

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

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

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

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

Introduction

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

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

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

*Corresponding author: Mahatma Lanuru, Department of Marine Science, Faculty of Marine Science and Fisheries, Hasanuddin University, Tamalanrea Km. 10, Makassar 90245, Indonesia, e-mail: mahat70@gmail.com

Rohani Ambo-Rappe and Khairul Amri: Department of Marine Science, Faculty of Marine Science and Fisheries, Hasanuddin University, Tamalanrea Km. 10, Makassar 90245, Indonesia

Susan L. Williams: Department of Evolution and Ecology, Bodega Marine Laboratory, University of California at Davis, PO Box 247, Bodega Bay, CA 94923-0247, USA

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-m² 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 Vetrino serial #VNO0224, Nortek AS, Rud, Norway) with Vetrino Plus software, a baud of 57600, and sampling rate of 200 Hz. The ADV was centered in the width of the working section for all measurements. The flume was calibrated by averaging velocity measurements without seagrass at 3, 5.5, 10, 15 and 25.5 cm above the bottom at 38 and 116 cm from the beginning of the working section. Seagrass measurements were made at midway along the length of the mesh (50 cm downstream from the edge of the seagrass bed) at 5.5, 10, 15 and 25.5 cm heights and in the middle of the seagrass bed. Due to the mesh, the closest the ADV could be positioned above the flume bottom was 5.5 cm.

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

To compare the experimental seagrass bed to the field and other studies, we counted the leaf shoots in the mesh and measured the leaf canopy height as the distance between the mesh surface and the longest leaf of 55 shoots of each species. We then clipped the leaves flush with the mesh and measured leaf area (Li-Cor meter, Model Li-3100, Lincoln, NE, USA) to calculate the leaf area index (LAI) as the one-sided leaf area (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

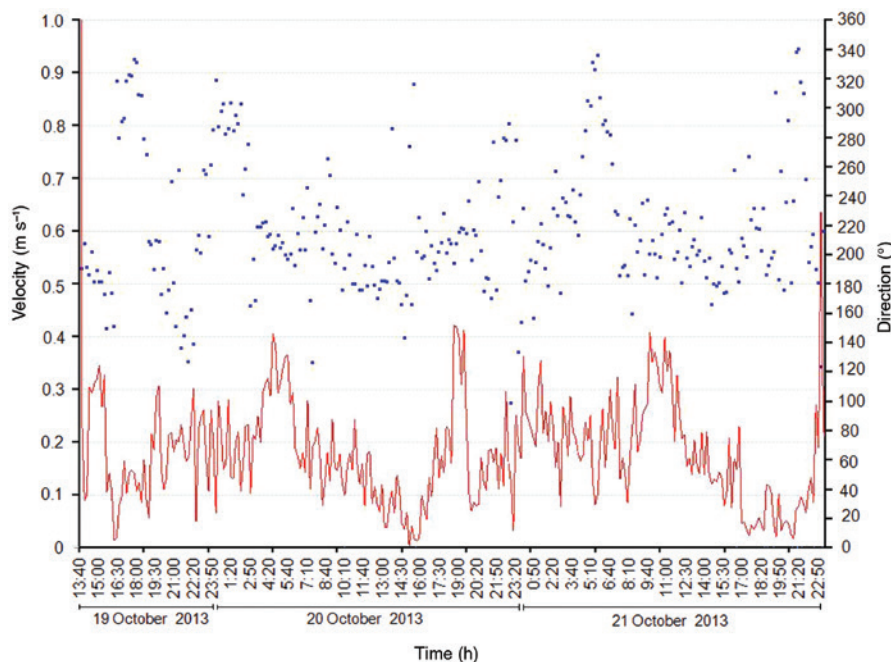


Figure 1: Current speed and direction over 48 h (19–21 October 2013) at the seagrass collection site, Barranglompo, Spermonde Islands, south Sulawesi, Indonesia.

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, r²=0.357; df=1, 4; LAI p=0.318, r²=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 |
|---------------------------------|--------------------|-------------|---------------------------------|--------------------------|--|---------------------------------------|----------------------|-----------------------------|---|
| <i>Enhalus aceroides</i> | 32 (1.2) | 1.4 | 0.393 (0.010) | 66 (3) | 0.005 | 1.256 | 36.2 | 82 | 123 (38) |
| <i>Cymodocea rotundata</i> | 10 (0.4) | 4.4 | 0.390 (0.014) | 66 (3) | 0.018 | 0.293 | 5.1 | 253 | 603 (190) |
| <i>Thalassia hemprichii</i> | 7.4 (0.4) | 5.9 | 0.378 (0.952) | 67 (6) | 0.001 | 0.275 | 4.1 | 229 | 701 (268) |
| <i>Syringodium isoetifolium</i> | 4.8 (0.2) | 9.2 | 0.383 (0.036) | 58 (13) | 0.091 | 0.157 | 2.9 | 651 | 1693 (658) |
| <i>Halodule uninervis</i> | 4.3 (0.2) | 10.3 | 0.400 (0.014) | 63 (1) | 0.016 | 0.050 | 0.8 | 522 | 1583 (540) |
| No seagrass | N/A | N/A | 0.398 (0.011) | 65 (1) | 0.104 (0.018) | N/A | N/A | N/A | N/A |

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

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

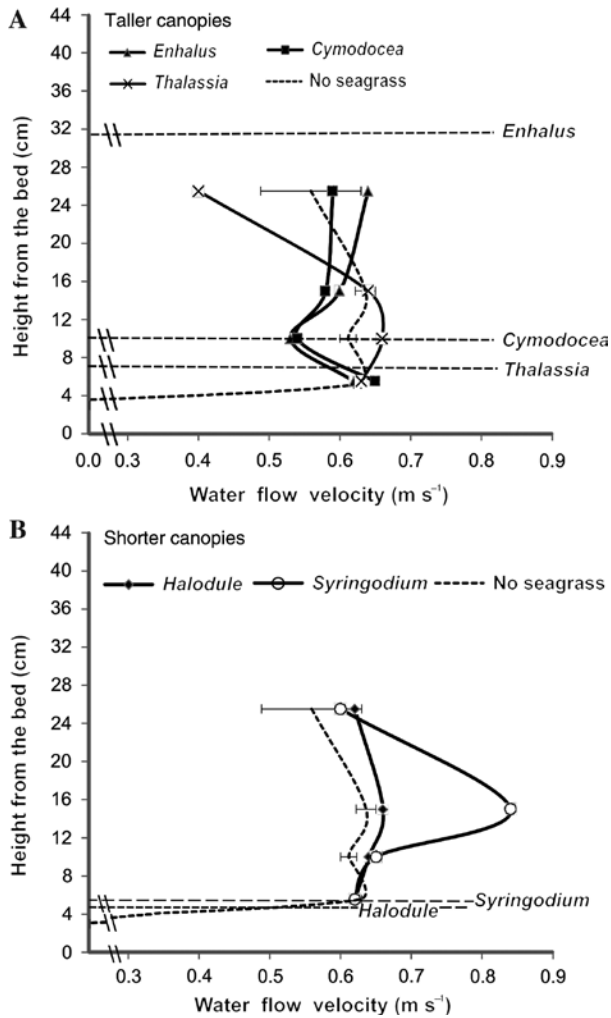


Figure 2: Water flow velocity profiles for a 1-m long seagrass bed of each of five seagrass species measured in a flume (44 cm water depth) at 0.60–0.65 m s⁻¹ freestream flow speeds. “A” is water flow velocity profiles for taller canopies, while “B” is water flow velocity profiles for shorter canopies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

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

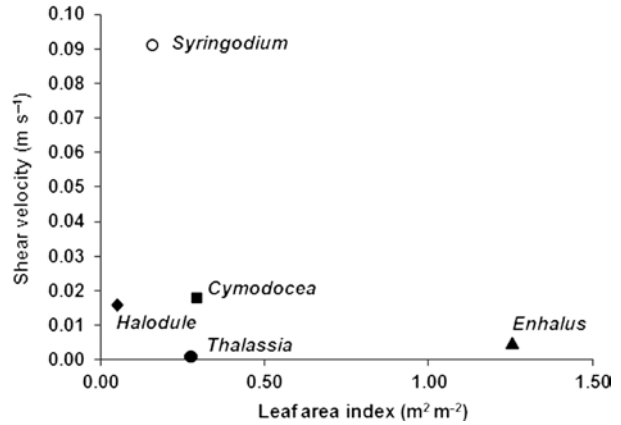


Figure 3: Shear velocity U* (m s⁻¹) versus leaf area index (m² m⁻²). U* scales with shear stress, the force resulting from the vertical velocity gradient. The leaf area index, a common predictor of U*, is the one-sided area of leaves per m² of substratum.

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

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

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

Submerged vegetation canopies are understood to strongly influence water flow, typically by slowing water flow and, under specific conditions including fast flow, creating skimming flow above the canopies and a vertical velocity maximum close to the substratum (Gambi et al. 1990, Nepf and Vivoni 2000, Madsen et al. 2001, Peterson et al. 2004, Hendriks et al. 2008). This understanding has been based on empirical and theoretical studies of seagrasses and mimics with generally much taller canopies than the seagrasses we studied. For example, studies of “short” species reported canopy heights ≥ 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



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 areas and habitat (seagrass) restoration. He has recently conducted research on a small island.



Rohani Ambo-Rappe

Department of Marine Science, Faculty of Marine Science and Fisheries, Hasanuddin University, Tamalanrea Km. 10, 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, Tamalanrea Km. 10, 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 bioindicators.

Susan L. Williams

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

Susan L. Williams is a Professor at the Bodega Marine Laboratory, which she directed from 2000 to 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.