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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Hydrodynamics in Short Indo-Pacific Seagrasses

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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

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 (Fonseca and Fisher 1986, van Katwijk et al. 2009).

In general, seagrass canopies modify the hydrodynamic environment within and around them by: 1) attenuating of water flow and dissipating wave energy, promoting the retention of sediments and biological particles, 2) changing the velocity profile close to the bottom and thus, 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 and Koch et al. 2006). These influences in turn govern the ecological processes mentioned above. These reviews and other references highlight that seagrass-hydrodynamic studies differ widely in their approach and results and more research is required to build a comprehensive understanding of the specific ways that 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 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 (*Thalassadendron, 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 under controlled conditions in a laboratory flume. *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 (hereafter referred to by genus) differ widely in their leaf morphology and thus canopy structure. They are common throughout the Indo-Pacific region where they form monospecific and mixed-species canopies, including some very short ones (see Results and Discussion).

Material and methods

Our field seagrass bed was located at Barranglompo Island (5^{o}03'S, 119^{o}20'E) in the Spermonde Archipelago, south Sulawesi, Indonesia. We measured freestream water flow speed and direction every minute for 48 hours (19-21 October 2013) using an Infinity Series ver. 0.10 current meter (JFE Advantech Co., Ltd. 3-48 Takahata-cho, Nishinomiya, Hyogo, Japan 63-8202), deployed at 1.5 m above the substratum (water depth = 4 m). We estimated the leaf shoot densities of *Enhalus, Cymocodea, Thalassia*, *Syringodium*, and *Halodule* in 1 m^2 quadrats (n = 4 per species) in monospecific stands before collecting intact rhizomes with attached leaf shoots. Seagrasses were cleaned of sediments and epiphytes, 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 in September 2014.

A straight flume (Model 504, Engineering Design Laboratory, Lake City, Minnesota 55041-0278, USA, working section 45 x 45 x 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 was not changed during the experiment. Measurements were made at a flume speeds of 0.60 - 0.65 m/s.

We created a seagrass bed (45 cm wide x 100 cm long) of each species using a plastic-coated wire mesh (0.5 cm x 0.5 cm mesh size**)** fitted across the width of 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. 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, Nebraska, USA) to calculate the leaf area index (LAI) as the one-sided leaf area (m^2) per m^2 of mesh. *Syringodium*'s cylindrical leaf area was calculated as the lateral area (leaf area multiplied by π). Leaves were oven-dried at 60°C until constant mass and weighed. LAI, leaf biomass, and density theoretically relate to the canopy's influence on hydrodynamics (Gambi et al. 1990, Koch et al. 2006, Peterson et al. 2004).

The water flow velocity in the flume was determined using an Acoustic Doppler Velocimeter (ADV, Field Vectrino serial #VNO0224, Nortek AS, Vangkroken 2, NO-1351 RUD, Norway) with Vectrino Plus software, a baud of 57600, and sampling rate of 200 Hz. The ADV was centered in the width of the working section. 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 5.5, 10, 15, and 25.5 cm heights; 5.5 cm was the closest ADV measurements could be made next to the flume bottom due to the mesh. After velocity stabilized upon repositioning the ADV, it was recorded over two minutes. The mesh itself without attached seagrasses slowed the flow minimally by 0.049 m/s at ≥ 5.5 cm above the bottom.

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/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:

K = von Karman's constant (0.41), U is the difference in velocity between two heights above the substratum (z_1 and z_2). 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, Koch et al. 2006, Peterson et al. 2004).

Results

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

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

The depth ratios (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 its canopy was at the transition between a depth-limited and emergent canopy. At this ratio, which is analogous to low tide in a shallow bed, a vertical exchange zone develops at the top of the canopy and density and morphology influence the hydrodynamics within the canopy, unlike in the unconfined condition of very short canopies.

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

Discussion

Our 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. Nevertheless, there are some general patterns worth noting. First, water flow speeds were lower within taller canopies such as *Enhalus* and *Cymodocea*, which is the expected hydrodynamic result. 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 shear velocity (U*). 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). Thus, smaller U* values indicate that very short canopies can reduce shear stress, providing increased sediment stabilization, such as found for short *Halodule uninervis* in the field (Christianen 2013). Sediment stabilization is an important coastal ecosystem function in itself but it also helps set the rate of seagrass community development and thus is important in seagrass restoration (Fonseca and Fisher1986, Williams 1990, van der Heide et al. 2007, van Katwijk et al. 2009, Lanuru 2011). Although the focus on much of the Indo-Pacific seagrass restoration has been on taller 'climax' seagrass such as *Enhalus* (Ambo-Rappe and Yasir, 2015, Lanuru, 2011), short but fast-growing species such as *Halodule* would not only cover the sediments more quickly but also provide some measure of sediment stabilization, 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 ≥ 5 cm (Fonseca and Fisher1986, 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. 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 (Christeanen et al. 2013). This basic lack of understanding of seagrass-hydrodynamic relationships constrains the creation of guidelines for seagrass restoration efforts (Bos and Katwijk 2007, van Katwijk et al. 2009), yet restoration is critical to combat the global seagrass decline. 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, there are many next steps in seagrass-hydrodynamic research, for example, manipulations of seagrass density, measurements of hydrodynamic conditions *in situ* and the shear strengths of different sediment types found in Indonesia's coastal habitats. 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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Table 1. Mean (SD) seagrass and hydrodynamic variables. '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^2 in flume. Leaf shoots/m^2 of 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^2/m^2)**	**Leaf biomass (g dry)**	**Leaf shoots/m^2**	**Natural bed leaf shoots/ m^2**
Enhalus	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
Cymodocea	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
Thalassia	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
Syringodium	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
Halodule	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

Figure Legends

Fig.1. Current speed and direction at the seagrass collection site, Barranglompo, Spermonde, south Sulawesi, Indonesia.

Fig. 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 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.

Fig. 3. Shear velocity U* (m/s) versus Leaf Area Index (m^2/m^2).

Figure 1

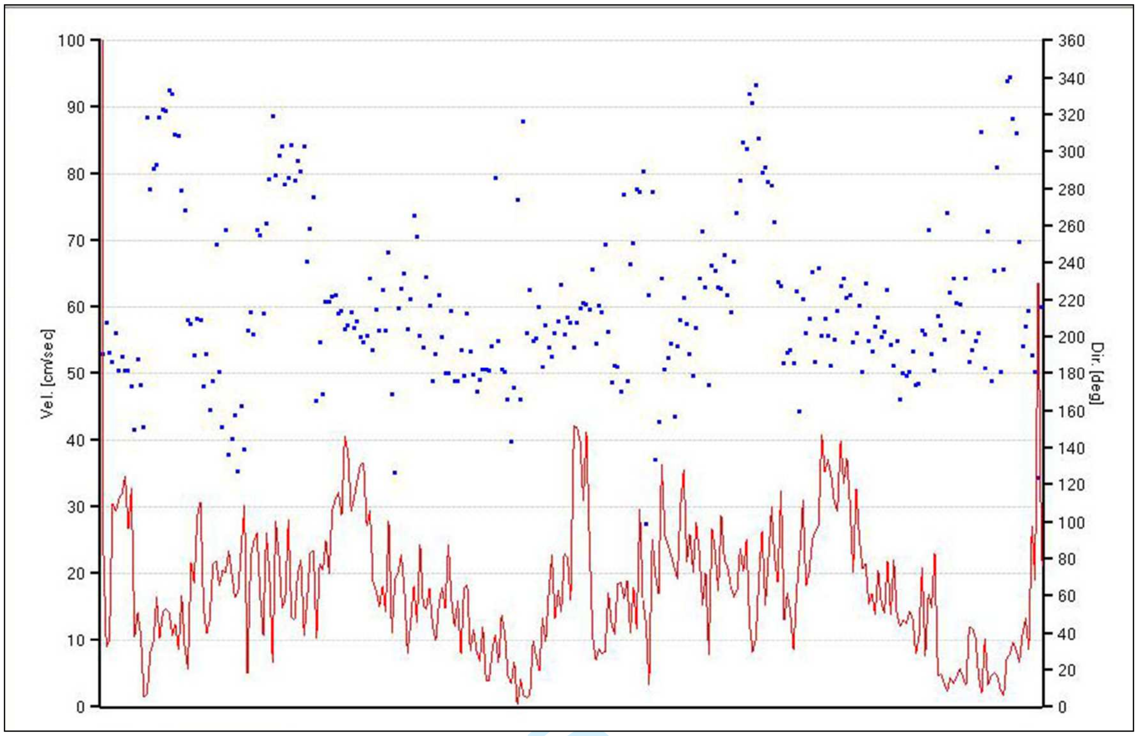

Vel. [cm/sec]
100
90
80
70
60
50
40
30
20
10
0
Dir. [deg]
360
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0

Figure 2

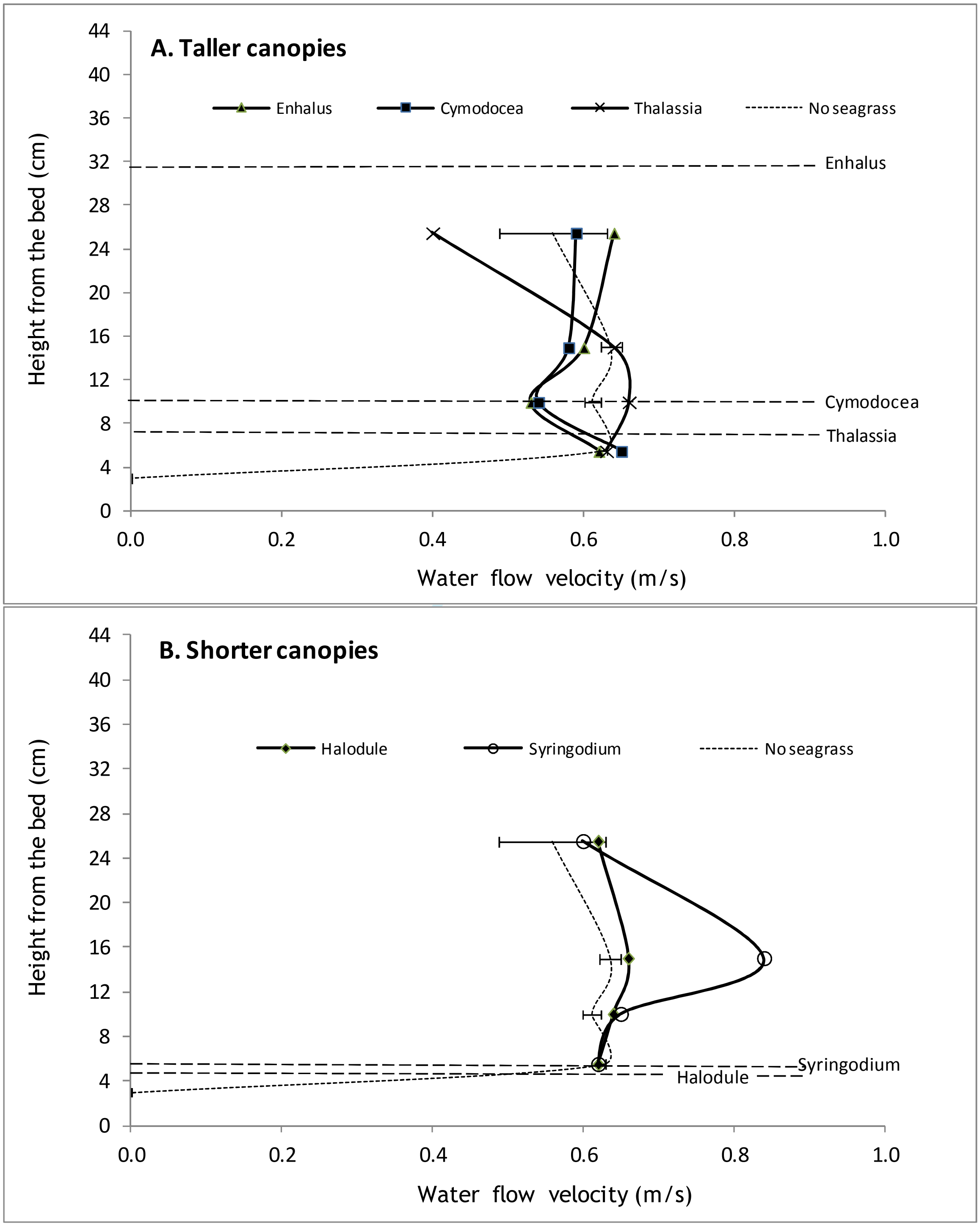
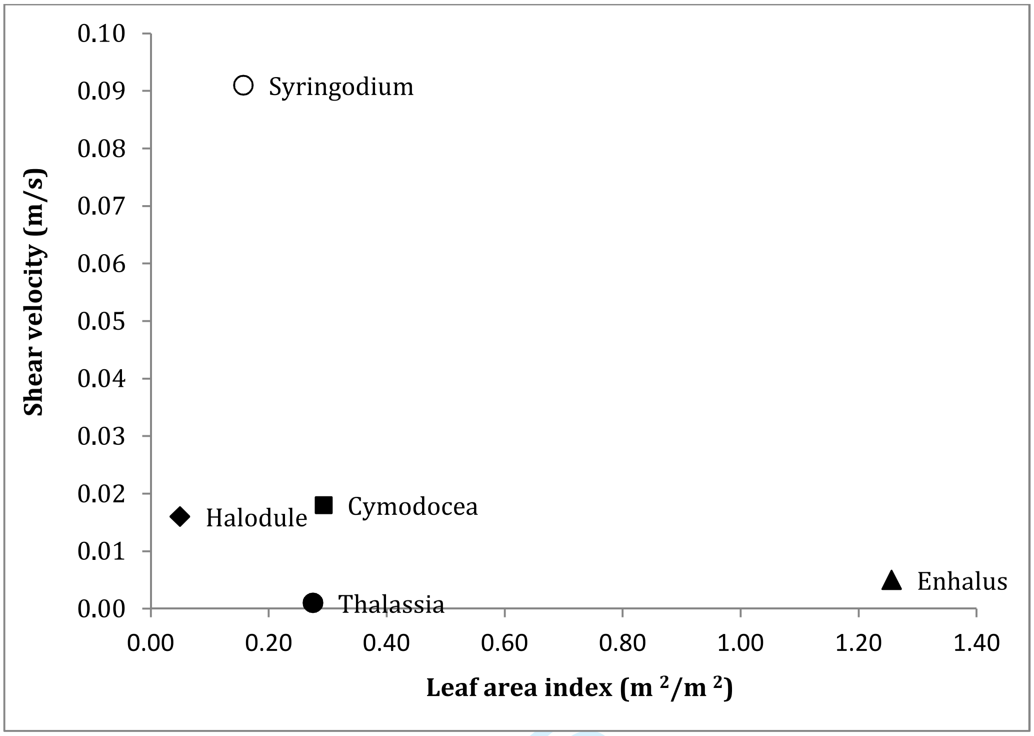

A. Taller canopies
Enhalus
Cymodocea
Thalassia
No seagrass
Enhalus
Cymodocea
Thalassia
Height from the bed (cm)
44
40
36
32
28
24
20
16
12
8
4
0
0.0
0.2
0.4
0.6
0.8
1.0
Water flow velocity (m/s)
B. Shorter canopies
Halodule
Syringodium
No seagrass
Syringodium
Halodule
Height from the bed (cm)
44
40
36
32
28
24
20
16
12
8
4
0
0.0
0.2
0.4
0.6
0.8
1.0
Water flow velocity (m/s)

Figure 3


Shear velocity (m/s)
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Syringodium
Halodule
Cymodocea
Enhalus
Thalassia
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Leaf area index (m 2/m 2)

453

Botanica Marina

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.

You may also click the below link to start the revision process (or continue the process if you have already started your revision) for your manuscript. If you use the below link you will not be required to login to ScholarOne Manuscripts.

PLEASE MAKE SURE TO CONFIRM YOUR CHOICE ON THE WEB PAGE AFTER CLICKING ON THE LINK

https://mc.manuscriptcentral.com/botmar?URL_MASK=276f0c2d09384a84af92afd01aa07433

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

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 epipytes 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 (= π x 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 (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?

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 *Limbong* 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*.

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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* 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

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 and 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 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 centre 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.

Material and methods

The field seagrass bed was located at Barranglompo Island (5^o03’S, 119^o20’E) in the Spermonde Archipelago, south Sulawesi, Indonesia. We measured freestream water flow speed and direction every minute for 48 hours (19-21 October 2013) using an Infinity Series ver. 0.10 current meter (JFE Advantech Co., Ltd. 3-48 Takahata-cho, Nishinomiya, Hyogo, Japan 63-8202). The current meter was deployed in 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 & Schweinfurth, *Enhalus acoroides* (Linnaeus f.) Royle, *Halodule uninervis* (Forsskål) Ascherson, *Syringodium isoetifolium* (Ascherson) Dandy, and *Thalassia hemprichii* (Ehrenberg) Ascherson were counted in 1-m^2 quadrats (n = 4 per species) in monospecific stands before collecting intact rhizomes with attached leaf shoots. Seagrasses were rinsed of sediments and epiphytes removed by gently wiping the leaves with a soft towel, cushioned by plastic fibre 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, Minnesota 55041-0278, USA, working section 45 x 45 x 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 speeds of 0.60 - 0.65 m/s.

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

We created a seagrass bed (45 cm wide x 100 cm long) of each species using a plastic-coated wire mesh (0.5 cm x 0.5 cm mesh size) fitted across the width of working section and centred 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. 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, Nebraska, USA) to calculate the leaf area index (LAI) as the one-sided leaf area (m^2) per m^2 of mesh. *Syringodium*'s cylindrical leaf area was calculated as the lateral area (leaf area multiplied by π). Leaves were oven-dried at 60°C until constant mass and weighed. LAI, leaf biomass, and density theoretically relate to the canopy's influence on hydrodynamics (Gambi et al. 1990, Koch et al. 2006, Peterson et al. 2004).

The water flow velocity in the flume was determined using an Acoustic Doppler Velocimeter (ADV, Field Vectrino serial #VNO0224, Nortek AS, Vangkroken 2, NO-1351 RUD, Norway) with Vectrino Plus software, a baud of 57600, and sampling rate of 200 Hz. The ADV was centred 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 two minutes. The mesh itself without attached seagrasses slowed the flow minimally by 0.049 m/s at ≥ 5.5 cm above the bottom.

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/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, Koch et al. 2006, Peterson et al. 2004).

Results

The mean water flow speed at the seagrass collection site was 0.160 m/s, ranging from 0.002 to 0.430 m/s (Fig. 1), which corresponded to freestream flow at 18 cm above the flume bottom (Fig. 2, Table 1).

In the flume, mean velocities differed depending on the species (Fig. 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 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* ($\leq$ 0.091 m/s) compared to the no seagrass value (0.104 m/s) (Table 1). There was no relationship between U* versus canopy height or LAI (Fig. 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 $p = 0.210$, $r^2 = 0.357$; df = 1, 4; LAI $p = 0.318$, $r^2 = 0.245$). Shoot densities, which were within the low range of natural canopies (Table 1), 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 points (Fig. 2 in Gambi et al. 1990; Fig.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 - 16 cm height above the bottom. The depth ratio for *Enhalus* (Table1), which in this study was measured in a situation analogous to low tide in a shallow bed, a vertical exchange zone is predicted to develop at the top of the canopy wherein the density and morphology influence the hydrodynamics within the canopy, unlike in the 'unconfined' condition of very short 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) and at the low end of natural densities (*Enhalus*) or even lower 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). Thus, smaller U* values indicate that very short canopies at relatively low densities, 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 set the rate of seagrass community development and thus is important in seagrass restoration (Fonseca and Fisher1986, Williams 1990, van der Heide et al. 2007, van Katwijk et al. 2009, Lanuru 2011). Although the focus on much of the Indo-Pacific seagrass restoration has been on taller 'climax' species such as *Enhalus* (Ambo-Rappe and Yasir 2015, Lanuru 2011), 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 Fisher1986, 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 (Christeanen 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 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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Table 1. Mean and standard deviation (in parenthesis) seagrass and hydrodynamic variables. '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^2 in flume. Leaf shoots/m^2 of 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^2/m^2)**	**Leaf biomass (g dry)**	**Leaf shoots/m^2**	**Natural bed leaf shoots/ m^2**
Enhalus aceroides	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
Cymodocea rotundata	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
Thalassia hemprichii	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
Syringodium isoetifolium	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
Halodule uninervis	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

Figure Legends

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

Fig. 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 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.

Fig. 3. Shear velocity U* (m/s) 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.

Figure 1

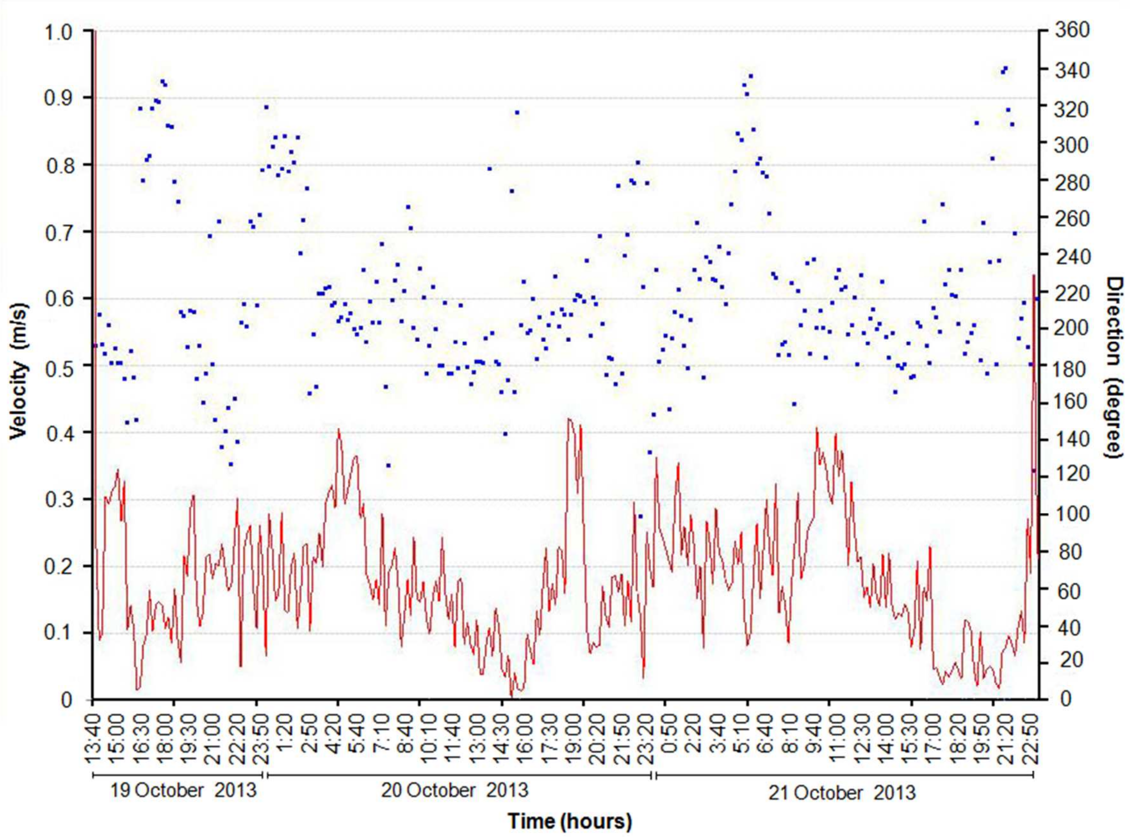

Velocity (m/s)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Direction (degree)
360
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
13:40
15:00
16:30
18:00
19:30
21:00
22:20
23:50
1:20
2:50
4:20
5:40
7:10
8:40
10:10
11:40
13:00
14:30
16:00
17:30
19:00
20:20
21:50
23:20
0:50
2:20
3:40
5:10
6:40
8:10
9:40
11:00
12:30
14:00
15:30
17:00
18:20
19:50
21:20
22:50
19 October 2013
20 October 2013
21 October 2013
Time (hours)

Figure 2

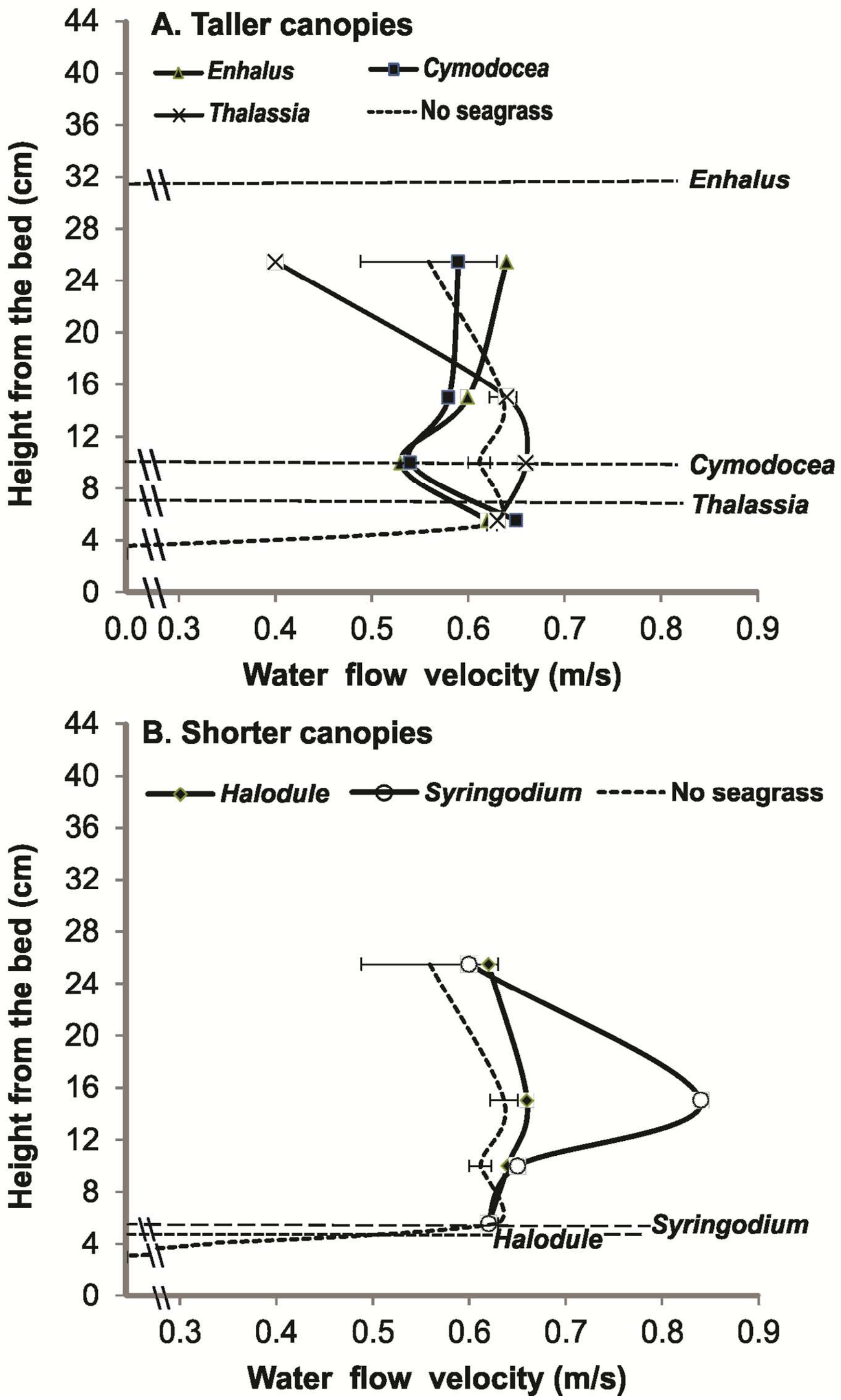
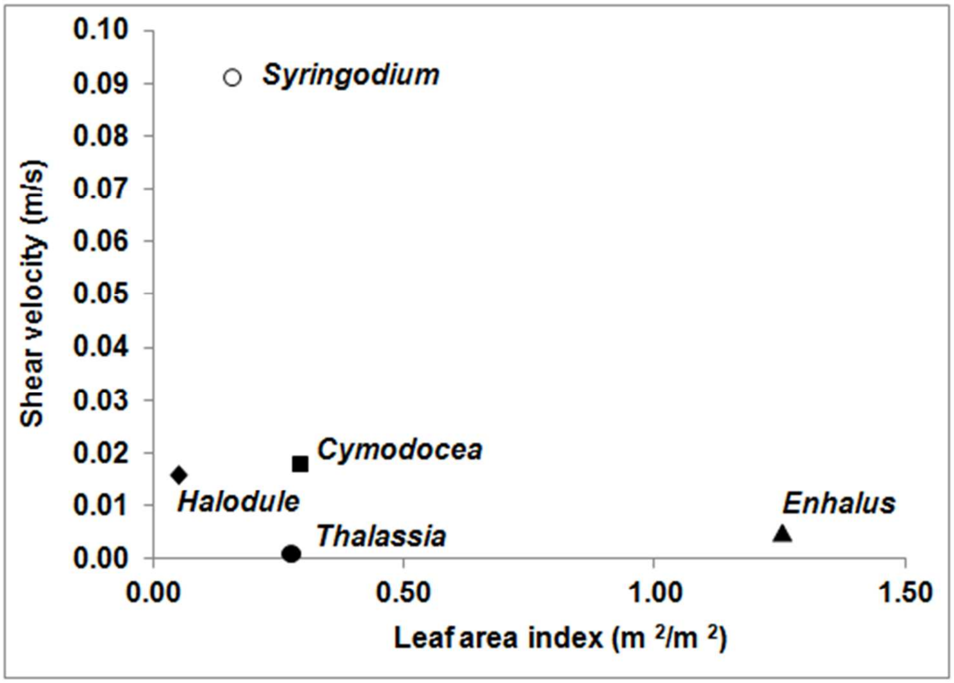

A. Taller canopies
Enhalus
Cymodocea
Thalassia
No seagrass
Enhalus
Cymodocea
Thalassia
Height from the bed (cm)
44
40
36
32
28
24
20
16
12
8
4
0
0.0 0.3 0.4 0.5 0.6 0.7 0.8 0.9
Water flow velocity (m/s)
B. Shorter canopies
Halodule
Syringodium
No seagrass
Syringodium
Halodule
Height from the bed (cm)
44
40
36
32
28
24
20
16
12
8
4
0
0.3 0.4 0.5 0.6 0.7 0.8 0.9
Water flow velocity (m/s)

Figure 3



Bionotes

Mahatma Lanuru

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

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 research interests are coastal oceanography, sediment dynamic (erosion/deposition) in the estuarine and coastal area, and habitat (seagrass) restoration. He has been recently conducted research on (i) Transplantation experiment for assessing the feasibility of using seagrass for coastal protection in Small Island, and (ii) small island coastal protection using '*Hybrid*' (combination of seagrass vegetation and submerged submerged wave breaker).

Rohani Ambo-Rappe

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Hasanuddin University, Jl. Perintis Kemerdekaan, Makassar 90245, INDONESIA.

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

Khairul Amri

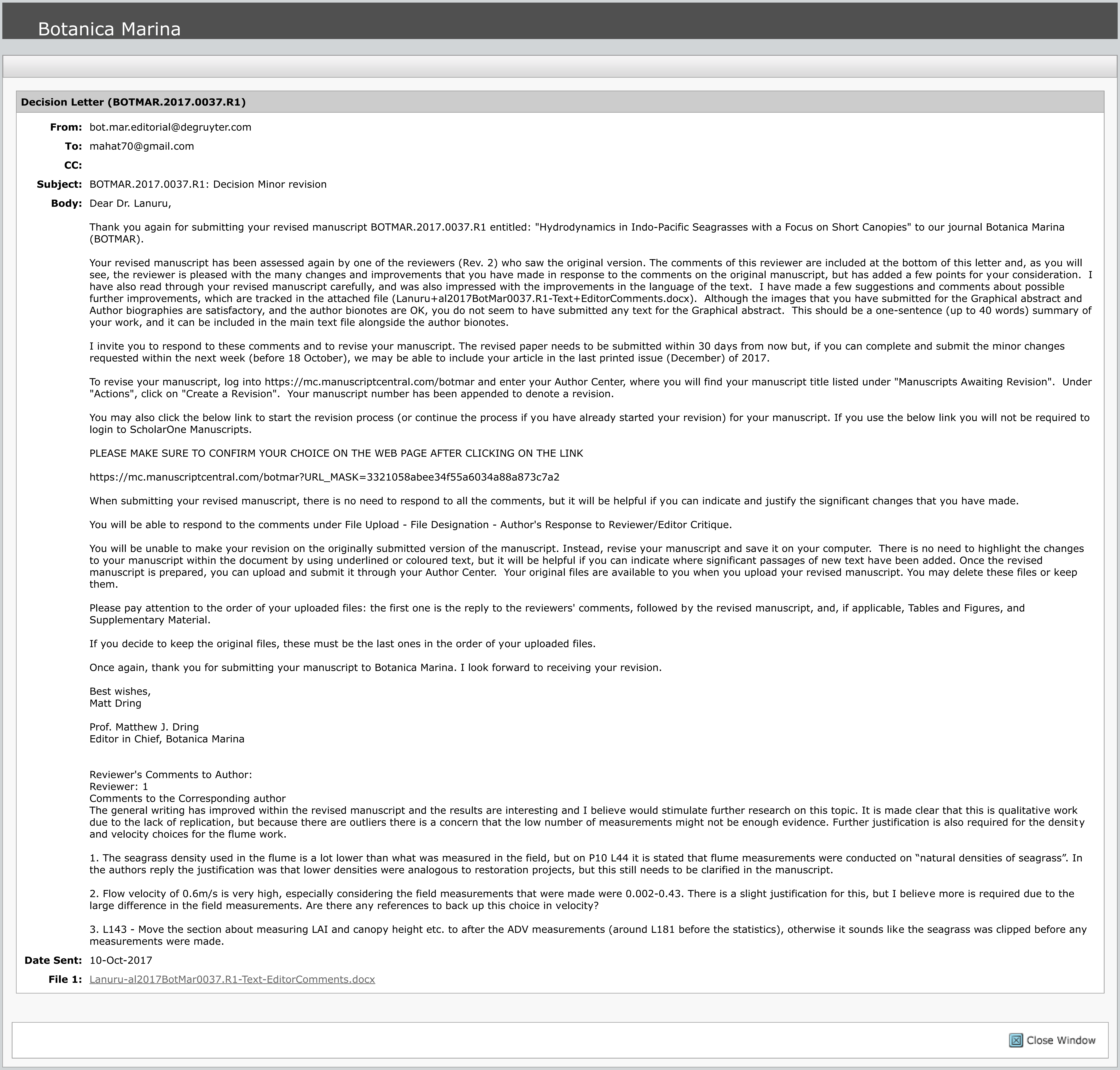
Department of Marine Science, Faculty of Marine Science and Fisheries, Hasanuddin University, Jl. Perintis Kemerdekaan, Makassar 90245, INDONESIA.

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.



Botanica Marina

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.

You may also click the below link to start the revision process (or continue the process if you have already started your revision) for your manuscript. If you use the below link you will not be required to login to ScholarOne Manuscripts.

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https://mc.manuscriptcentral.com/botmar?URL_MASK=3321058abee34f55a6034a88a873c7a2

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

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

Professor Matthew Dring
Editor in Chief, *Botanica Marina*

Dear Professor Dring:

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Dr Mahatma Lanuru

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.

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

Mahatma Lanuru[1], Rohani Ambo-Rappe[1], Khairul Amri[1], Susan L. Williams[2]

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[2]Department of Evolution and Ecology, Bodega Marine Laboratory, University of California at Davis, PO Box 247, Bodega Bay, California 94923-0247, USA

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Running title: Seagrass hydrodynamics

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 and 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 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 centre 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.

Material 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 63-8202). The current meter was deployed in freestream flow at 1.5 m above the substratum (water depth = 4 m) and over a metre 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^2 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 fibre 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, Minnesota 55041-0278, USA, working section 45 x 45 x 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^{-1}.

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 x 100 cm long) of each species using a plastic-coated wire mesh (0.5 x 0.5 cm mesh size**)** fitted across the width of working section and centred 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 Vectrino serial #VNO0224, Nortek AS, Vangkroken 2, NO-1351 RUD, Norway) with Vectrino Plus software, a baud of 57600, and sampling rate of 200 Hz. The ADV was centred 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 m s^{-1} at $\geq$ 5.5 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, Nebraska, USA) to calculate the leaf area index (LAI) as the one-sided leaf area (m^2) per m^2 of mesh. *Syringodium*'s cylindrical leaf area was calculated as the lateral area (leaf area multiplied by π). Leaves were oven-dried at 60°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 m s^{-1}, ranging from 0.002 to 0.430 m s^{-1} (Fig. 1). 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).

In the flume, mean velocities differed depending on the species (Fig. 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^{-1}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* ($\leq$ 0.091 m s^{-1}) compared to the no-seagrass value (0.104 m s^{-1}; Table 1). There was no relationship between U* versus canopy height or LAI (Fig. 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 $p = 0.210$, $r^2 = 0.357$; df = 1, 4; LAI $p = 0.318$, $r^2 = 0.245$). 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 points (Fig. 2 in Gambi et al. 1990; Fig.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 this condition, 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' condition of very short 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 (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). 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 on much of the Indo-Pacific seagrass restoration has been on taller 'climax' species such as *Enhalus* (Ambo-Rappe and Yasir 2015, Lanuru 2011), 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 (Christeanen 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 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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Table 1. Mean and standard deviation (in parenthesis) for seagrass and hydrodynamic variables. '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 $\geq$ 5.5 cm above the bottom (n = 4). LAI: one-sided leaf area m^{-2} in flume. Leaf shoots m^{-2} of 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^{-1})**	**Turbulence intensity (%)**	**Shear velocity U* (m s^{-1})**	**LAI (m^{2} m^{-2})**	**Leaf biomass (g dry)**	**Leaf shoots m^{-2}**	**Natural bed leaf shoots m^{-2}**
Enhalus aceroides	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
Cymodocea rotundata	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
Thalassia hemprichii	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
Syringodium isoetifolium	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
Halodule uninervis	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

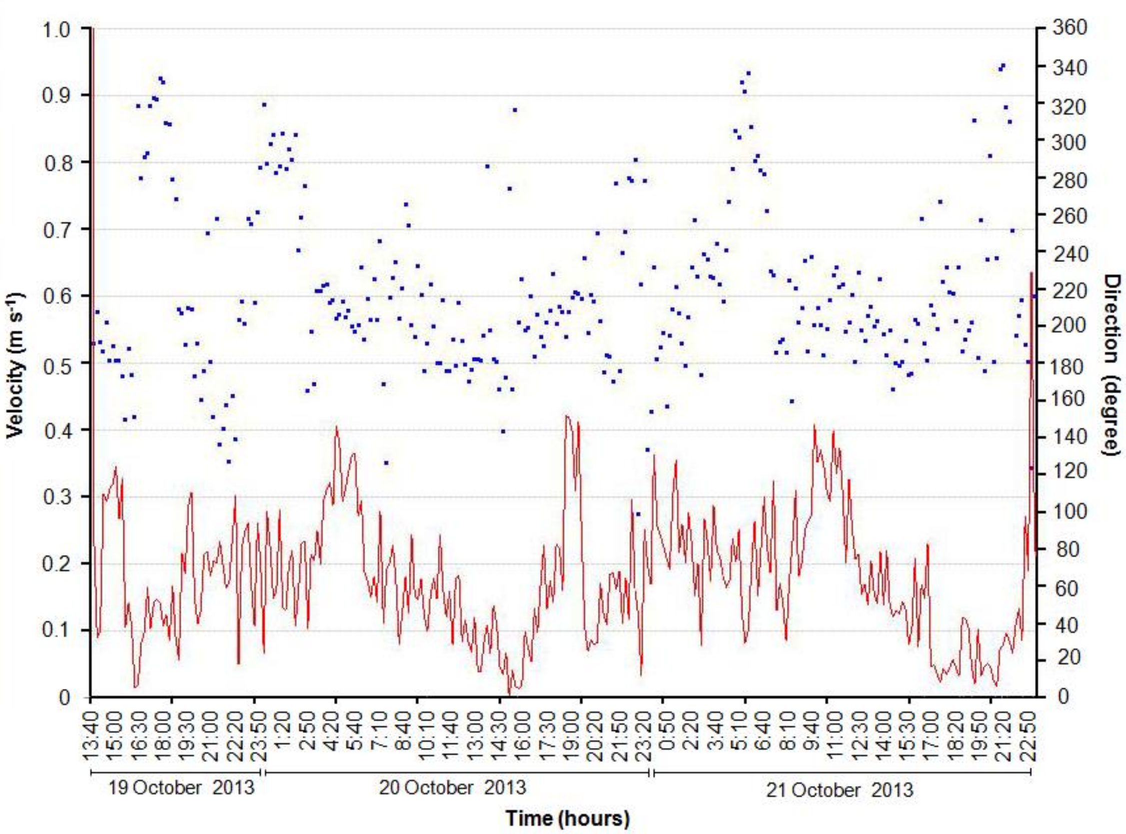
Figure Legends

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

Fig. 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. 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.

Fig. 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.

Figure 1



Velocity (m s⁻¹)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Direction (degree)
360
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
13:40
15:00
16:30
18:00
19:30
21:00
22:20
23:50
1:20
2:50
4:20
5:40
7:10
8:40
10:10
11:40
13:00
14:30
16:00
17:30
19:00
20:20
21:50
23:20
0:50
2:20
3:40
5:10
6:40
8:10
9:40
11:00
12:30
14:00
15:30
17:00
18:20
19:50
21:20
22:50
19 October 2013
20 October 2013
21 October 2013
Time (hours)

Figure 2

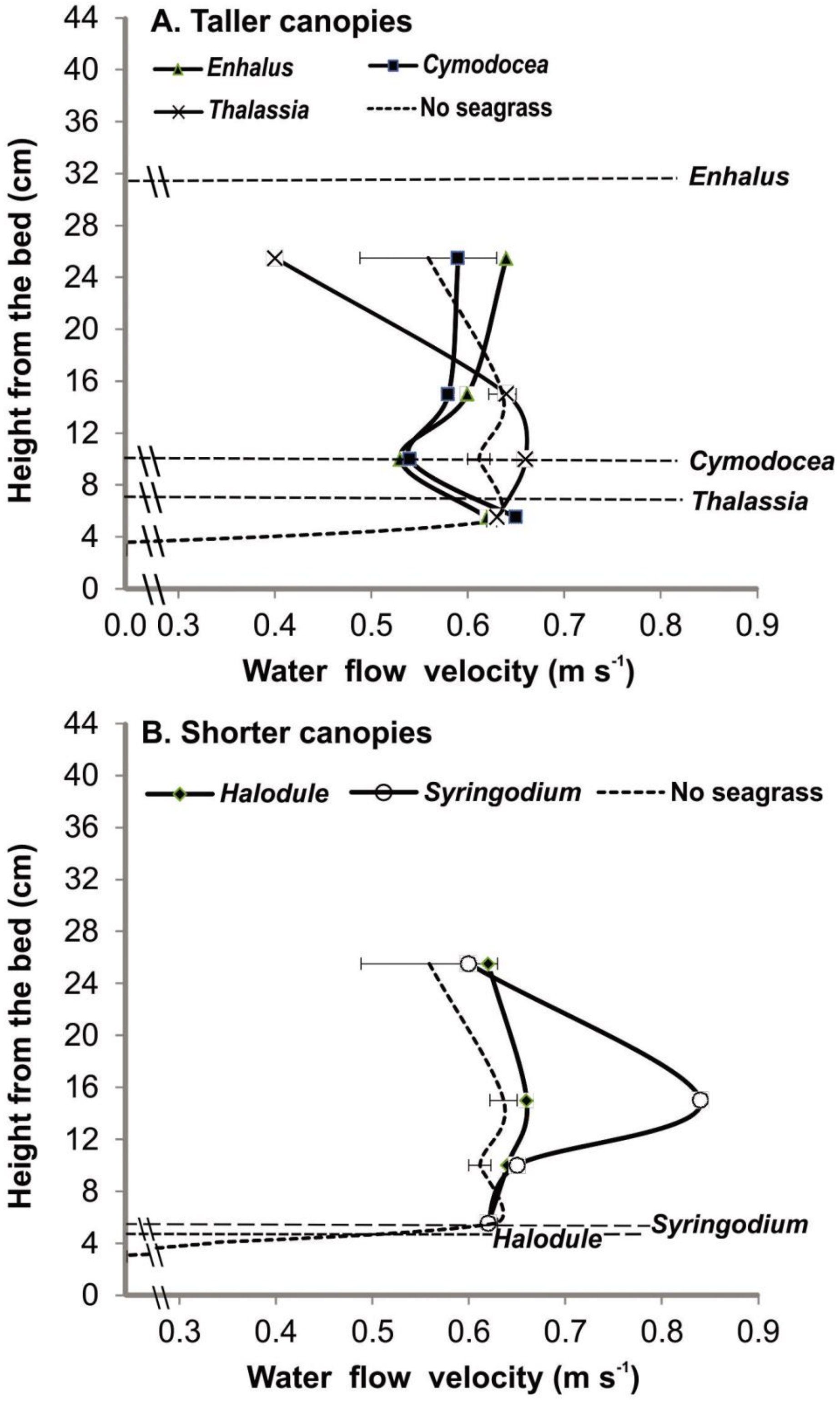
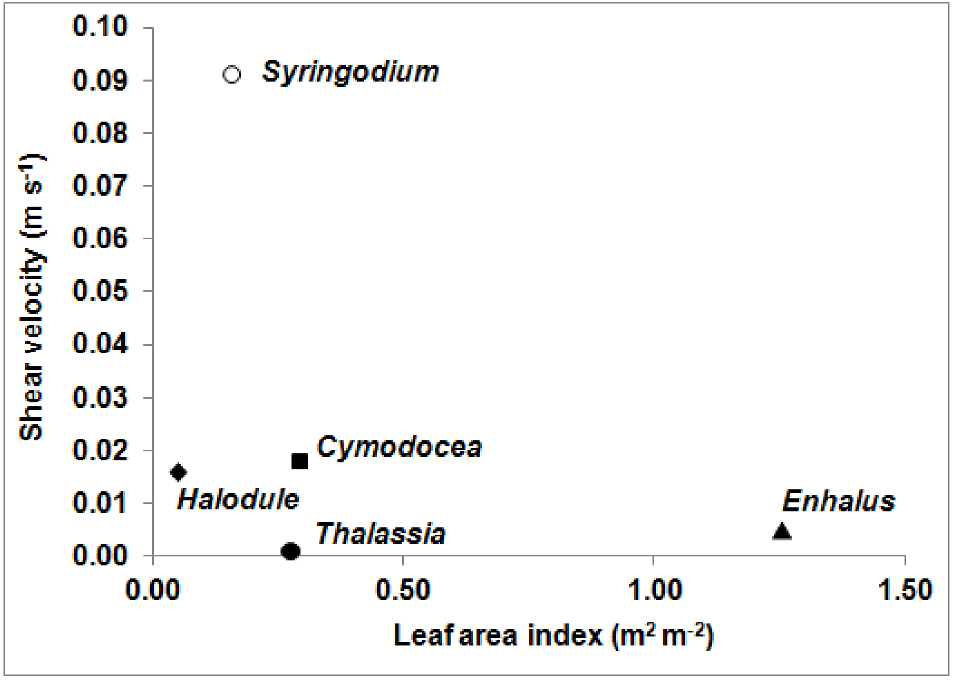

A. Taller canopies
Enhalus
Cymodocea
Thalassia
No seagrass
Enhalus
Cymodocea
Thalassia
Height from the bed (cm)
44
40
36
32
28
24
20
16
12
8
4
0
0.0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Water flow velocity (m s-1)
B. Shorter canopies
Halodule
Syringodium
No seagrass
Syringodium
Halodule
Height from the bed (cm)
44
40
36
32
28
24
20
16
12
8
4
0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Water flow velocity (m s-1)

Figure 3



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Graphic abstract

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

Botanica Marina

Decision Letter (BOTMAR.2017.0037.R2)

From: bot.mar.editorial@degruyter.com

To: mahat70@gmail.com

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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

File 1: Lanuru-al2017BotMar0037.R2-FinalText.docx

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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.

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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^2 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^{-1}. 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 Vectrino serial #VNO0224, Nortek AS, Rud, Norway) with Vectrino 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 m s^{-1} at ≥5.5 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 (m^2) per m^2 of mesh. *Syringodium's* cylindrical leaf area was calculated as the lateral area (leaf area multiplied by π). Leaves were oven-dried at 60°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 m s^{-1}, ranging from 0.002 to 0.430 m s^{-1} (Figure 1). The seagrass densities in the field were higher than in the flume for all species except *Enhalus*, for which

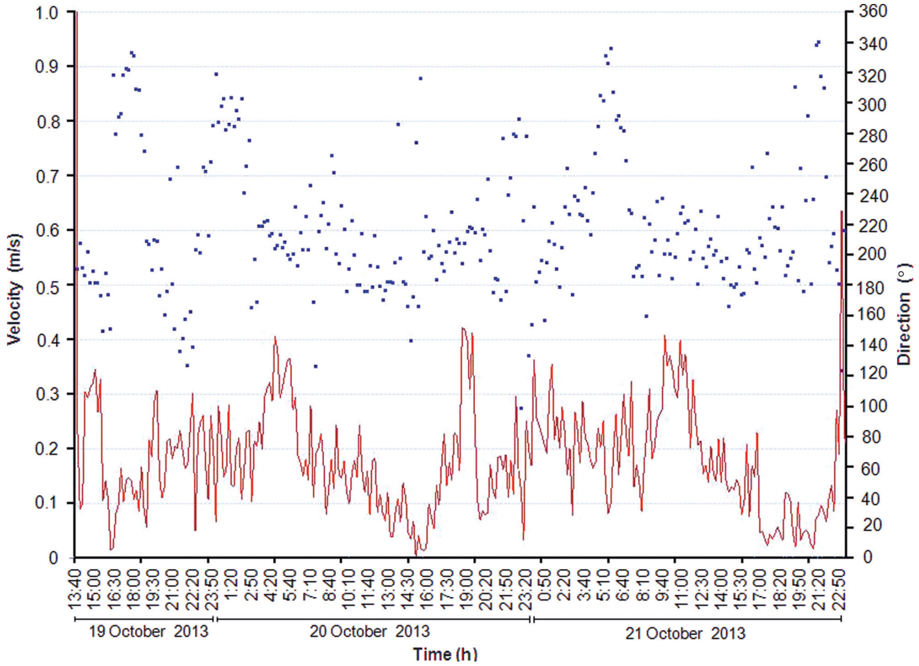

Figure 1: Current speed and direction over 48 h (19–21 October 2013) at the seagrass collection site, Barranglompo, Spermonde Islands, south Sulawesi, Indonesia.

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^{-1} 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^{-1}) compared to the no-seagrass value (0.104 m s^{-1}; 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 $p = 0.210$, $r^2 = 0.357$; df = 1, 4; LAI $p = 0.318$, $r^2 = 0.245$). 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 ($m\ s^{-1}$)	Turbulence intensity (%)	Shear velocity U* ($m\ s^{-1}$)	LAI ($m^2\ m^{-2}$)	Leaf biomass (g dry)	Leaf shoots m^{-2}	Natural bed leaf shoots m^{-2}
Enhalus acoroides	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
Cymodocea rotundata	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
Thalassia hemprichii	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
Syringodium isoetifolium	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
Halodule uninervis	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^{-2} in flume. Leaf shoots m^{-2} of mesh in flume. Natural bed leaf shoot density from 1 m × 1 m quadrats (n = 4).

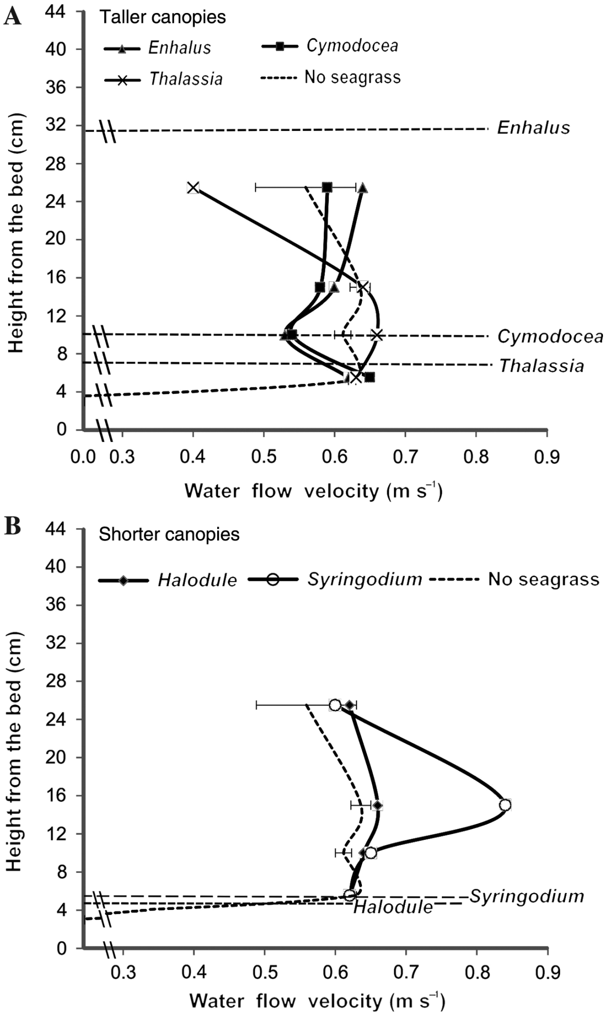

Figure 2: Water flow velocity profiles for a 1-m long seagrass bed of each of five seagrass species measured in a flume (44 cm water depth) at 0.60–0.65 m s^{-1} freestream flow speeds.
Dashed line indicates the mean height of the leaf canopy by species. Two velocity profiles were averaged for the flume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

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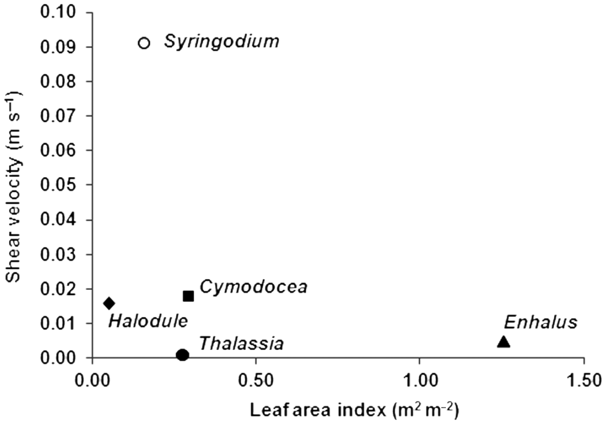

Figure 3: Shear velocity U* (m s^{-1}) versus leaf area index (m^2 m^{-2}). U* scales with shear stress, the force resulting from the vertical velocity gradient. The leaf area index, a common predictor of U*, is the one-sided area of leaves per m^2 of substratum.

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 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 ≥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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Bionotes

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Q4:
In the sentences “He has recently conducted research on ……”should this rather read “on a small island”. Please check and amend

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Graphical abstract

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

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

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

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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^2 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^{-1}. 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 Vectrino serial #VNO0224, Nortek AS, Rud, Norway) with Vectrino 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 m s^{-1} at ≥5.5 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 (m^2) per m^2 of mesh. *Syringodium's* cylindrical leaf area was calculated as the lateral area (leaf area multiplied by π). Leaves were oven-dried at 60°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 m s^{-1}, ranging from 0.002 to 0.430 m s^{-1} (Figure 1). The seagrass densities in the field were higher than in the flume for all species except *Enhalus*, for which

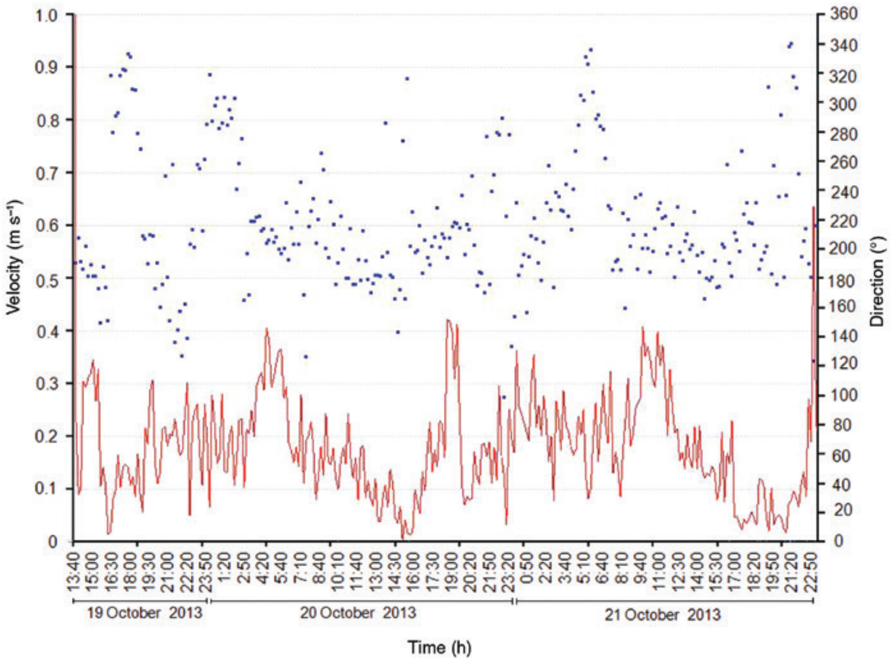

Figure 1: Current speed and direction over 48 h (19–21 October 2013) at the seagrass collection site, Barranglompo, Spermonde Islands, south Sulawesi, Indonesia.

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^{-1} 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^{-1}) compared to the no-seagrass value (0.104 m s^{-1}; 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, $r^2 = 0.357$; df = 1, 4; LAI p = 0.318, $r^2 = 0.245$). 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^{-1})	Turbulence intensity (%)	Shear velocity U* (m s^{-1})	LAI (m^2 m^{-2})	Leaf biomass (g dry)	Leaf shoots m^{-2}	Natural bed leaf shoots m^{-2}
Enhalus aceroides	32 (1.2)	1.4	0.393 (0.010)	66 (3)	0.005	1.256	36.2	82	123 (38)
Cymodocea rotundata	10 (0.4)	4.4	0.390 (0.014)	66 (3)	0.018	0.293	5.1	253	603 (190)
Thalassia hemprichii	7.4 (0.4)	5.9	0.378 (0.952)	67 (6)	0.001	0.275	4.1	229	701 (268)
Syringodium isoetifolium	4.8 (0.2)	9.2	0.383 (0.036)	58 (13)	0.091	0.157	2.9	651	1693 (658)
Halodule uninervis	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^{-2} in flume. Leaf shoots m^{-2} of mesh in flume. Natural bed leaf shoot density from 1 m × 1 m quadrats (n = 4).

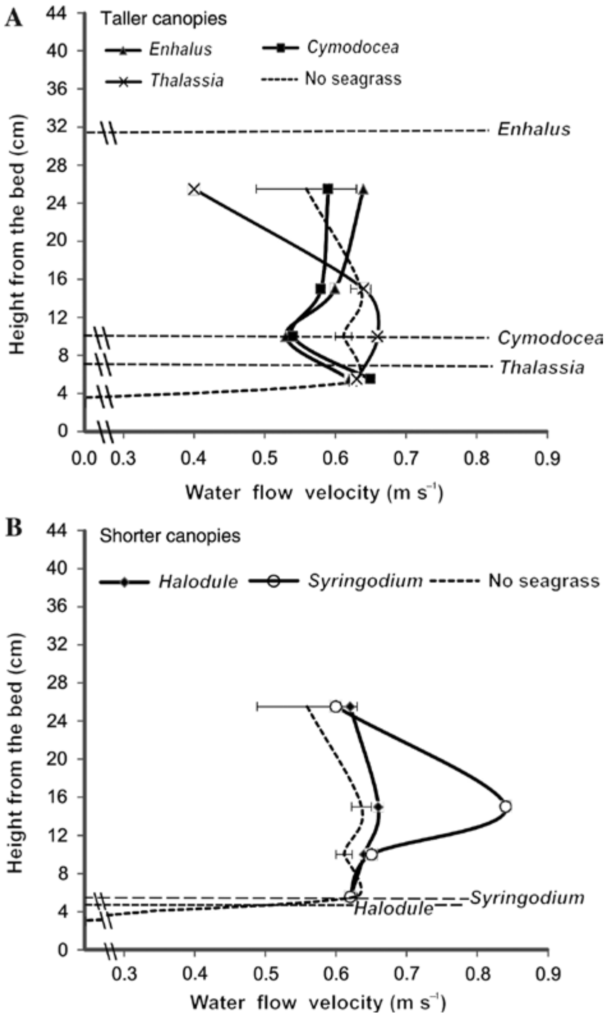

Figure 2: Water flow velocity profiles for a 1-m long seagrass bed of each of five seagrass species measured in a flume (44 cm water depth) at 0.60–0.65 m s^{-1} freestream flow speeds.
"A" is water flow velocity profiles for taller canopies, while "B" is water flow velocity profiles for shorter canopies 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.

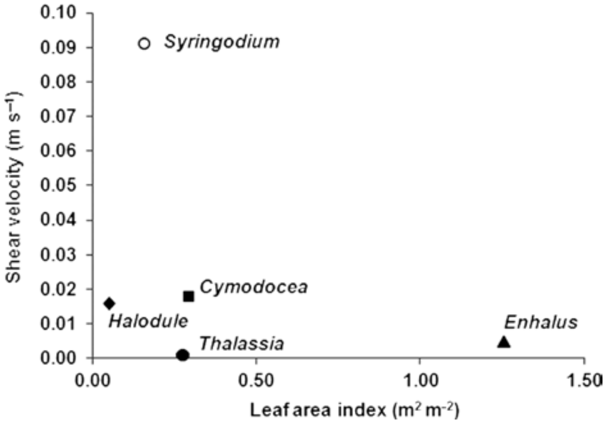

Figure 3: Shear velocity U* (m s^{-1}) versus leaf area index (m^2 m^{-2}). U* scales with shear stress, the force resulting from the vertical velocity gradient. The leaf area index, a common predictor of U*, is the one-sided area of leaves per m^2 of substratum.

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 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 ≥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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