2</sup> of mesh in flume. Natural bed leaf shoot density from 1 m x 1 m quadrats (n = 4).

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<b>Canopy type</b>	<b>Canopy height (cm)</b>	<b>Depth ratio</b>	<b>Turbulence (m s<sup>-1</sup>)</b>	<b>Turbulence intensity (%)</b>	<b>Shear velocity U* (m s<sup>-1</sup>)</b>	<b>LAI (m<sup>2</sup> m<sup>-2</sup>)</b>	<b>Leaf biomass (g dry)</b>	<b>Leaf shoots m<sup>-2</sup></b>	<b>Natural bed leaf shoots m<sup>-2</sup></b>
<i>Enhalus aceroides</i>	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
<i>Cymodocea rotundata</i>	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
<i>Thalassia hemprichii</i>	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
<i>Syringodium isoetifolium</i>	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
<i>Halodule uninervis</i>	4.3 (0.2)	10.3	0.400 (0.014)	63 (1)	0.016	0.050	0.8	522	1583 (540)
No seagrass	N/A	N/A	0.398 (0.011)	65 (1)	0.104 (0.018)	N/A	N/A	N/A	N/A

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421

422 **Figure Legends**

423

424 Fig.1. Current speed and direction over 48 hours (19-21 October 2013) at the seagrass  
425 collection site, Barranglompo, Spermonde Islands, south Sulawesi, Indonesia.

426

427 Fig. 2. Water flow velocity profiles for a 1-m long seagrass bed of each of five seagrass  
428 species measured in a flume (44 cm water depth) at 0.60 - 0.65 m s<sup>-1</sup> freestream flow  
429 speeds. Dashed line indicates the mean height of the leaf canopy by species. Two velocity  
430 profiles were averaged for the flume calibration without seagrass. The error bars indicate  
431 standard errors of two replicate profiles.

432

433 Fig. 3. Shear velocity U\* (m s<sup>-1</sup>) versus Leaf Area Index (m<sup>2</sup> m<sup>-2</sup>). U\* scales with shear  
434 stress, the force resulting from the vertical velocity gradient. The Leaf Area Index, a  
435 common predictor of U\*, is the one-sided area of leaves per m<sup>2</sup> of substratum.

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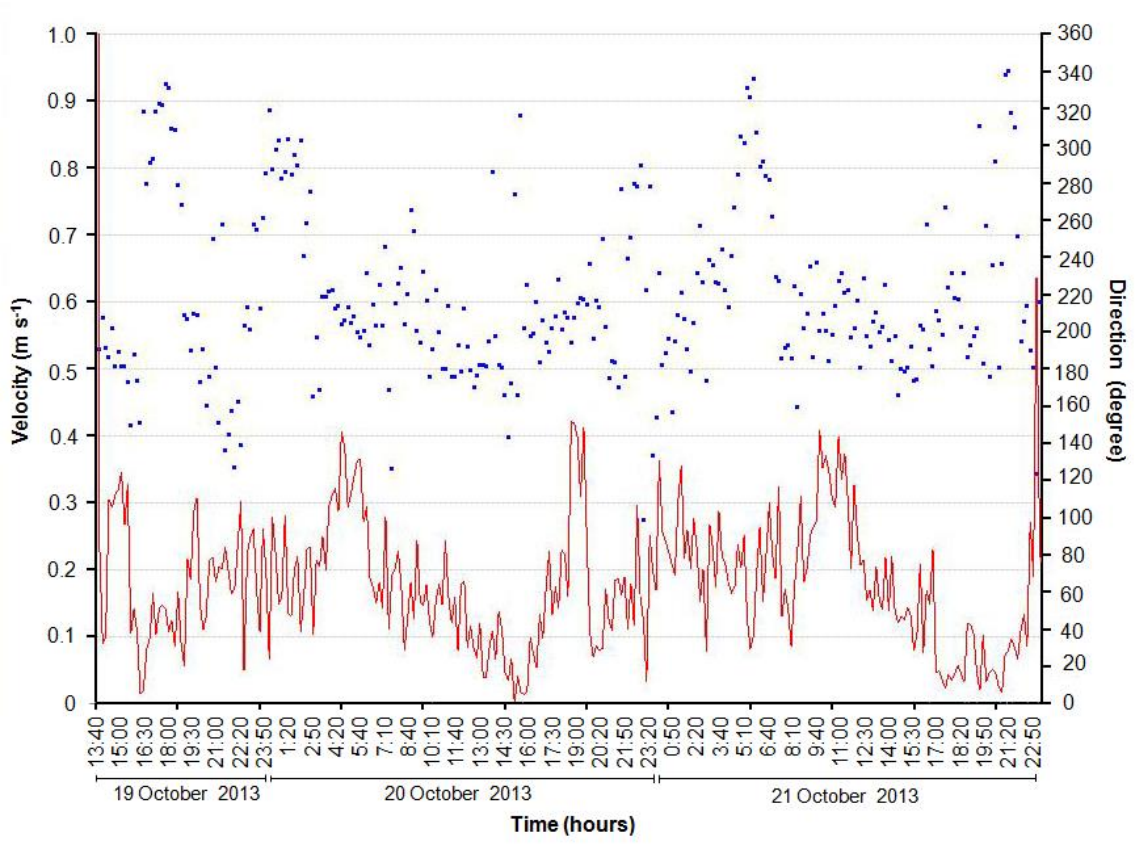
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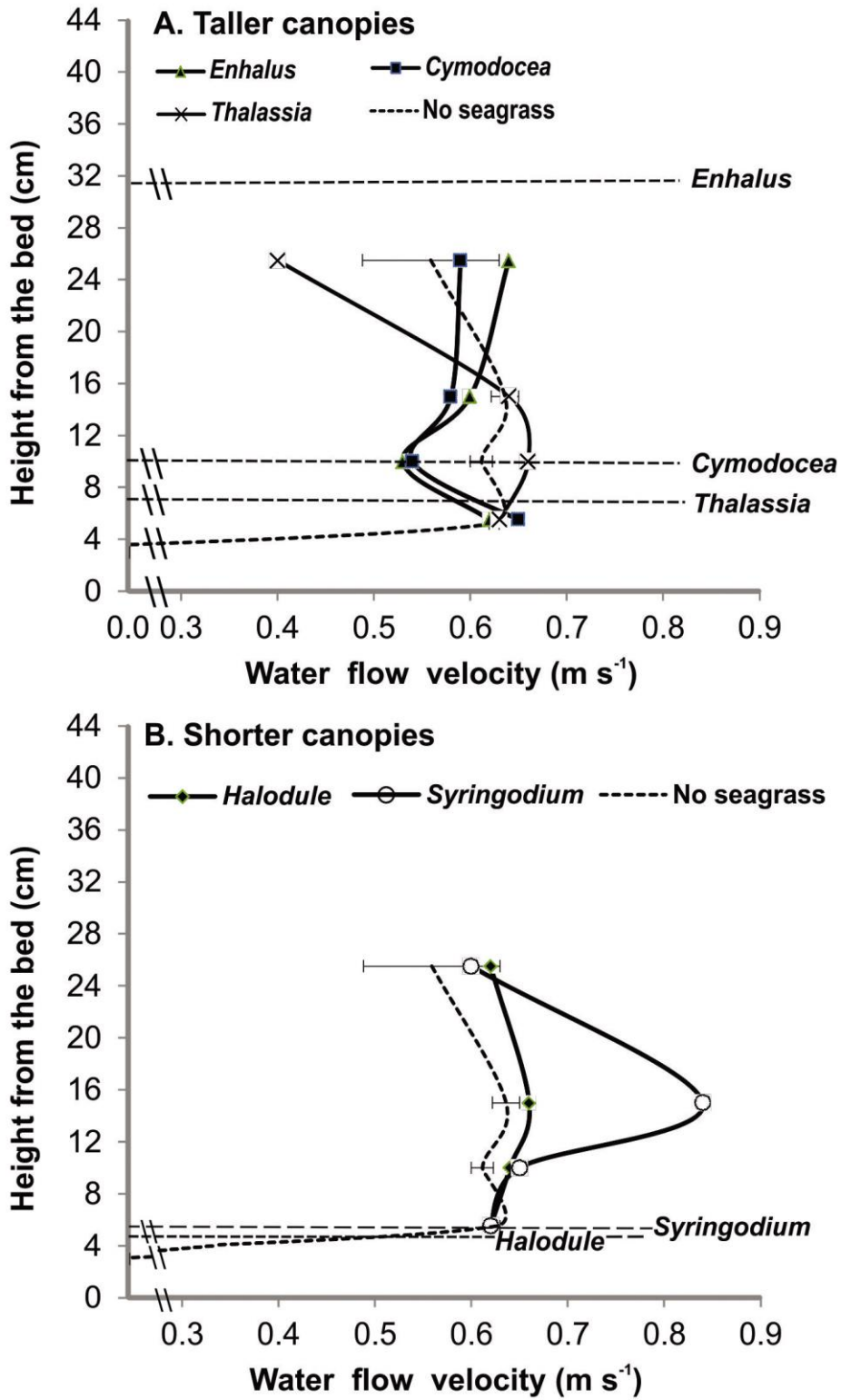
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443 **Figure 1**  
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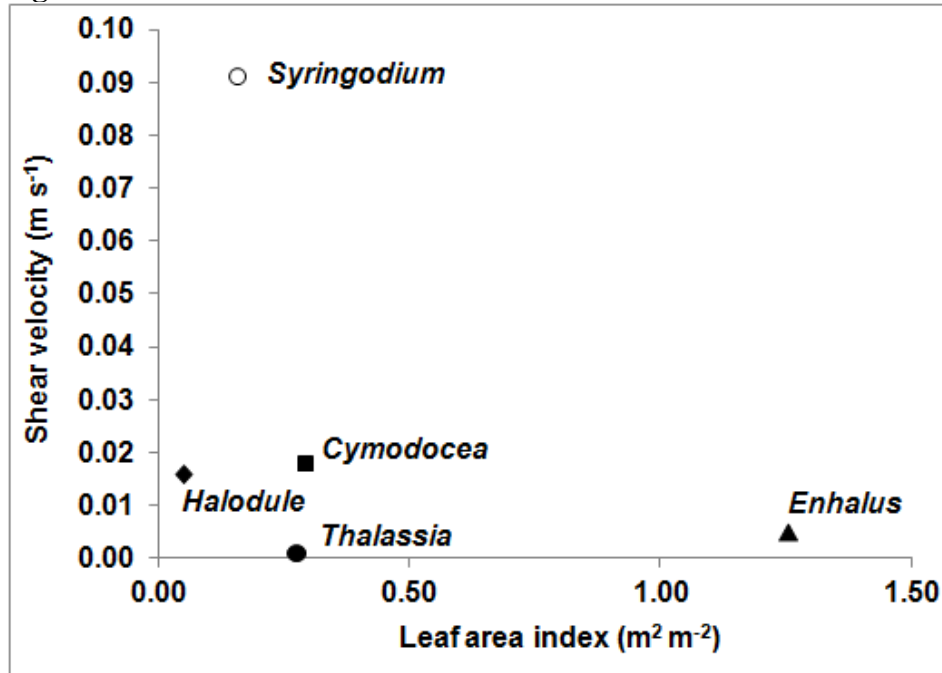
447 **Figure 2**  
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**Figure 3**



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**Bionotes**

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481 seagrass for coastal protection in Small Island, and (ii) small island coastal protection  
482 using 'Hybrid' (combination of seagrass vegetation and submerged wave breaker).  
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500 various topics related to seagrass ecosystem services and restoration.

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533 from 2000-2009. She is a marine ecologist whose research focuses on seagrasses and

534 seaweeds and their conservation and management. Her previous research on

535 hydrodynamics focused on coral reef algal turfs.

536

537

538 Graphic abstract

539

540 The hydrodynamic effects of five species of seagrasses from Indonesia were studied in a

541 flume.

542

## Decision Letter (BOTMAR.2017.0037.R2)

**From:** bot.mar.editorial@degruyter.com

**To:** mahat70@gmail.com

**CC:**

**Subject:** BOTMAR.2017.0037.R2 - Decision Accept

**Body:** 20-Oct-2017

Dear Dr. Lanuru:

Many thanks for responding so quickly and carefully to my message of 6 October, requesting a few minor changes to your manuscript entitled "Hydrodynamics in Indo-Pacific Seagrasses with a Focus on Short Canopies". After making a few very minor linguistic and typographical corrections, which are tracked in the attached file of the final text (this is for your information only - there is no need to submit another revision), I am completely satisfied with this revised version, and it is a pleasure to accept it for publication in Botanica Marina.

The Botanica Marina production office will contact you for proofreading in the near future. Your article will be published ahead of print as soon as possible, and in the printed edition at a later time. Once it is published, please promote your paper as actively as possible by sending the pdf file to others working in this field, and encouraging them to refer to your paper in their own publications.

Thank you for your interesting and valuable contribution, and for your willingness to respond to our reviewers' comments. I hope that your experience of publishing in Botanica Marina has been rewarding, and that you will consider the Journal as a home for your manuscripts in the future.

Best wishes,  
Matt Dring

Prof. Matthew J. Dring  
Editor in Chief, Botanica Marina

**Date Sent:** 20-Oct-2017

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Mahatma Lanuru\*, Rohani Ambo-Rappe, Khairul Amri and Susan L. Williams

# Hydrodynamics in Indo-Pacific seagrasses with a focus on short canopies

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**Abstract:** Seagrass hydrodynamic regimes are important to understand and also to guide seagrass restoration, which is of great interest in Indonesia because of environmental threats to the exceptionally high seagrass species richness. Hydrodynamic regimes influence the physical stability of seagrass beds, sedimentation rates, and the advection of nutrients and food to seagrasses and associated organisms. In a flume, we determined the effect of canopies of *Cymodocea rotundata*, *Enhalus acoroides*, *Halodule uninervis*, *Syringodium isoetifolium* and *Thalassia hemprichii* on water velocity, turbulence, turbulence intensity and shear velocity. The taller canopies of *Enhalus* and *Cymodocea* slowed water flow, but the shorter canopies (<5 cm) had little effect. Seagrasses did not influence turbulence and turbulence intensity (turbulence normalized to mean velocity) but they reduced shear velocity  $U^*$ . Our results indicate that *Enhalus* is a good candidate for transplantation in terms of reducing mean water flow and shear velocities, but that *Halodule* should also be considered as it also reduced shear velocities and it spreads quickly after transplantation. Our results extend the understanding of seagrass-hydrodynamic relationships to include very short canopies, unlike the taller canopies studied to date.

**Keywords:** *Cymodocea*; *Enhalus*; hydrodynamics; Indonesia; seagrass.

## Introduction

Seagrass leaf canopies profoundly influence water flow dynamics. In turn, water flow dynamics influence both the physical marine environment by affecting sediment deposition and resuspension and the associated biological communities through effects on physiological processes, food availability, larval recruitment and dispersal (Eckman 1987, Thomas et al. 2000, Williams and Heck 2001, Koch et al. 2006, González-Ortiz et al. 2014). Understanding the seagrass-hydrodynamic relationship is also important for successful restoration efforts because currents or wave action can uproot fragile seagrass transplants (Fonseca and Fisher 1986, van Katwijk et al. 2009).

In general, seagrass canopies modify the hydrodynamic environment within and around them by: (1) attenuating the water flow and dissipating wave energy, promoting the retention of sediments and biological particles, (2) changing the velocity profile close to the bottom and affecting the boundary layer of more viscous, slower flow, (3) increasing or decreasing the turbulence and thus advection (the transport of materials), and (4) propagating monamis, or leaf waving, which enhances advection (reviewed in Madsen et al. 2001, Koch et al. 2006). These influences in turn govern the ecological processes mentioned above. For example, very slow water flow, decreased turbulence and advection can create mass transfer limitation of critical substrates including carbon dioxide and dissolved nutrients to seagrass and associated primary producers (Thomas et al. 2000, Koch et al. 2006). Reduced advective fluxes of food particles and larvae can limit the recruitment, survival and growth of animals living within the seagrass bed. High flow speeds can rip seagrasses from the substratum. The reviews by Madsen et al. (2001) and Koch et al. (2006) highlight that seagrass-hydrodynamic studies differ widely in their approach and results, and that more research is required to build a comprehensive understanding of the specific ways in which seagrasses influence water flow. Of note for our study is that most seagrass-hydrodynamic studies have been devoted to temperate species and to canopies that are relatively tall (>5 cm, see Discussion).

The influence of a seagrass canopy on water flow depends on its physical structure. Most simply, in the case

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of a continuous monospecific canopy, structure is dictated by leaf morphology (including stiffness and length relative to water depth), density and arrangement, while patchiness in the meadow influences water flow at the larger landscape scale (references above; Nepf and Vivoni 2000, Bouma et al. 2005, Fonseca et al. 2007, Peralta et al. 2008). Leaf morphology varies widely in size and shape across seagrass genera and species (Duarte 1991), ranging from straps (*Enhalus*, *Posidonia*, *Thalassia*, *Zostera*, *Cymodocea*, *Halodule*), small ovals (*Halophila*), cylinders (*Syringodium*), to more complex shapes (*Thalassodendron*, *Amphibolis*). Seagrass morphology itself adjusts plastically to hydrodynamic regimes (Peralta et al. 2006).

The objective of our study was to generate some basic understanding of the effect of common Indonesian seagrass species on water flow dynamics. Although Indonesia is a center of seagrass species richness (Green and Short 2003, Short et al. 2007), its seagrasses have been studied relatively little compared to coral reefs and mangroves (Orth et al. 2006), despite the fact that Indonesian seagrasses are threatened by many factors (Nadiarti et al. 2012). To generate baseline information, we measured basic hydrodynamic descriptors of the canopies of five species, which differ widely in leaf morphology and thus canopy structure, under controlled conditions in a laboratory flume. The species are common throughout the Indo-Pacific region where they form monospecific and mixed-species canopies, including ones with very short leaves.

## Materials and methods

The field seagrass bed was located at Barranglompo Island (5°03'S, 119°20'E) in the Spermonde Archipelago, south Sulawesi, Indonesia. We measured freestream water flow speed and direction every minute for 48 h (19–21 October 2013) using an Infinity Series ver. 0.10 current meter (JFE Advantech Co., Ltd. 3-48 Takahata-cho, Nishinomiya, Hyogo, Japan). The current meter was deployed in a freestream flow at 1.5 m above the substratum (water depth = 4 m) and over a meter above the seagrass canopy. Freestream flow, i.e. where there are no boundary layer influences caused by friction with the bottom and the seagrass, was measured to estimate flow speeds to be used in the flume study described below. Measurements were recorded during a spring tide cycle and under calm wind and wave conditions.

In September 2014, the leaf shoots of *Cymodocea rotundata* Ascherson et Schweinfurth, *Enhalus acoroides*

(Linnaeus f.) Royle, *Halodule uninervis* (Forsskål) Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii* (Ehrenberg) Ascherson were counted in 1-m<sup>2</sup> quadrats (n = 4 per species) in monospecific stands before collecting intact rhizomes with attached leaf shoots. Seagrasses were rinsed of sediments, and epiphytes were removed by gently wiping the leaves with a soft towel, cushioned by plastic fiber batting, and placed in coolers for air shipment to the Bodega Marine Laboratory, University of California at Davis, USA, where flume studies were conducted.

A straight flume (Model 504, Engineering Design Laboratory, Lake City, MN, USA, working section 45 × 45 × 250 cm) was used to characterize the effect of the leaf canopy on water flow dynamics. The flume was filled with seawater to a depth of 44 cm above the bottom and the seawater was not changed during the experiment. Measurements were made at a flume speed of 0.60–0.65 m s<sup>-1</sup>. The velocity was chosen to be at the high end of the field conditions recorded over 48 h because undoubtedly the velocity would reach higher levels under less calm field conditions.

We created a seagrass bed (45 cm wide × 100 cm long) of each species using a plastic-coated wire mesh (0.5 × 0.5 cm mesh size) fitted across the width of the working section and centered in the middle of the working section's length. To secure the buoyant seagrass in the flume, we placed the rhizomes between two pieces of mesh, spacing them irregularly to mimic their natural arrangement, added small lead fishing sinkers, and threaded the leaf shoots through the top mesh layer. The edges of the mesh were smoothed with duct tape. The mesh was placed as close to the flume bottom as possible (average height above bottom: 1.8 cm ± 0.43 SD, n = 275 measurements). The mesh created a rough bottom generally analogous to the rough bottoms created by small pieces of coral rubble and animal tubes in Indo-Pacific seagrass beds.

The water flow velocity in the flume was determined using an Acoustic Doppler Velocimeter (ADV, Field Vetrino serial #VNO0224, Nortek AS, Rud, Norway) with Vetrino Plus software, a baud of 57600, and sampling rate of 200 Hz. The ADV was centered in the width of the working section for all measurements. The flume was calibrated by averaging velocity measurements without seagrass at 3, 5.5, 10, 15 and 25.5 cm above the bottom at 38 and 116 cm from the beginning of the working section. Seagrass measurements were made at midway along the length of the mesh (50 cm downstream from the edge of the seagrass bed) at 5.5, 10, 15 and 25.5 cm heights and in the middle of the seagrass bed. Due to the mesh, the closest the ADV could be positioned above the flume bottom was 5.5 cm.

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After velocity stabilized upon repositioning the ADV, it was recorded over 2 min. The mesh itself without attached seagrasses slowed the flow minimally by  $0.049 \text{ m s}^{-1}$  at  $\geq 5.5 \text{ cm}$  above the bottom.

To compare the experimental seagrass bed to the field and other studies, we counted the leaf shoots in the mesh and measured the leaf canopy height as the distance between the mesh surface and the longest leaf of 55 shoots of each species. We then clipped the leaves flush with the mesh and measured leaf area (Li-Cor meter, Model Li-3100, Lincoln, NE, USA) to calculate the leaf area index (LAI) as the one-sided leaf area ( $\text{m}^2$ ) per  $\text{m}^2$  of mesh. *Syringodium*'s cylindrical leaf area was calculated as the lateral area (leaf area multiplied by  $\pi$ ). Leaves were oven-dried at  $60^\circ\text{C}$  until constant mass and weighed. LAI, leaf biomass, and density theoretically relate to the canopy's influence on hydrodynamics (Gambi et al. 1990, Peterson et al. 2004, Koch et al. 2006).

We calculated the mean velocity as the square root of the sum of squares of the ADV's three velocity components averaged across instantaneous recordings made during the measurement period. Turbulence, the measure of the variation in the average flow, was calculated as the root mean square of the standard deviation of each velocity component (Denny 1988, Gambi et al. 1990). Turbulence intensity (%) was calculated as the turbulence divided by the mean velocity. The depth ratio (water depth divided by the canopy height) was calculated to compare

hydrodynamic environments due to differences in canopy heights in the flume (Nepf and Vivoni 2000).

The shear velocity  $U^*$  was determined from the von Karman-Prandtl velocity-depth profile relationship (Denny 1988, Gambi et al. 1990):

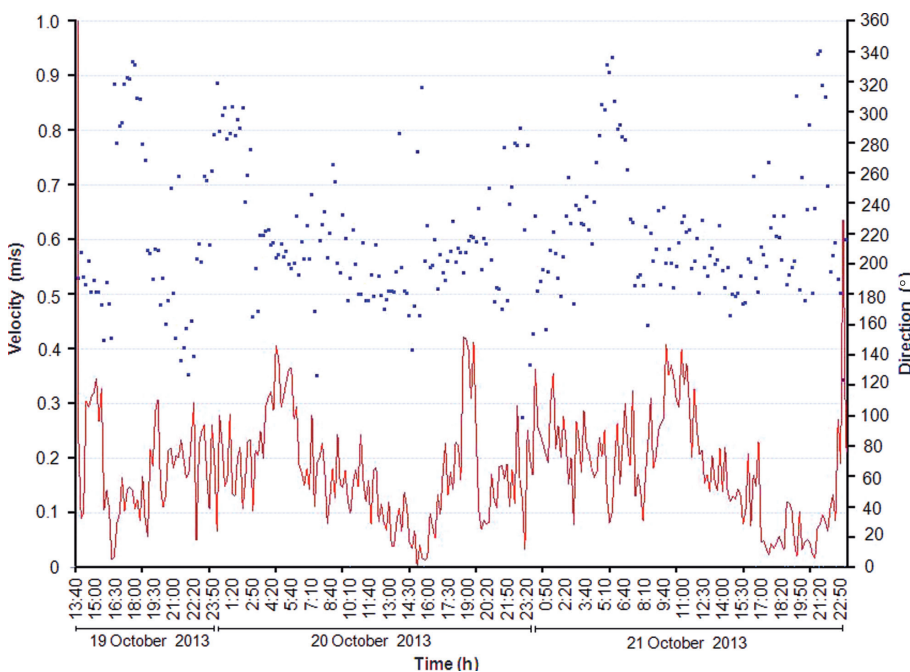
$$U(z) = U^*/K (\ln(z_2/z_1)),$$

where:

$U$  is the difference in velocity between two heights above the substratum ( $z_1$  and  $z_2$ ) and  $K$  = von Karman's constant (0.41). Depth  $z_1$  was 5.5 cm and  $z_2$  was 25.5 cm for *Enhalus* and *Cymodocea*, 5.5 and 15 for *Syringodium* and *Halodule*, and 3 and 25.5 upstream, respectively, to conform to the log relationship between velocity and height above the bottom. We performed linear regressions of  $U^*$  versus LAI, canopy height, and density, which can be predictors of the canopy's influence on hydrodynamics (Gambi et al. 1990, Peterson et al. 2004, Koch et al. 2006).

## Results

The mean water flow speed at the seagrass collection site was  $0.160 \text{ m s}^{-1}$ , ranging from  $0.002$  to  $0.430 \text{ m s}^{-1}$  (Figure 1). The seagrass densities in the field were higher than in the flume for all species except *Enhalus*, for which



**Figure 1:** Current speed and direction over 48 h (19–21 October 2013) at the seagrass collection site, Barranglompo, Spermonde Islands, south Sulawesi, Indonesia.

the flume density was towards the low end of the range of natural densities (Table 1).

In the flume, mean velocities differed depending on the species (Figure 2). The two short species (*Syringodium*, *Halodule*, <5 cm tall, Table 1) had no observable effect on mean velocities compared to upstream (no seagrass, 0.600–0.650 m s<sup>-1</sup> freestream flow above 3 cm). Water flow decreased between 10 and 16 cm height above the bottom in the *Enhalus* and *Cymodocea* experimental beds. At 24 cm, which was well above the *Cymodocea* canopy's mean maximum height (Table 1) and approaching *Enhalus*'s mean maximum canopy height, flow was equivalent to freestream conditions. Due to lack of replication, the outliers at 24 cm in the *Thalassia* and at 16 cm in the *Syringodium* profiles cannot be explained.

The depth ratio (Table 1) for all species except *Enhalus* was >2, indicating they experienced similar hydrodynamic environments unconfined by water depth in the flume (Nepf and Vivoni 2000) and that some cross comparisons can be made. The ratio for *Enhalus* indicated that its canopy was at the transition between a depth-limited and emergent canopy.

Seagrass canopies had minimal effects on turbulence and turbulence intensity (Table 1). The taller canopies (*Enhalus*, *Cymodocea*, *Thalassia*) increased values only 2–3% compared to upstream (no seagrass) values.

All species reduced U\* (≤0.091 m s<sup>-1</sup>) compared to the no-seagrass value (0.104 m s<sup>-1</sup>; Table 1). There was no relationship between U\* versus canopy height or LAI (Figure 3), which was highly correlated to leaf biomass (Pearson correlation coefficient=0.988). These potential predictors of U\* explained only 25–36% of U\* variation (height p=0.210, r<sup>2</sup>=0.357; df=1, 4; LAI p=0.318, r<sup>2</sup>=0.245). Shoot densities explained <0.1% of U\* variation (p=0.976).

## Discussion

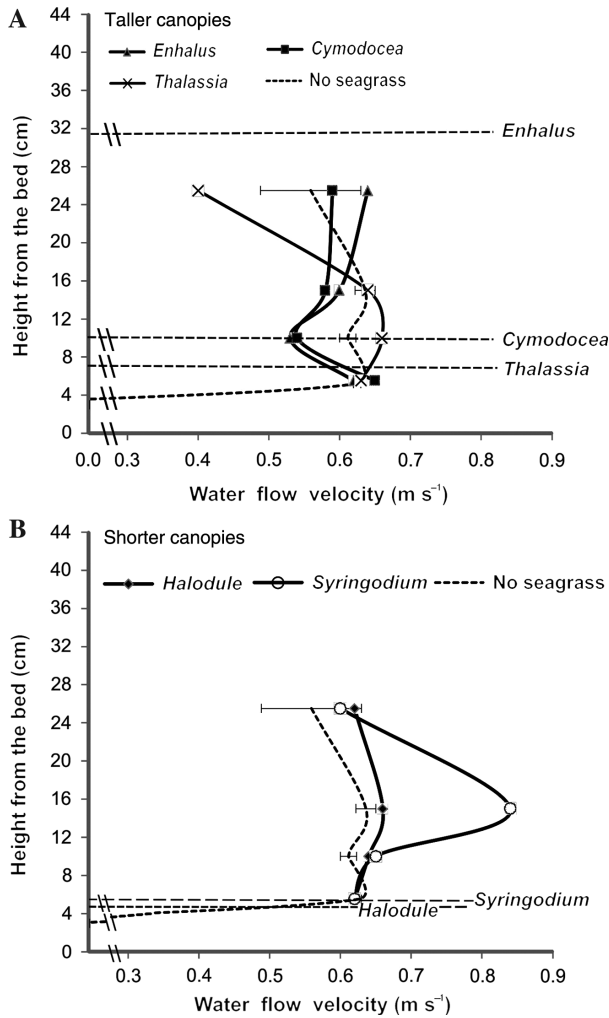
The data are limited to qualitative comparisons across species because there was no replication within a species due to the logistical limitations inherent in bringing seagrasses from Indonesia to the flume facility in California and keeping them in good condition. We therefore cannot explain whether extreme points in the velocity profiles are outliers or represent a seagrass effect. Outliers in flume velocity profiles are not unusual and can result from a transient wobble in the ADV or a transient difference in flume conditions, such as could result from a power surge. For example, published velocity profiles also show outlier

**Table 1:** Mean and standard deviation (in parenthesis) for seagrass and hydrodynamic variables.

Canopy type	Canopy height (cm)	Depth ratio	Turbulence (m s <sup>-1</sup> )	Turbulence intensity (%)	Shear velocity U* (m s <sup>-1</sup> )	LAI (m <sup>2</sup> m <sup>-2</sup> )	Leaf biomass (g dry)	Leaf shoots m <sup>-2</sup>	Natural bed leaf shoots m <sup>-2</sup>
<i>Enhalus aceroides</i>	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
<i>Cymodocea rotundata</i>	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
<i>Thalassia hemprichii</i>	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
<i>Syringodium isoetifolium</i>	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
<i>Halodule uninervis</i>	4.3 (0.2)	10.3	0.400 (0.014)	63 (1)	0.016	0.050	0.8	522	1583 (540)
No seagrass	N/A	N/A	0.398 (0.011)	65 (1)	0.104 (0.018)	N/A	N/A	N/A	N/A

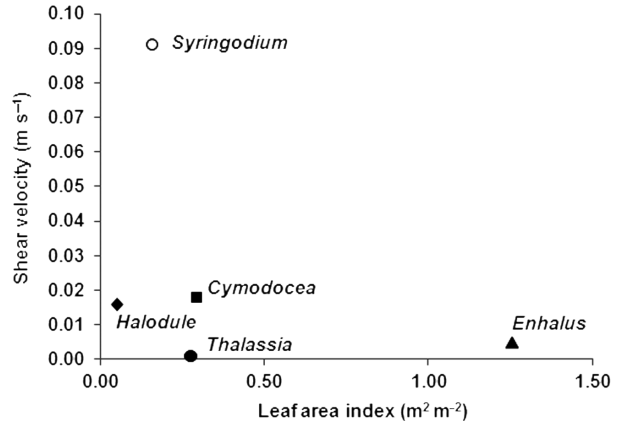
"No seagrass" is the average of two flume calibrations without seagrass (N/A: not applicable).

Canopy height in flume (n = 55 leaves). Depth ratio: flume water depth/canopy height. Turbulence and turbulence intensity: average of heights ≥5.5 cm above the bottom (n = 4). LAI: one-sided leaf area m<sup>-2</sup> in flume. Leaf shoots m<sup>-2</sup> of mesh in flume. Natural bed leaf shoot density from 1 m × 1 m quadrats (n = 4).



**Figure 2:** Water flow velocity profiles for a 1-m long seagrass bed of each of five seagrass species measured in a flume (44 cm water depth) at 0.60–0.65 m s<sup>-1</sup> freestream flow speeds. Dashed line indicates the mean height of the leaf canopy by species. Two velocity profiles were averaged for the flume calibration without seagrass. The error bars indicate standard errors of two replicate profiles.

points (figure 2 in Gambi et al. 1990; figure 1 in Fonseca and Koehl 2006). Despite the lack of replication, there are some general patterns worth noting that can be addressed in future studies. First, water flow speeds in *Enthalus* and *Cymodocea* canopies were reduced between 4 and 16 cm height above the bottom. The depth ratio for *Enthalus* (Table 1) was measured in a situation analogous to low tide in a shallow bed. Under these conditions, the depth ratio suggests that a vertical exchange zone could develop at the top of the canopy wherein the density and morphology influence the hydrodynamics within the canopy, in contrast to the “unconfined” conditions of very short canopies (Nepf and Vivoni 2000). Second, seagrasses had



**Figure 3:** Shear velocity  $U^*$  (m s<sup>-1</sup>) versus leaf area index (m<sup>2</sup> m<sup>-2</sup>).  $U^*$  scales with shear stress, the force resulting from the vertical velocity gradient. The leaf area index, a common predictor of  $U^*$ , is the one-sided area of leaves per m<sup>2</sup> of substratum.

minimal influence on turbulence, the variation in the time-averaged mean velocity, which is important for the advection of essential elements, pollutants, and biological and non-biological particles (Denny 1988, Koch et al. 2006).

Another important finding is that even the shorter canopies (<5 cm) reduced the  $U^*$  (shear velocity).  $U^*$  scales with shear stress, the force resulting from the vertical velocity gradient, which is responsible for initiating movements of sediment and other particles at and near the bottom (Denny 1988, Koch et al. 2006). The finding that short canopies can reduce  $U^*$  is conservative because measurements were made at low seagrass densities (Table 1), such as would occur early in seagrass restoration projects. The velocities in the flume were also higher than those measured under calm conditions. The flume velocities created a steeper vertical gradient that better represents the conditions on less calm days at the study site, which was a small island exposed to the open ocean. The flow speed in the flume was similar to the high flow speeds in other studies (Fonseca and Kenworthy 1987, Hizon-Fradejas et al. 2009). Thus, smaller  $U^*$  values indicate that very short canopies at relatively low densities and high freestream velocities can reduce shear stress, providing increased sediment stabilization, such as found for short *Halodule uninervis* in the field (Christianen et al. 2013). Sediment stabilization is an important coastal ecosystem function in itself but it also helps to set the rate of seagrass community development and thus is important in seagrass restoration (Fonseca and Fisher 1986, Williams 1990, van der Heide et al. 2007, van Katwijk et al. 2009, Lanuru 2011). Although the focus of much of the Indo-Pacific seagrass restoration has been on taller “climax”

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species such as *Enhalus* (Lanuru 2011, Ambo-Rappe and Yasir 2015), short but fast-growing species such as *Halodule* would not only cover the sediments more quickly but also provide some measure of sediment stabilization, even early in restoration when densities are low, based on our result and that of Christianen et al. (2013).

Submerged vegetation canopies are understood to strongly influence water flow, typically by slowing water flow and, under specific conditions including fast flow, creating skimming flow above the canopies and a vertical velocity maximum close to the substratum (Gambi et al. 1990, Nepf and Vivoni 2000, Madsen et al. 2001, Peterson et al. 2004, Hendriks et al. 2008). This understanding has been based on empirical and theoretical studies of seagrasses and mimics with generally much taller canopies than the seagrasses we studied. For example, studies of “short” species reported canopy heights  $\geq 5$  cm (Fonseca and Fisher 1986, Heis et al. 2000, Peterson et al. 2004, Bouma et al. 2005, Widdows et al. 2008, Paul and Gillis 2015). Thus, our study expands the understanding of seagrass-hydrodynamic relationships by demonstrating that in very short seagrass canopies, such as commonly occur in intertidal to shallow waters in the Indo-Pacific region, seagrasses do not necessarily exert a strong influence on hydrodynamics, yet nevertheless they can decrease shear velocity and thus provide increased sediment stabilization.

Several predictions can be made about short seagrass canopies, to be tested empirically. For example, very short canopies do not necessarily enhance the retention of organic matter or larvae by reducing velocity. On the other hand, the supply of resources, e.g. nutrients for primary producers and phytoplankton for filter feeders (Thomas et al. 2000, González-Ortiz et al. 2014), could be less limiting in shorter canopies. When waves are present along with currents, a canopy of short seagrass will oscillate and open and close more than taller seagrass under the same current speed, which theoretically enhances the supply of resources (Paul and Gillis 2015).

Our results provide some basic information to guide future studies, in addition to highlighting the dearth of information on short seagrass canopies, which are common close to shore or where herbivory is intense (Christianen et al. 2013). There are many avenues for future hydrodynamic research on Indo-Pacific seagrasses. Examples of important future studies include seagrass effects at varying water speeds and under oscillating conditions when waves are the dominant hydrodynamic driver. There is also a need to study the effect of different patch sizes and mixtures of species. This basic lack of understanding of seagrass-hydrodynamic

relationships constrains the creation of guidelines for seagrass restoration efforts (Bos and van Katwijk 2007, van Katwijk et al. 2009), yet restoration is critical to combat the global seagrass decline. Hydrodynamics can influence loss of leaves in transplanted seagrass or even the transplantation itself (van Katwijk et al. 2009). There is great interest in Indonesia in establishing guidelines for seagrass restoration to combat loss and conserve its high seagrass diversity, dependent organisms and ecosystem functions. To this end, measurements of hydrodynamic conditions *in situ* and the shear strengths of different sediment types found in Indonesia’s coastal habitats are also needed to expand laboratory studies to field applications. In our study, the predictive relationship typically reported between seagrass density, biomass, and leaf area and hydrodynamic parameters (Gambi et al. 1990, Peterson et al. 2004, Koch et al. 2006, Widdows et al. 2008, Paul and Gillis 2015) seemed to break down in the short canopies, as Christianen et al. (2013) also reported. If this is the general case for very short canopies, then an easy-to-measure canopy metric that predicts seagrass-hydrodynamic relations would be especially valuable in regions such as Indonesia where state-of-the-art facilities for hydrodynamic studies are lacking.

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## Graphical abstract

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Mahatma Lanuru, Rohani Ambo-Rappe,  
Khairul Amri and Susan L. Williams  
**Hydrodynamics in Indo-Pacific seagrasses  
with a focus on short canopies**

<https://doi.org/10.1515/bot-2017-0037>  
Botanica Marina 2017; x(x): xxx–xxx

**Research article:** The hydrodynamic effects of five species of seagrasses from Indonesia were studied in a flume.

**Keywords:** *Cymodocea*; *Enhalus*; hydrodynamics; Indonesia; seagrass.



Mahatma Lanuru\*, Rohani Ambo-Rappe, Khairul Amri and Susan L. Williams

# Hydrodynamics in Indo-Pacific seagrasses with a focus on short canopies

<https://doi.org/10.1515/bot-2017-0037>

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**Abstract:** Seagrass hydrodynamic regimes are important to understand and also to guide seagrass restoration, which is of great interest in Indonesia because of environmental threats to the exceptionally high seagrass species richness. Hydrodynamic regimes influence the physical stability of seagrass beds, sedimentation rates, and the advection of nutrients and food to seagrasses and associated organisms. In a flume, we determined the effect of canopies of *Cymodocea rotundata*, *Enhalus acoroides*, *Halodule uninervis*, *Syringodium isoetifolium* and *Thalassia hemprichii* on water velocity, turbulence, turbulence intensity and shear velocity. The taller canopies of *Enhalus* and *Cymodocea* slowed water flow, but the shorter canopies (<5 cm) had little effect. Seagrasses did not influence turbulence and turbulence intensity (turbulence normalized to mean velocity) but they reduced shear velocity  $U^*$ . Our results indicate that *Enhalus* is a good candidate for transplantation in terms of reducing mean water flow and shear velocities, but that *Halodule* should also be considered as it also reduced shear velocities and it spreads quickly after transplantation. Our results extend the understanding of seagrass-hydrodynamic relationships to include very short canopies, unlike the taller canopies studied to date.

**Keywords:** *Cymodocea*; *Enhalus*; hydrodynamics; Indonesia; seagrass.

## Introduction

Seagrass leaf canopies profoundly influence water flow dynamics. In turn, water flow dynamics influence both the physical marine environment by affecting sediment deposition and resuspension and the associated biological communities through effects on physiological processes, food availability, larval recruitment and dispersal (Eckman 1987, Thomas et al. 2000, Williams and Heck 2001, Koch et al. 2006, González-Ortiz et al. 2014). Understanding the seagrass-hydrodynamic relationship is also important for successful restoration efforts because currents or wave action can uproot fragile seagrass transplants (Fonseca and Fisher 1986, van Katwijk et al. 2009).

In general, seagrass canopies modify the hydrodynamic environment within and around them by: (1) attenuating the water flow and dissipating wave energy, promoting the retention of sediments and biological particles, (2) changing the velocity profile close to the bottom and affecting the boundary layer of more viscous, slower flow, (3) increasing or decreasing the turbulence and thus advection (the transport of materials), and (4) propagating monamis, or leaf waving, which enhances advection (reviewed in Madsen et al. 2001, Koch et al. 2006). These influences in turn govern the ecological processes mentioned above. For example, very slow water flow, decreased turbulence and advection can create mass transfer limitation of critical substrates including carbon dioxide and dissolved nutrients to seagrass and associated primary producers (Thomas et al. 2000, Koch et al. 2006). Reduced advective fluxes of food particles and larvae can limit the recruitment, survival and growth of animals living within the seagrass bed. High flow speeds can rip seagrasses from the substratum. The reviews by Madsen et al. (2001) and Koch et al. (2006) highlight that seagrass-hydrodynamic studies differ widely in their approach and results, and that more research is required to build a comprehensive understanding of the specific ways in which seagrasses influence water flow. Of note for our study is that most seagrass-hydrodynamic studies have been devoted to temperate species and to canopies that are relatively tall (>5 cm, see Discussion).

The influence of a seagrass canopy on water flow depends on its physical structure. Most simply, in the case

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of a continuous monospecific canopy, structure is dictated by leaf morphology (including stiffness and length relative to water depth), density and arrangement, while patchiness in the meadow influences water flow at the larger landscape scale (references above; Nepf and Vivoni 2000, Bouma et al. 2005, Fonseca et al. 2007, Peralta et al. 2008). Leaf morphology varies widely in size and shape across seagrass genera and species (Duarte 1991), ranging from straps (*Enhalus*, *Posidonia*, *Thalassia*, *Zostera*, *Cymodocea*, *Halodule*), small ovals (*Halophila*), cylinders (*Syringodium*), to more complex shapes (*Thalassodendron*, *Amphibolis*). Seagrass morphology itself adjusts plastically to hydrodynamic regimes (Peralta et al. 2006).

The objective of our study was to generate some basic understanding of the effect of common Indonesian seagrass species on water flow dynamics. Although Indonesia is a center of seagrass species richness (Green and Short 2003, Short et al. 2007), its seagrasses have been studied relatively little compared to coral reefs and mangroves (Orth et al. 2006), despite the fact that Indonesian seagrasses are threatened by many factors (Nadiarti et al. 2012). To generate baseline information, we measured basic hydrodynamic descriptors of the canopies of five species, which differ widely in leaf morphology and thus canopy structure, under controlled conditions in a laboratory flume. The species are common throughout the Indo-Pacific region where they form monospecific and mixed-species canopies, including ones with very short leaves.

## Materials and methods

The field seagrass bed was located at Barranglompo Island (5°03'S, 119°20'E) in the Spermonde Archipelago, south Sulawesi, Indonesia. We measured freestream water flow speed and direction every minute for 48 h (19–21 October 2013) using an Infinity Series ver. 0.10 current meter (JFE Advantech Co., Ltd. 3-48 Takahata-cho, Nishinomiya, Hyogo, Japan). The current meter was deployed in a freestream flow at 1.5 m above the substratum (water depth = 4 m) and over a meter above the seagrass canopy. Freestream flow, i.e. where there are no boundary layer influences caused by friction with the bottom and the seagrass, was measured to estimate flow speeds to be used in the flume study described below. Measurements were recorded during a spring tide cycle and under calm wind and wave conditions.

In September 2014, the leaf shoots of *Cymodocea rotundata* Ascherson et Schweinfurth, *Enhalus acoroides*

(Linnaeus f.) Royle, *Halodule uninervis* (Forsskål) Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii* (Ehrenberg) Ascherson were counted in 1-m<sup>2</sup> quadrats (n = 4 per species) in monospecific stands before collecting intact rhizomes with attached leaf shoots. Seagrasses were rinsed of sediments, and epiphytes were removed by gently wiping the leaves with a soft towel, cushioned by plastic fiber batting, and placed in coolers for air shipment to the Bodega Marine Laboratory, University of California at Davis, USA, where flume studies were conducted.

A straight flume (Model 504, Engineering Design Laboratory, Lake City, MN, USA, working section 45 × 45 × 250 cm) was used to characterize the effect of the leaf canopy on water flow dynamics. The flume was filled with seawater to a depth of 44 cm above the bottom and the seawater was not changed during the experiment. Measurements were made at a flume speed of 0.60–0.65 m s<sup>-1</sup>. The velocity was chosen to be at the high end of the field conditions recorded over 48 h because undoubtedly the velocity would reach higher levels under less calm field conditions.

We created a seagrass bed (45 cm wide × 100 cm long) of each species using a plastic-coated wire mesh (0.5 × 0.5 cm mesh size) fitted across the width of the working section and centered in the middle of the working section's length. To secure the buoyant seagrass in the flume, we placed the rhizomes between two pieces of mesh, spacing them irregularly to mimic their natural arrangement, added small lead fishing sinkers, and threaded the leaf shoots through the top mesh layer. The edges of the mesh were smoothed with duct tape. The mesh was placed as close to the flume bottom as possible (average height above bottom: 1.8 cm ± 0.43 SD, n = 275 measurements). The mesh created a rough bottom generally analogous to the rough bottoms created by small pieces of coral rubble and animal tubes in Indo-Pacific seagrass beds.

The water flow velocity in the flume was determined using an Acoustic Doppler Velocimeter (ADV, Field Vetrino serial #VNO0224, Nortek AS, Rud, Norway) with Vetrino Plus software, a baud of 57600, and sampling rate of 200 Hz. The ADV was centered in the width of the working section for all measurements. The flume was calibrated by averaging velocity measurements without seagrass at 3, 5.5, 10, 15 and 25.5 cm above the bottom at 38 and 116 cm from the beginning of the working section. Seagrass measurements were made at midway along the length of the mesh (50 cm downstream from the edge of the seagrass bed) at 5.5, 10, 15 and 25.5 cm heights and in the middle of the seagrass bed. Due to the mesh, the closest the ADV could be positioned above the flume bottom was 5.5 cm.

After velocity stabilized upon repositioning the ADV, it was recorded over 2 min. The mesh itself without attached seagrasses slowed the flow minimally by  $0.049 \text{ m s}^{-1}$  at  $\geq 5.5 \text{ cm}$  above the bottom.

To compare the experimental seagrass bed to the field and other studies, we counted the leaf shoots in the mesh and measured the leaf canopy height as the distance between the mesh surface and the longest leaf of 55 shoots of each species. We then clipped the leaves flush with the mesh and measured leaf area (Li-Cor meter, Model Li-3100, Lincoln, NE, USA) to calculate the leaf area index (LAI) as the one-sided leaf area ( $\text{m}^2$ ) per  $\text{m}^2$  of mesh. *Syringodium*'s cylindrical leaf area was calculated as the lateral area (leaf area multiplied by  $\pi$ ). Leaves were oven-dried at  $60^\circ\text{C}$  until constant mass and weighed. LAI, leaf biomass, and density theoretically relate to the canopy's influence on hydrodynamics (Gambi et al. 1990, Peterson et al. 2004, Koch et al. 2006).

We calculated the mean velocity as the square root of the sum of squares of the ADV's three velocity components averaged across instantaneous recordings made during the measurement period. Turbulence, the measure of the variation in the average flow, was calculated as the root mean square of the standard deviation of each velocity component (Denny 1988, Gambi et al. 1990). Turbulence intensity (%) was calculated as the turbulence divided by the mean velocity. The depth ratio (water depth divided by the canopy height) was calculated to compare

hydrodynamic environments due to differences in canopy heights in the flume (Nepf and Vivoni 2000).

The shear velocity  $U^*$  was determined from the von Karman-Prandtl velocity-depth profile relationship (Denny 1988, Gambi et al. 1990):

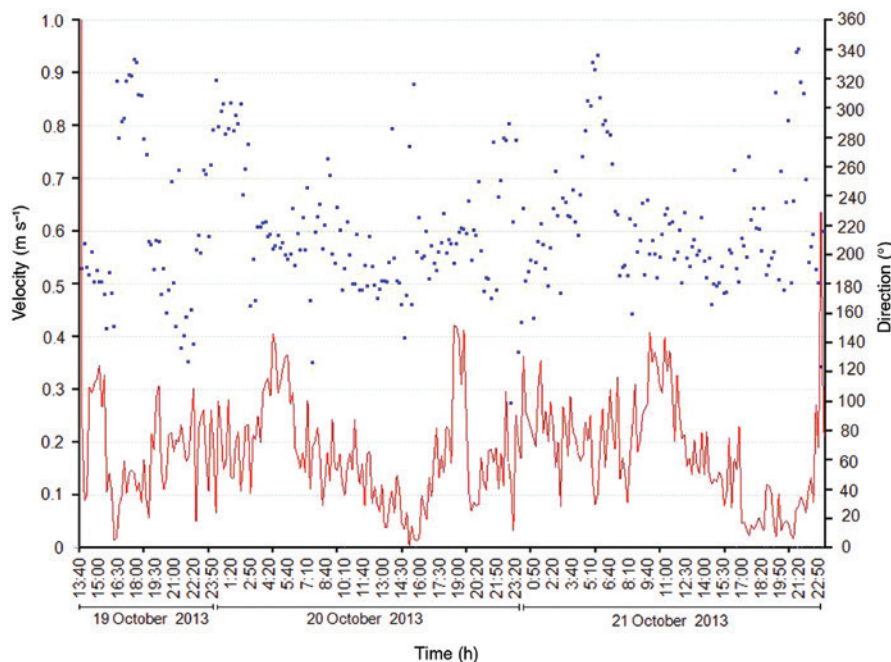
$$U(z) = U^*/K (\ln(z_2/z_1)),$$

where:

$U$  is the difference in velocity between two heights above the substratum ( $z_1$  and  $z_2$ ) and  $K$  = von Karman's constant (0.41). Depth  $z_1$  was 5.5 cm and  $z_2$  was 25.5 cm for *Enhalus* and *Cymodocea*, 5.5 and 15 for *Syringodium* and *Halodule*, and 3 and 25.5 upstream, respectively, to conform to the log relationship between velocity and height above the bottom. We performed linear regressions of  $U^*$  versus LAI, canopy height, and density, which can be predictors of the canopy's influence on hydrodynamics (Gambi et al. 1990, Peterson et al. 2004, Koch et al. 2006).

## Results

The mean water flow speed at the seagrass collection site was  $0.160 \text{ m s}^{-1}$ , ranging from  $0.002$  to  $0.430 \text{ m s}^{-1}$  (Figure 1). The seagrass densities in the field were higher than in the flume for all species except *Enhalus*, for which



**Figure 1:** Current speed and direction over 48 h (19–21 October 2013) at the seagrass collection site, Barranglompo, Spermonde Islands, south Sulawesi, Indonesia.

the flume density was towards the low end of the range of natural densities (Table 1).

In the flume, mean velocities differed depending on the species (Figure 2). The two short species (*Syringodium*, *Halodule*, <5 cm tall, Table 1) had no observable effect on mean velocities compared to upstream (no seagrass, 0.600–0.650 m s<sup>-1</sup> freestream flow above 3 cm). Water flow decreased between 10 and 16 cm height above the bottom in the *Enhalus* and *Cymodocea* experimental beds. At 24 cm, which was well above the *Cymodocea* canopy's mean maximum height (Table 1) and approaching *Enhalus*'s mean maximum canopy height, flow was equivalent to freestream conditions. Due to lack of replication, the outliers at 24 cm in the *Thalassia* and at 16 cm in the *Syringodium* profiles cannot be explained.

The depth ratio (Table 1) for all species except *Enhalus* was >2, indicating they experienced similar hydrodynamic environments unconfined by water depth in the flume (Nepf and Vivoni 2000) and that some cross comparisons can be made. The ratio for *Enhalus* indicated that its canopy was at the transition between a depth-limited and emergent canopy.

Seagrass canopies had minimal effects on turbulence and turbulence intensity (Table 1). The taller canopies (*Enhalus*, *Cymodocea*, *Thalassia*) increased values only 2–3% compared to upstream (no seagrass) values.

All species reduced U\* (≤0.091 m s<sup>-1</sup>) compared to the no-seagrass value (0.104 m s<sup>-1</sup>; Table 1). There was no relationship between U\* versus canopy height or LAI (Figure 3), which was highly correlated to leaf biomass (Pearson correlation coefficient=0.988). These potential predictors of U\* explained only 25–36% of U\* variation (height p=0.210, r<sup>2</sup>=0.357; df=1, 4; LAI p=0.318, r<sup>2</sup>=0.245). Shoot densities explained <0.1% of U\* variation (p=0.976).

## Discussion

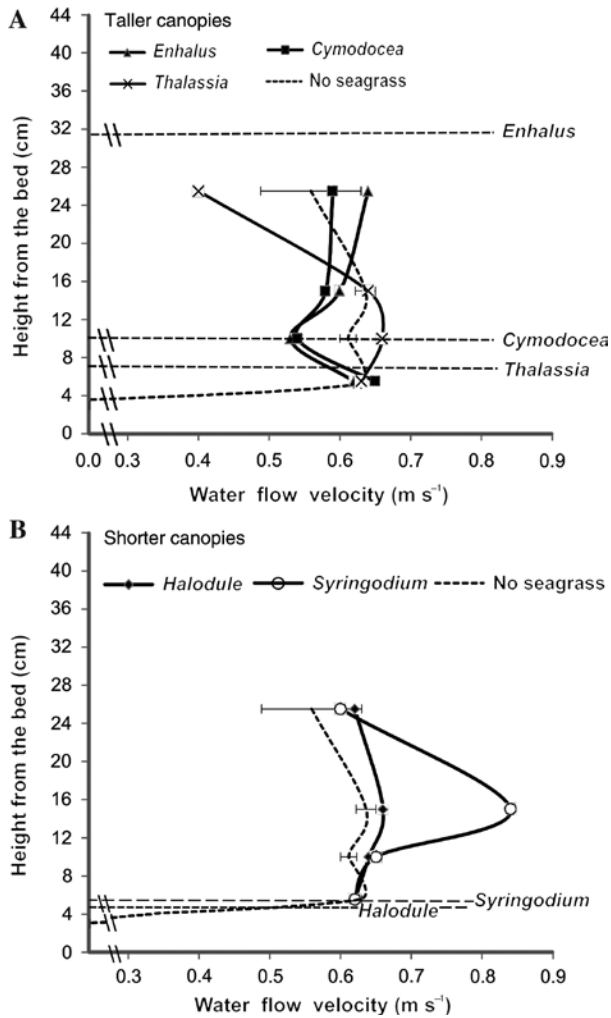
The data are limited to qualitative comparisons across species because there was no replication within a species due to the logistical limitations inherent in bringing seagrasses from Indonesia to the flume facility in California and keeping them in good condition. We therefore cannot explain whether extreme points in the velocity profiles are outliers or represent a seagrass effect. Outliers in flume velocity profiles are not unusual and can result from a transient wobble in the ADV or a transient difference in flume conditions, such as could result from a power surge. For example, published velocity profiles also show outlier

**Table 1:** Mean and standard deviation (in parenthesis) for seagrass and hydrodynamic variables.

Canopy type	Canopy height (cm)	Depth ratio	Turbulence (m s <sup>-1</sup> )	Turbulence intensity (%)	Shear velocity U* (m s <sup>-1</sup> )	LAI (m <sup>2</sup> m <sup>-2</sup> )	Leaf biomass (g dry)	Leaf shoots m <sup>-2</sup>	Natural bed leaf shoots m <sup>-2</sup>
<i>Enhalus aceroides</i>	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
<i>Cymodocea rotundata</i>	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
<i>Thalassia hemprichii</i>	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
<i>Syringodium isoetifolium</i>	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
<i>Halodule uninervis</i>	4.3 (0.2)	10.3	0.400 (0.014)	63 (1)	0.016	0.050	0.8	522	1583 (540)
No seagrass	N/A	N/A	0.398 (0.011)	65 (1)	0.104 (0.018)	N/A	N/A	N/A	N/A

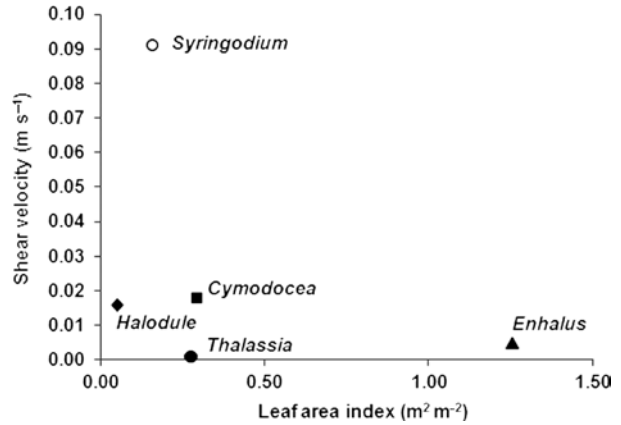
"No seagrass" is the average of two flume calibrations without seagrass (N/A: not applicable).

Canopy height in flume (n = 55 leaves). Depth ratio: flume water depth/canopy height. Turbulence and turbulence intensity: average of heights ≥5.5 cm above the bottom (n = 4). LAI: one-sided leaf area m<sup>-2</sup> in flume. Leaf shoots m<sup>-2</sup> of mesh in flume. Natural bed leaf shoot density from 1 m × 1 m quadrats (n = 4).



**Figure 2:** Water flow velocity profiles for a 1-m long seagrass bed of each of five seagrass species measured in a flume (44 cm water depth) at 0.60–0.65  $m s^{-1}$  freestream flow speeds. “A” is water flow velocity profiles for taller canopies, while “B” is water flow velocity profiles for shorter canopies seagrass species. Dashed line indicates the mean height of the leaf canopy by species. Two velocity profiles were averaged for the flume calibration without seagrass. The error bars indicate standard errors of two replicate profiles.

points (figure 2 in Gambi et al. 1990; figure 1 in Fonseca and Koehl 2006). Despite the lack of replication, there are some general patterns worth noting that can be addressed in future studies. First, water flow speeds in *Enhalus* and *Cymodocea* canopies were reduced between 4 and 16 cm height above the bottom. The depth ratio for *Enhalus* (Table 1) was measured in a situation analogous to low tide in a shallow bed. Under these conditions, the depth ratio suggests that a vertical exchange zone could develop at the top of the canopy wherein the density and morphology influence the hydrodynamics within the canopy, in contrast to the “unconfined” conditions of very short



**Figure 3:** Shear velocity  $U^*$  ( $m s^{-1}$ ) versus leaf area index ( $m^2 m^{-2}$ ).  $U^*$  scales with shear stress, the force resulting from the vertical velocity gradient. The leaf area index, a common predictor of  $U^*$ , is the one-sided area of leaves per  $m^2$  of substratum.

canopies (Nepf and Vivoni 2000). Second, seagrasses had minimal influence on turbulence, the variation in the time-averaged mean velocity, which is important for the advection of essential elements, pollutants, and biological and non-biological particles (Denny 1988, Koch et al. 2006).

Another important finding is that even the shorter canopies (<5 cm) reduced the  $U^*$  (shear velocity).  $U^*$  scales with shear stress, the force resulting from the vertical velocity gradient, which is responsible for initiating movements of sediment and other particles at and near the bottom (Denny 1988, Koch et al. 2006). The finding that short canopies can reduce  $U^*$  is conservative because measurements were made at low seagrass densities (Table 1), such as would occur early in seagrass restoration projects. The velocities in the flume were also higher than those measured under calm conditions. The flume velocities created a steeper vertical gradient that better represents the conditions on less calm days at the study site, which was a small island exposed to the open ocean. The flow speed in the flume was similar to the high flow speeds in other studies (Fonseca and Kenworthy 1987, Hizon-Fradejas et al. 2009). Thus, smaller  $U^*$  values indicate that very short canopies at relatively low densities and high freestream velocities can reduce shear stress, providing increased sediment stabilization, such as found for short *Halodule uninervis* in the field (Christianen et al. 2013). Sediment stabilization is an important coastal ecosystem function in itself but it also helps to set the rate of seagrass community development and thus is important in seagrass restoration (Fonseca and Fisher 1986, Williams 1990, van der Heide et al. 2007, van Katwijk et al. 2009, Lanuru 2011). Although the focus of much of the Indo-Pacific seagrass

restoration has been on taller “climax” species such as *Enhalus* (Lanuru 2011, Ambo-Rappe and Yasir 2015), short but fast-growing species such as *Halodule* would not only cover the sediments more quickly but also provide some measure of sediment stabilization, even early in restoration when densities are low, based on our result and that of Christianen et al. (2013).

Submerged vegetation canopies are understood to strongly influence water flow, typically by slowing water flow and, under specific conditions including fast flow, creating skimming flow above the canopies and a vertical velocity maximum close to the substratum (Gambi et al. 1990, Nepf and Vivoni 2000, Madsen et al. 2001, Peterson et al. 2004, Hendriks et al. 2008). This understanding has been based on empirical and theoretical studies of seagrasses and mimics with generally much taller canopies than the seagrasses we studied. For example, studies of “short” species reported canopy heights  $\geq 5$  cm (Fonseca and Fisher 1986, Heis et al. 2000, Peterson et al. 2004, Bouma et al. 2005, Widdows et al. 2008, Paul and Gillis 2015). Thus, our study expands the understanding of seagrass-hydrodynamic relationships by demonstrating that in very short seagrass canopies, such as commonly occur in intertidal to shallow waters in the Indo-Pacific region, seagrasses do not necessarily exert a strong influence on hydrodynamics, yet nevertheless they can decrease shear velocity and thus provide increased sediment stabilization.

Several predictions can be made about short seagrass canopies, to be tested empirically. For example, very short canopies do not necessarily enhance the retention of organic matter or larvae by reducing velocity. On the other hand, the supply of resources, e.g. nutrients for primary producers and phytoplankton for filter feeders (Thomas et al. 2000, González-Ortiz et al. 2014), could be less limiting in shorter canopies. When waves are present along with currents, a canopy of short seagrass will oscillate and open and close more than taller seagrass under the same current speed, which theoretically enhances the supply of resources (Paul and Gillis 2015).

Our results provide some basic information to guide future studies, in addition to highlighting the dearth of information on short seagrass canopies, which are common close to shore or where herbivory is intense (Christianen et al. 2013). There are many avenues for future hydrodynamic research on Indo-Pacific seagrasses. Examples of important future studies include seagrass effects at varying water speeds and under oscillating conditions when waves are the dominant hydrodynamic driver. There is also a need to study the effect of different patch sizes and mixtures of species. This basic

lack of understanding of seagrass-hydrodynamic relationships constrains the creation of guidelines for seagrass restoration efforts (Bos and van Katwijk 2007, van Katwijk et al. 2009), yet restoration is critical to combat the global seagrass decline. Hydrodynamics can influence loss of leaves in transplanted seagrass or even the transplantation itself (van Katwijk et al. 2009). There is great interest in Indonesia in establishing guidelines for seagrass restoration to combat loss and conserve its high seagrass diversity, dependent organisms and ecosystem functions. To this end, measurements of hydrodynamic conditions *in situ* and the shear strengths of different sediment types found in Indonesia’s coastal habitats are also needed to expand laboratory studies to field applications. In our study, the predictive relationship typically reported between seagrass density, biomass, and leaf area and hydrodynamic parameters (Gambi et al. 1990, Peterson et al. 2004, Koch et al. 2006, Widdows et al. 2008, Paul and Gillis 2015) seemed to break down in the short canopies, as Christianen et al. (2013) also reported. If this is the general case for very short canopies, then an easy-to-measure canopy metric that predicts seagrass-hydrodynamic relations would be especially valuable in regions such as Indonesia where state-of-the-art facilities for hydrodynamic studies are lacking.

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