

# Ecological connectivity with mangroves influences tropical seagrass population longevity and meadow traits within an island ecosystem

Amrit Kumar Mishra\*, Deepak Apte

Marine Conservation Department, Bombay Natural History Society, Hornbill House, Dr. Salim Ali Chowk, Shaheed Bhagat Singh Road, Opp. Lion Gate, Mumbai, 400001, India

**ABSTRACT:** Seagrass meadows around the Andaman Sea are globally significant, but declining rapidly. Assessment of the existing seagrass population dynamics is essential to facilitate effective conservation measures. We studied population dynamics of the seagrass *Thalassia hemprichii* at 3 locations in the Andaman and Nicobar Islands in the Andaman Sea. At each location, 2 sites were assessed, one with mangroves (MG) and another without mangroves (WMG). Quadrat and corer sampling techniques were used to collect seagrass and sediment samples. Reconstruction techniques were used to derive population dynamics of *T. hemprichii*. Sand fractions dominated (>90%) the *T. hemprichii* meadows, with silt comprising a higher percentage only at the MG sites. The density, biomass, productivity and horizontal meadow migration of *T. hemprichii* were higher at the MG sites. The number of leaves shoot<sup>-1</sup>, vertical rhizome (VR), VR internode length, number of VRs shoot<sup>-1</sup> and vertical growth were higher at the WMG sites. *T. hemprichii* required less time to produce a single leaf at the MG sites than at the WMG sites. Plants associated with mangroves had 4 to 5 yr of longevity, with higher numbers of younger plants. Population growth rates were positive at all sites except at the WMG site of Burmanallah. Our results provide evidence that mangrove ecosystems have a positive impact on seagrass meadow traits and population dynamics. Therefore, it is crucial to focus on the ecological connectivity between seagrasses and associated coastal ecosystems, as it is pivotal to increase our understanding of the important link between coastal ecosystems and ecosystem functioning.

**KEY WORDS:** Population dynamics · Ecological connectivity · Reconstruction techniques · *Thalassia hemprichii* · Coastal ecosystems · Tropical islands

Resale or republication not permitted without written consent of the publisher

## 1. INTRODUCTION

Seagrass meadows are among the most diverse and widely distributed submerged coastal ecosystems that inhabit the tropical and temperate bioregions of the world (Spalding et al. 2003, Short et al. 2007). These ecosystems provide 24 different types of services (Nordlund et al. 2016), including habitat and nurseries for commercially important fish populations and endangered sea cows (Unsworth et al. 2019), carbon sequestration and storage (Duarte et al. 2013), shoreline protection from storm surges and prevention

of coastal erosion (Ondiviela et al. 2014, Potouroglou et al. 2017) and regulation of nutrient cycles (Costanza et al. 2014). These ecosystem services are critical for the functioning of seagrass-dependent trophic levels and they also aid millions of coastal communities that depend on these ecosystems for their livelihoods and food security (Cullen-Unsworth et al. 2014, Nordlund et al. 2016, 2018). Although coastal communities across the world reap the benefits of these ecosystems, human activities including modification to and destruction of coastal habitats have led to a 30% decline in seagrass populations worldwide in the last

\*Corresponding author: a.mishra@bnhs.org

3 to 4 decades, with a decline of 7 % yr<sup>-1</sup> (Waycott et al. 2009, Pendleton et al. 2012, Howard et al. 2014). Much of this decline has occurred in the bioregion of Asia in the Andaman Sea, Java Sea, South China Sea and Gulf of Thailand (Short et al. 2011, Saenger et al. 2013), which could hold negative consequences for the native biodiversity.

Seagrasses are marine angiosperms that inhabit sheltered or shallow-water coastal ecoscapes (Hemminga & Duarte 2000). Seagrasses form mono-specific or mixed meadows and are found associated with mangroves, saltmarsh or coral reefs in certain bioregions. However, research on seagrass species, their associated ecosystems (such as mangroves or coral reefs) and the effects of these associations on seagrass population traits and ecosystem functioning has received less attention (Nagelkerken et al. 2008, Kathiresan & Alikunhi 2011). Both seagrass and mangrove ecosystems are physico-chemically linked at the macro-level of connectivity, and evidence indicates that organic matter, nutrients and trace metals from these ecosystems are exported into the surrounding coastal environment (Holmer & Olsen 2002, Kristensen et al. 2008, Kathiresan & Alikunhi 2011, Huxham et al. 2018, Mishra & Kumar 2020). Mangrove ecosystems play an important role in nutrient and sediment retention, thereby influencing adjacent seagrass meadows (Holmer & Olsen 2002, Gillis et al. 2017). Previous studies of 10 seagrass species (including *Thalassia hemprichii*) have indicated an increase in seagrass percentage cover and biomass when associated with mangrove ecosystems off the coast of Thailand in the Andaman Sea (Poovachiranon & Chansang 1994). Seasonality influences the mangrove run-off, which in turn affects seagrass growth, survivorship and distribution (Lirman & Cropper 2003). Interconnectivity between seagrass and mangrove ecosystems, resulting in significantly higher species richness, fish assemblages, density, diversity and population structure, has been reported from the Indo-Pacific region (Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2002, Dorenbosch et al. 2007, Berkström et al. 2013, Saenger et al. 2013). Such interlinkage or habitat connectivity enables seagrasses and mangroves to complement each other in increasing one another's productivity, thus facilitating an increase in the associated biodiversity, plant fitness and overall ecosystem functioning (Dorenbosch et al. 2007, Medina-Gómez et al. 2016).

In India, 13 out of the total 16 seagrass species are reported from the Andaman and Nicobar Islands (ANI) in the Andaman Sea, covering an area of 29.3 km<sup>2</sup> (Jagtap et al. 2003, Ragavan et al. 2016,

Thangaradjou & Bhatt 2018). One of the keystone seagrass species of ANI is *T. hemprichii*, which is found in intertidal sandy regions and coral rubble up to a depth of 15 m (Jagtap et al. 2003, Thangaradjou & Bhatt 2018). *T. hemprichii* is closely associated with mangrove ecosystems or with other seagrass species such as *Halophila ovalis* or *Halodule pinifolia* (Ragavan et al. 2016) or *Cymodocea rotundata* (authors' unpubl.). In terms of ecological connectivity, the movements of animals (like fish) between mangroves and surrounding coral reef ecosystems have been explored in these islands (Swapna et al. 2016), whereas there have been no such reports on the ecological connectivity involving seagrasses. Although *T. hemprichii* is found in association with mangroves, the ecological connectivity between these ecosystems and its impact on seagrass population dynamics and ecosystem functioning have seldom been explored (Kathiresan & Alikunhi 2011). Earlier studies on *T. hemprichii* in ANI investigated its occurrence (Jagtap 1991, Das 1996), composition, distribution and diversity (Saxena et al. 2010, Ragavan et al. 2016), density, biomass and morphometrics (Savurirajan et al. 2018), heavy metal contents (Nobi et al. 2010) and leaf reddening (Ragavan et al. 2014). However, these studies did not provide evidence of the population structure and growth dynamics of *T. hemprichii*.

In the wake of a severe decline of seagrasses globally, leading to the extinction risk of 11 seagrass species (Short et al. 2011, Saenger et al. 2013), understanding the population trends (i.e. stable or declining) of seagrasses is of utmost importance if their ecosystem services are to be maintained. In India, seagrass beds are declining due to various anthropogenic disturbances (Thangaradjou et al. 2009, Nobi et al. 2010). In this scenario, a unidirectional approach (without considering the inter-connectedness of ecosystems) for restoration/management and conservation efforts can lead to a failure in managing these important seagrass bioregions (Crook et al. 2015, Bayraktarov et al. 2016, Gillis et al. 2017, Valdez et al. 2020). It is well established that individual coastal ecosystems (such as seagrasses, mangroves and coral reef ecosystems) act as ecosystem engineers and can modify their individual traits to control the important coastal fluxes, like waves, sediment inflow and nutrient levels that influence the associated coastal seascapes (Sheaves 2009, Guannel et al. 2016, Gillis et al. 2017). Among these ecosystem engineers, both mangroves and seagrasses can act as either donors or recipients of the coastal fluxes (Saenger et al. 2013, Gillis et al. 2014, 2017) and can influence each other's population dynamics (Hanski

1998). However, the influence of mangroves (as donor ecosystem engineers) on the population traits of the adjacent seagrass ecosystem (as recipient ecosystem) is less understood, because most studies involving seagrasses along with mangroves or coral reefs have focussed on the movement of only animals (mostly fish or invertebrates) between these ecosystems (Nagelkerken et al. 2008, Campbell et al. 2011, Berkström et al. 2013, Saenger et al. 2013, Guannel et al. 2016).

Here we assessed the ecological association of seagrass ecosystems with mangroves, and quantified the influence of this association on seagrass population and meadow traits within an island ecosystem. We surveyed *T. hemprichii* meadows of Shahid Dweep (formerly Neil) and Swaraj Dweep (formerly Havelock) Islands and at Burmanallah in the ANI associated with mangrove ecosystems and contrasted them with areas without mangroves to assess the positive/negative effects of mangrove association. Hereafter we will use the names Neil, Havelock and Burmanallah for convenience. We tested the hypothesis that ecosystem connectivity between seagrass and mangroves can influence seagrass meadows and their population traits positively in an island ecosystem.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

We surveyed and sampled the coastal regions of Neil and Havelock Islands and Burmanallah in the ANI, India (Fig. 1), where seagrass and mangroves (*Rhizophora apiculata*) co-existed, during the period of February to March 2019 (summer/dry season). At each location, 2 sites, one associated with mangroves (MG) and another without being associated with mangroves (WMG) were selected (Fig. 2). The seagrass meadow edges were close (0.2–0.5 m) to the wave-breaking zone at the WMG sites, whereas at the MG sites, they were farther away from the wave-breaking zone, which was located coastward of the mangroves (Fig. 2). The ecosystem matrix of these sites consisted of coral reefs towards the open sea, seagrasses in the middle and mangroves towards the landward zone (Fig. 2), all within a close range. These study locations exhibited a semi-diurnal tidal amplitude of 2.45 m, with temperatures ranging from 26.28–35.67°C and salinity from 32–35.

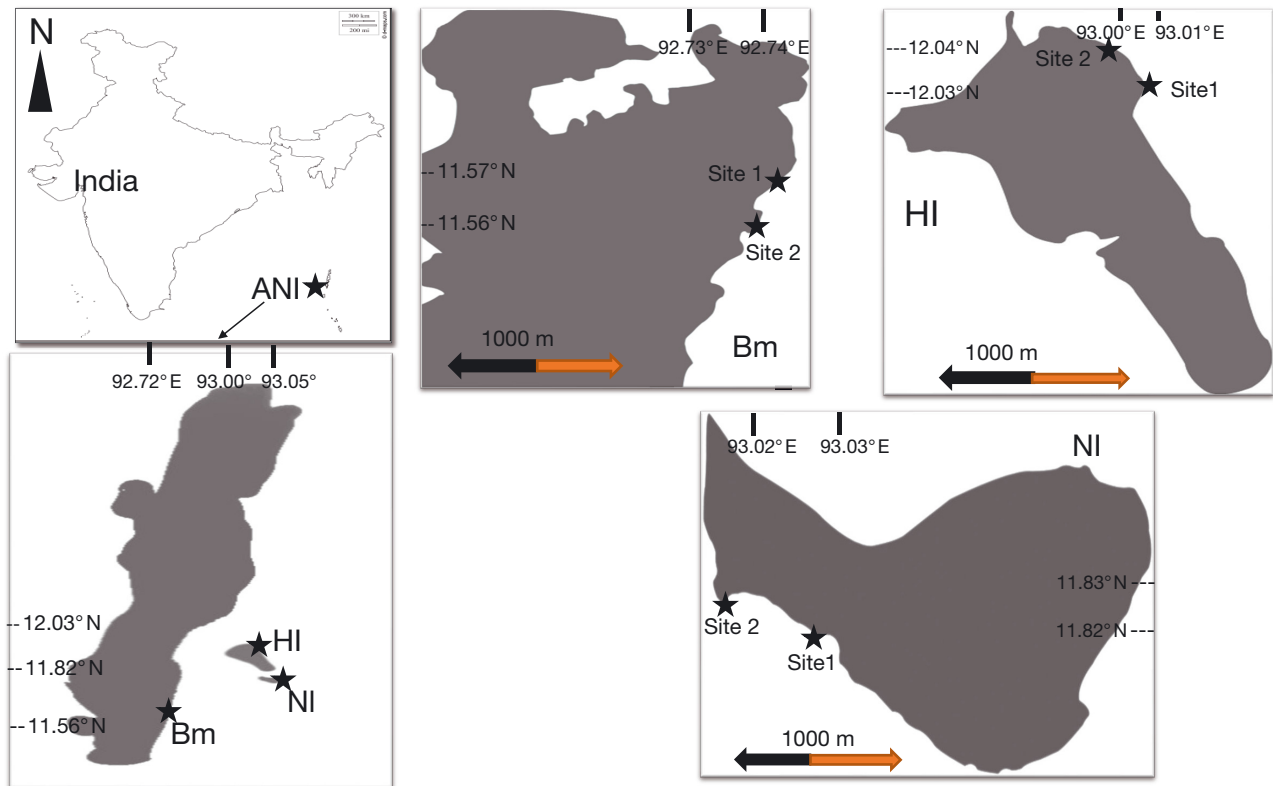


Fig. 1. Study area in the Andaman and Nicobar Islands (ANI), India: Neil Island, NI (Shahid Dweep), Havelock Island, HI (Swaraj Dweep) and Burmanallah, Bm. At all 3 locations, site 1 represents an area with mangroves and site 2 represents an area without mangroves



Fig. 2. Representative matrices of the island ecosystems (a) in association with and (b) without mangroves at Neil Island, showing the wave-breaking zones, mangroves, seagrasses, dead coral reefs and open sea

#### 2.1.1. Neil Island

Neil Island is situated in the south-east region of ANI (Fig. 1). The 2 sites selected here were 1000 m apart and were separated by dead coral patches. The *Thalassia hemprichii* population was sampled at both MG and WMG sites within a depth of 0.5 m during low tide. The *T. hemprichii* meadows in this area were 1.5 m apart from the mangrove root areas.

#### 2.1.2. Havelock Island

Havelock Island is also situated in the south-east of ANI, north of Neil Island (Fig. 1). The 2 sites (MG and WMG) here were 900–1000 m apart, and each site was surrounded by dead coral patches. At both sites, the *T. hemprichii* population was found in monospecific patches or in mixed patches along with *Halophila ovalis* or *Halodule uninervis* when sheltered by dead corals. The mono-specific *T. hemprichii* population was sampled here at a depth of 0.5 m during low tide, and 2–3 m apart from the mangrove root areas.

#### 2.1.3. Burmanallah

Burmanallah is also situated in the south-east region of ANI (Fig. 1). This location, lined with rocky intertidal beaches, is influenced by anthropogenic pollution from human-made coastal concrete walls, boat anchorages and an outlet which discharges land run-off into this area. The *T. hemprichii* meadows within the mangrove area were monospecific and were 3–4 m apart from the mangrove root areas. Mixed meadows of *Cymodocea rotundata* and *T. hemprichii* were found near the WMG site. The sites here were 1000 m apart from each other. *T. hemprichii* was sampled at a depth of 0.3 m during low tide.

### 2.2. Sediment sampling

Sediment cores ( $n = 10$ ) were collected from each quadrat at all sites where seagrass was sampled (see Section 2.3), using a 5 cm wide and 10 cm long plastic core. The corer was pushed at least 5 cm into the sediment while sampling. As many of the WMG sampling sites were full of coral rubble, it was difficult to dig deeper. Sediments were collected in plastic bags and transferred to the laboratory. In the laboratory, the sediment samples were oven dried at 60°C for 72 h before sieving to collect various grain size fractions (500, 150, 75, 63  $\mu\text{m}$ ).

### 2.3. Seagrass sampling

Ten quadrats (40 × 40 cm) were collected randomly from a transect of 20 × 30 m perpendicular to the beach at both sites (at all 3 locations), within a depth of 0.3–0.5 m during low tide. We used a quadrat and a hand shovel to dig out seagrass samples up to 10 cm depth. From each quadrat, seagrass leaves, rhizomes and roots were collected, rinsed off carefully in the field with seawater and brought to the lab for further analysis. In the laboratory, the seagrass tissues were rinsed carefully again with fresh water, keeping the plant rhizome mat intact, as required for reconstruction techniques (Duarte et al. 1994, Fourqurean et al. 2003). Epiphytes were scraped from leaf surfaces with a plastic razor.

### 2.4. Seagrass traits

At each site in the 3 locations, we measured and analysed a variety of *T. hemprichii* traits, such as



(1) meadow abundance (total shoot density, total apical density, reproductive density and effort, total biomass, above ground [AG] biomass, below ground [BG] biomass and the ratios of AG:BG biomass), (2) rhizome growth and production (vertical and horizontal), (3) population traits (age frequency distribution) and (4) population dynamics (long-term shoot recruitment, present shoot recruitment rate and net population growth rate).

Total shoot and apical densities (shoots  $\text{m}^{-2}$ ) were estimated by counting the number of shoots and apicals of physically independent individuals per sample. The presence of male or female reproductive structures in each shoot was recorded to estimate the reproductive shoot density (fruits or flowers  $\text{m}^{-2}$ ). The reproductive effort (%) was calculated by dividing the reproductive density by the total number of shoots multiplied by 100. The biomasses of leaves, rhizomes (vertical and horizontal) and roots were obtained by weighing the samples after separation, and oven drying the separated plant tissues for 48 h at  $60^{\circ}\text{C}$ . These weight values were then used for production estimations and biomass (g dry weight [DW]  $\text{m}^{-2}$ ) calculations. The AG (leaves) and BG (rhizomes+ roots) biomass values were used to estimate the AB:BG biomass ratios. *T. hemprichii* morphometric traits such as horizontal rhizome length, leaf length, leaf width and internode lengths were measured using a Vernier calliper (accuracy: 0.02 mm). The canopy height of *T. hemprichii*, i.e. the leaf length of the longest leaf from the sediment to the leaf tip, was measured using a ruler, and the longest 20% of the length values were excluded from the calculations (McKenzie & Campbell 2002).

Plant rhizome growth and production, population age structure and associated population dynamics were estimated using reconstruction techniques (Duarte et al. 1994, Fourqurean et al. 2003). The age of *T. hemprichii* shoots was estimated by counting the number of leaf scars on the vertical rhizomes plus the number of standing leaves in each shoot multiplied by the leaf plastochrome interval (PI). To estimate the PI of each study site, i.e. the time needed to produce a new leaf, the sequence of average internodal length of *T. hemprichii* shoots collected with the quadrats plus additional plants collected by hand was plotted. A running average was applied to filter short-term seasonal variability, and the difference in the number of vertical leaf scars between 2 consecutive length modes was counted. The modes represent annual growth periods, and thus the average number of leaf scars produced between modes was averaged to estimate the leaf PI of the population (Duarte et

al. 1994, Short & Duarte 2001). Shoot age frequency distribution was constructed to reveal the plant age structure and maximum longevity and to calculate the population dynamics parameters.

Vertical rhizome elongation rates ( $\text{cm yr}^{-1}$ ) for each site were derived as the slope of a linear regression between the lengths of vertical rhizomes and their age (Duarte et al. 1994). Horizontal rhizome elongation rate was estimated based on the linear regression of the number of horizontal internodes between 2 consecutive shoots against the age difference of these shoots. The slope (internodes  $\text{yr}^{-1}$ ) was then multiplied by the mean internodal length ( $\text{cm internode}^{-1}$ ) to obtain the horizontal elongation ( $\text{cm yr}^{-1}$ ). The horizontal and vertical rhizome production rates ( $\text{g DW m}^{-2} \text{yr}^{-1}$ ) were estimated by multiplying the elongation rates ( $\text{cm yr}^{-1}$ ) by density (shoots  $\text{m}^{-2}$ ) and by the specific dry weight of rhizomes ( $\text{g DW cm}^{-1}$ ). The number of leaves per shoot was counted from intact shoots with leaves in each sample ( $n > 150$ ).

The long-term average recruitment ( $R$ ) was estimated from the shoot age structure using the general model:  $N_x = N_0 e^{-Rx}$ , where  $N_x$  is the number of shoots in age class  $x$  and  $N_0$  is the number of shoots recruited into the population. This model assumes that mortality and recruitment have remained constant over the lifespan of the oldest shoots, with year to year random variation around some mean value of mortality and recruitment (Fourqurean et al. 2003, Cunha & Duarte 2005). The recruitment for the current year (2019) of sampling ( $R_0 \text{ yr}^{-1}$ ) was estimated as the difference of total number of shoots and the number of shoots older than a year in the shoot population (Duarte et al. 1994). The population growth rate ( $r$ ) was estimated as:  $r = R_0 - M$ , where  $M$  is the long-term mortality rate, which equals the long-term recruitment rate ( $R$ ) under the assumptions of near steady state (Fourqurean et al. 2003). A population was considered growing if  $r$  was positive ( $R_0 > R$ ), shrinking if  $r$  was negative ( $R_0 < R$ ), or on the same trajectory pattern if  $R_0$  was not significantly different from  $R$  (Fourqurean et al. 2003).

## 2.5. Statistical analysis

Significant differences between *T. hemprichii* traits such as density, biomass, morphometric features, growth and production estimates between the 2 sites (MG and WMG) and the 3 locations (Neil, Havelock and Burmanallah) were investigated using 2-way ANOVA. All data was pre-checked for normality (Shapiro-Wilks test) and homogeneity of variance

(*F*-test). When variances were not homogeneous, the corresponding data were  $\ln(x + 1)$  transformed. When there were significant interaction effects, the Holm-Sidak test was performed for *a posteriori* comparisons among factor levels (sites and locations).

A *t*-test for the difference between 2 regression lines was used to compare the vertical rhizome elongation rates, as these are equal to the slopes of the linear regression between the age and size of the rhizomes. Statistical analyses were not performed for the horizontal rhizome elongation rate, because just 1 value was obtained for each site. The confidence limits of the exponential decay regression model used to estimate the long-term average recruitment rate (*R*) allowed its statistical comparison to the present recruitment rate (*R*<sub>0</sub>) as described by Fourqurean et al. (2003). Significant differences in the long-term recruitment rate among sites were tested using 1-way ANOVA. Results were considered significant at  $p < 0.05$  (Sokal & Rohlf 2012). Data are presented as mean and SE. All statistical analysis was carried out using SIGMAPLOT (Ver. 11.02) software.

### 3. RESULTS

#### 3.1. Sediment characteristics

The sediment sand fraction was higher than silt at both sites with and without mangroves at all 3 locations (Table 1). The sediment silt content was higher at the MG sites compared to the WMG sites. Among the MG sites, Neil Island ( $27.86 \pm 0.07\%$ ) recorded the highest silt content and Burmanallah ( $10.55 \pm 1.2\%$ ) the lowest. The silt content was significantly different between the sites and locations except between Neil and Havelock (Table 1).

#### 3.2. Meadow traits

Mangrove-associated *Thalassia hemprichii* meadows had higher shoot and apex densities, i.e. number of individual plants (Fig. 3). The MG site of Neil Island had the highest shoot ( $2741.3 \pm 97.3$  shoots  $m^{-2}$ ) and

Table 1. Results of grain size analysis of sediments and biomass and morphometrics of *Thalassia hemprichii* beds associated with mangroves (MG) and without mangroves (WMG) at the Neil Island, Havelock Island and Burmanallah locations. Values are mean  $\pm$  SE. Lowercase superscript letters: significant differences ( $p < 0.05$ ; ns: not significant) between sites (MG and WMG); uppercase superscript letters: significant differences between locations (A: Neil vs. Havelock; B: Neil vs. Burmanallah; C: Havelock vs. Burmanallah; X: no difference) derived from 2-way ANOVA. DW: dry weight; S: sand; Si: silt; AG: above ground; BG: below ground; VR: vertical rhizome; HR: horizontal rhizome. \*Significance,  $p < 0.05$ , derived from *t*-test. #. Not tested

Variables		Neil		Havelock		Burmanallah	
		MG	WMG	MG	WMG	MG	WMG
Sediment grain size (%)	S	$82.14 \pm 6.13^{ns}$	$99.98 \pm 6.81^{ns}$	$85.23 \pm 5.28^{ns}$	$95.69 \pm 8.33^{ns}$	$89.45 \pm 3.33^{ns}$	$99.69 \pm 3.33^{ns}$
	Si	$27.86 \pm 0.07^{BXa}$	$0.02 \pm 0.0^{BXb}$	$14.73 \pm 2.13^{XCc}$	$4.41 \pm 0.65^{XCd}$	$10.55 \pm 1.2^{BCe}$	$0.41 \pm 0.01^{BCf}$
Biomass (g DW $m^{-2}$ )	AG:BG	$0.57 \pm 0.08^{XXa}$	$0.27 \pm 0.02^{XXb}$	$0.33 \pm 0.02^{XCc}$	$0.36 \pm 0.04^{XCc}$	$0.57 \pm 0.01^{XCd}$	$0.42 \pm 0.01^{XCd}$
No. of leaves shoot <sup>-1</sup>		$3.98 \pm 0.01^{AXa}$	$3.80 \pm 0.03^{AXb}$	$3.25 \pm 0.07^{ACc}$	$3.14 \pm 0.07^{ACd}$	$3.91 \pm 0.03^{CXe}$	$3.75 \pm 0.06^{CXf}$
No. of leaves $yr^{-1}$		$14.31^{\#}$	$13.62^{\#}$	$15.65^{\#}$	$12.53^{\#}$	$14.02^{\#}$	$12.89^{\#}$
Leaf length (cm)		$10.57 \pm 0.21^{ABa}$	$12.28 \pm 0.18^{ABb}$	$9.41 \pm 0.28^{ACc}$	$10.48 \pm 0.20^{ACd}$	$9.82 \pm 0.25^{BCe}$	$9.15 \pm 0.23^{BCf}$
Leaf width (cm)		$0.76 \pm 0.23^{ABa}$	$0.57 \pm 0.01^{ABb}$	$0.61 \pm 0.01^{ACc}$	$0.56 \pm 0.01^{ACd}$	$0.55 \pm 0.01^{BCe}$	$0.49 \pm 0.01^{BCf}$
Canopy height (cm)		$19.15 \pm 0.23^{ABa}$	$17.47 \pm 0.21^{ABb}$	$15.06 \pm 0.33^{ACc}$	$14.06 \pm 0.20^{ACd}$	$14.88 \pm 0.24^{BXe}$	$13.10 \pm 0.16^{BXf}$
Leaf elongation (cm $yr^{-1}$ )		$0.41 \pm 0.01^{ABa}$	$0.45 \pm 0.01^{ABb}$	$0.40 \pm 0.01^{ACc}$	$0.36 \pm 0.07^{ACd}$	$0.38 \pm 0.01^{BCe}$	$0.28 \pm 0.01^{BCf}$
No. of VRs shoot <sup>-1</sup>		$1.24 \pm 0.03^{ABa}$	$1.3 \pm 0.04^{ABa}$	$1.45 \pm 0.08^{ABb}$	$1.43 \pm 0.08^{ABb}$	$1.48 \pm 0.06^{BXc}$	$1.42 \pm 0.07^{BXc}$
Rhizome length (cm)	VR	$1.58 \pm 0.1^{ABa}$	$1.77 \pm 0.11^{ABb}$	$1.22 \pm 0.07^{ACc}$	$0.97 \pm 0.44^{AXd}$	$1.59 \pm 0.11^{BXe}$	$1.63 \pm 0.11^{BXf}$
	HR	$8.3 \pm 0.40^{XXa}$	$8.65 \pm 0.44^{XXb}$	$7.8 \pm 0.30^{XXc}$	$6.67 \pm 0.43^{XXd}$	$10 \pm 0.98^{XXe}$	$9.41 \pm 0.53^{XXf}$
Internode length (cm)	VR	$0.50 \pm 0.01^{AXa}$	$0.52 \pm 0.01^{AXa}$	$0.36 \pm 0.01^{ACb}$	$0.37 \pm 0.01^{ACb}$	$0.48 \pm 0.02^{XCc}$	$0.51 \pm 0.01^{XCc}$
	HR	$0.34 \pm 0.06^{ABa}$	$0.34 \pm 0.06^{ABb}$	$0.42 \pm 0.01^{ACc}$	$0.41 \pm 0.01^{ACd}$	$0.29 \pm 0.08^{BCe}$	$0.28 \pm 0.07^{BCf}$
Elongation rate (cm $yr^{-1}$ )	VR	$1.33 \pm 0.58^{a*}$	$2.22 \pm 0.74^{a*}$	$0.85 \pm 0.29^{b*}$	$1.18 \pm 0.38^{b*}$	$1.65 \pm 0.35^{c*}$	$1.56 \pm 0.88^{c*}$
	HR	$10.1^{\#}$	$9.58^{\#}$	$2.86^{\#}$	$1.96^{\#}$	$4.68^{\#}$	$3.82^{\#}$

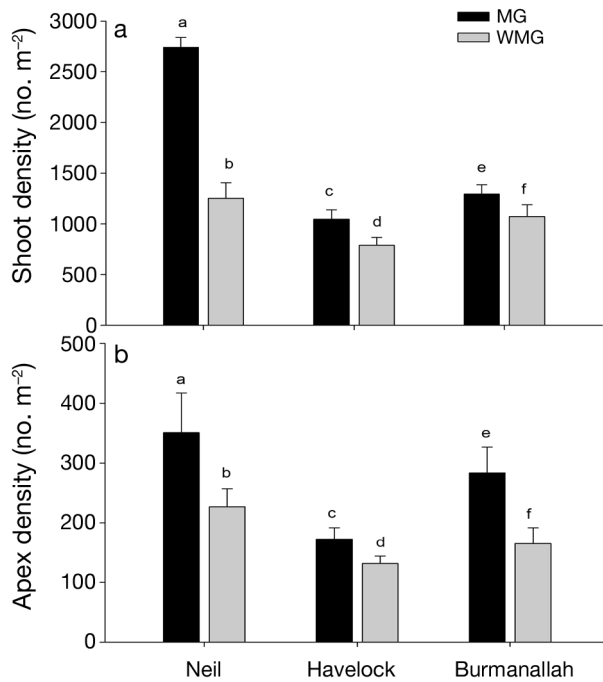


Fig. 3. Shoot and apex density of *Thalassia hemprichii* at the Neil Island, Havelock Island and Burmanallah locations associated with mangroves (MG) and without mangroves (WMG). Error bars: SE. Lowercase letters: significant differences ( $p < 0.001$ ) between the 2 sites (MG and WMG) derived from 2-way ANOVA results with sites as fixed factors

apex ( $350.43 \pm 66.5$  apex  $m^{-2}$ ) densities. The lowest shoot ( $1046.1 \pm 91.6$  shoot  $m^{-2}$ ) and apex ( $172.6 \pm 19.2$  apex  $m^{-2}$ ) densities were recorded at the MG site of Havelock Island. For Neil Island, the shoot density at the MG site was 2-fold higher than that of the WMG site (Fig. 3a), whereas at Burmanallah, the apex density of the MG site was 1.7-fold higher than that of the WMG site (Fig. 3b). The shoot and apex densities were significantly different between the sites (Fig. 3). The reproductive density and effort were not significantly different between sites but were different between locations.

A mixed response was observed for seagrass morphometric features between sites and locations (Tables 1 & 2). The number of leaves per shoot at the MG sites ( $3.25\text{--}3.98$  leaves shoot<sup>-1</sup>) was higher than at the WMG sites ( $3.14\text{--}3.80$  leaves shoot<sup>-1</sup>) (Table 1). The average leaf length of plants was lower at the MG sites than at the WMG sites. The leaf length was longer ( $12.28 \pm 0.18$  cm) at Neil and shorter ( $9.82 \pm 0.23$  cm) at Burmanallah WMG sites when compared to their respective MG sites. Contrastingly, the leaves of *T. hemprichii* were wider at the MG sites of Neil Island, and the leaf width at the MG site was 1.2-fold higher than that of the WMG site. Coinciding with

increased leaf lengths, the leaf elongation rates were also higher at the WMG sites than at the MG sites. In Burmanallah, the rate of leaf elongation at the WMG site was 1.3-fold higher than that of the MG site. At the WMG sites, longer leaf lengths did not result in increased canopy height. Contrastingly, in terms of canopy height at the MG sites, Neil ( $19.15 \pm 0.23$  cm) had the highest and Burmanallah ( $14.88 \pm 0.24$  cm) had the lowest (Table 1).

Although the number of vertical rhizomes per shoot was not significantly different, the vertical rhizome length did differ significantly between sites (Table 1). Following the similar pattern of leaf length, the vertical and horizontal rhizome lengths were higher at the WMG sites than at the MG sites. The plant vertical rhizome lengths were 1.1-fold (Neil), 1.2-fold (Havelock) and 1-fold (Burmanallah) higher at the WMG sites than at the MG sites, respectively (Table 1). The longest horizontal rhizome was recorded at the WMG site of Burmanallah ( $10 \pm 0.98$  cm) and the shortest ( $6.67 \pm 0.30$  cm) at the MG site of Havelock. Vertical internode lengths differed significantly between locations, and horizontal internode lengths were significantly different between both sites and locations (Table 1). The highest ( $10.1$  cm  $yr^{-1}$ ) and the lowest ( $2.86$  cm  $yr^{-1}$ ) horizontal elongation rates were recorded at Neil and Havelock Islands, respectively (Table 1).

The AG and BG biomasses of *T. hemprichii* were significantly different between sites (Fig. 4). The AG and BG biomass measures were higher at the MG sites than at the WMG sites at all 3 locations (Fig. 4). The highest AG ( $380.9 \pm 29.7$  g DW  $m^{-2}$   $yr^{-1}$ ) and BG ( $668.56 \pm 38.4$  g DW  $m^{-2}$   $yr^{-1}$ ) biomass was observed at the MG site of Neil Island. The AG biomass of the Neil Island MG site was 3.35-fold higher than that of its WMG site (Fig. 4a), whereas at Havelock, the BG biomass of the MG site was 1.6-fold higher than that of the WMG site (Fig. 4b). The AG:BG biomass ratio was 2-fold higher at the MG site than at the WMG site in Neil Island (Table 1).

Seagrass rhizome (vertical and horizontal) production rates were significantly different between sites, except for the vertical rhizome production at Burmanallah (Fig. 5). A clear pattern of higher vertical rhizome production at MG sites was observed for Neil and Havelock Islands, with similar rhizome production (between MG and WMG sites) at Burmanallah (Fig. 5a). The horizontal rhizome production was higher at the MG sites and lower at the WMG sites (Fig. 5b). The highest vertical ( $233.8 \pm 63.4$  g DW  $m^{-2}$   $yr^{-1}$ ) and horizontal production ( $206.3 \pm 39.5$  g DW  $m^{-2}$   $yr^{-1}$ ) was observed at the MG site of Neil Island. The highest

Table 2. Two-way ANOVA differences in sediment grain size fraction and *Thalassia hemprichii* biomass and morphometrics between locations (3 levels; N: Neil Island, H: Havelock Island, B: Burmanallah); and between sites (2 variables; MG: with mangroves, WMG: without mangroves). Two-way ANOVA degrees of freedom (df) between groups and within groups, mean squares (MS), *F*-statistic and p-values and Holm-Sidak post hoc significance test results ( $p < 0.05$ ) are presented for locations and sites. **Bold:** differences that were significant. S: sand; Si: silt; AG: above ground; BG: below ground; VR: vertical rhizome; HR: horizontal rhizome; nv: no value

Variables	Variation	Two-way ANOVA			Holm-Sidak p-values				Sites		
		df	MS	F	p	N vs H	Location N vs B	H vs B	Neil MG vs WMG	Havelock MG vs WMG	Burmanallah MG vs WMG
Sediment (S)	Location	2, 101	210.84	0.128	0.880	nv	nv	nv	nv	nv	nv
	Sites		791.22	0.480	0.620						
Sediment (Si)	Location	2, 101	167.79	10.867	<0.001	0.906	0.002	0.002	<0.001	0.001	0.012
	Sites		805.90	52.192	<0.001						
Biomass (AG:BG)	Location	2, 55	0.070	4.299	0.022	0.119	0.286	0.007	<0.001	0.649	0.104
	Sites		0.197	10.409	0.003						
No. of leaves shoot <sup>-1</sup>	Location	2, 301	6.529	16.830	<0.001	<0.001	0.341	<0.001	<0.001	<0.001	0.002
	Sites		3.601	9.282	<0.001						
Leaf length	Location	2, 301	175.118	62.640	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Sites		751.490	268.811	<0.001						
Leaf width	Location	2, 301	0.589	53.500	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	Sites		0.550	49.930	<0.001						
Canopy height	Location	2, 115	110.784	114.784	<0.001	<0.001	<0.001	0.575	<0.001	<0.001	<0.001
	Sites		19.730	20.520	<0.001						
Leaf elongation	Location	2, 301	0.370	78.607	<0.001	0.002	<0.001	<0.001	<0.001	<0.001	0.010
	Sites		0.862	182.953	<0.001						
No. of VRs shoot <sup>-1</sup>	Location	2, 301	0.247	3.595	0.029	0.008	0.017	1.00	<0.001	<0.001	<0.001
	Sites		0.169	2.454	0.063				0.524	0.523	1.00
Rhizome length (VR)	Location	2, 301	2.652	2.893	0.057	0.015	0.715	0.018	<0.001	<0.001	0.006
	Sites		9.159	9.992	<0.001						
Rhizome length (HR)	Location	2, 301	4.159	0.315	0.730	nv	nv	nv	<0.001	0.004	0.016
	Sites		88.549	6.715	<0.001				<0.001		
Internode length (VR)	Location	2, 301	0.242	25.607	<0.001	<0.001	0.573	<0.001	<0.001	<0.001	nv
	Sites		0.006	0.724	0.538				nv	nv	nv
Internode length (HR)	Location	2, 301	0.411	17.083	<0.001	<0.001	<0.001	0.006	0.005	0.008	0.021
	Sites		0.082	3.406	0.018						



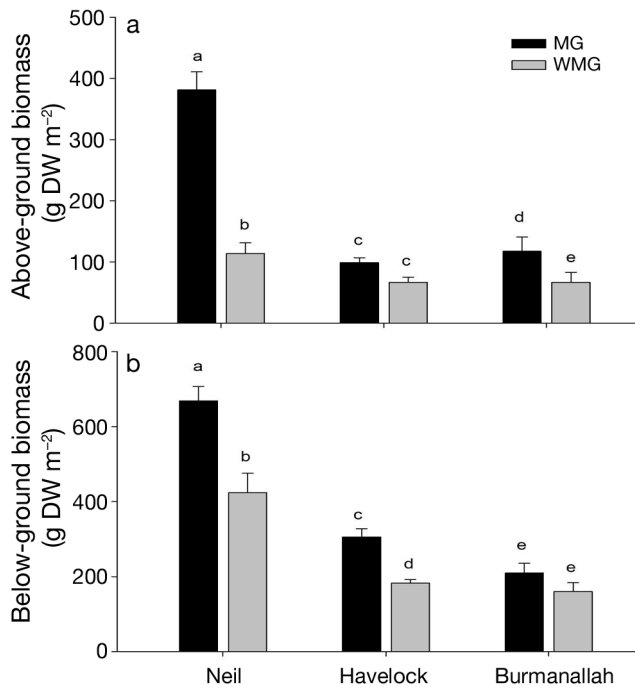


Fig. 4. (a) Above ground and (b) below ground biomass of *Thalassia hemprichii* at the Neil Island, Havelock Island and Burmanallah locations associated with mangroves (MG) and without mangroves (WMG). Error bars: SE. Lowercase letters: significant differences ( $p < 0.001$ ) between the 2 sites (MG and WMG) derived from 2-way ANOVA results with sites as fixed factors

difference in vertical production (2-fold) and horizontal production (2.4-fold) between sites was observed for Neil (Fig. 5a) and Havelock Islands, respectively (Fig. 5b).

### 3.3. Population traits

*T. hemprichii* associated with mangroves needed fewer days to produce a single leaf than the plants without mangroves, as observed from the PI (Fig. 6). The MG site of Havelock Island took the least amount of time (23.31 d) to produce a single leaf, whereas its WMG site took the most (29.11 d) for the production of a single leaf (Fig. 6b,c). The average shoot age of the plants associated with mangroves was significantly different between sites and locations, except between Havelock and Burmanallah (Table 3). The differences in the average shoot age was within similar range (ca. 1-fold) of the MG sites at Neil and Burmanallah and the WMG site of Havelock. No significant differences were observed for the long-term average recruitment ( $R$ ) between the MG and the WMG sites (Table 3).

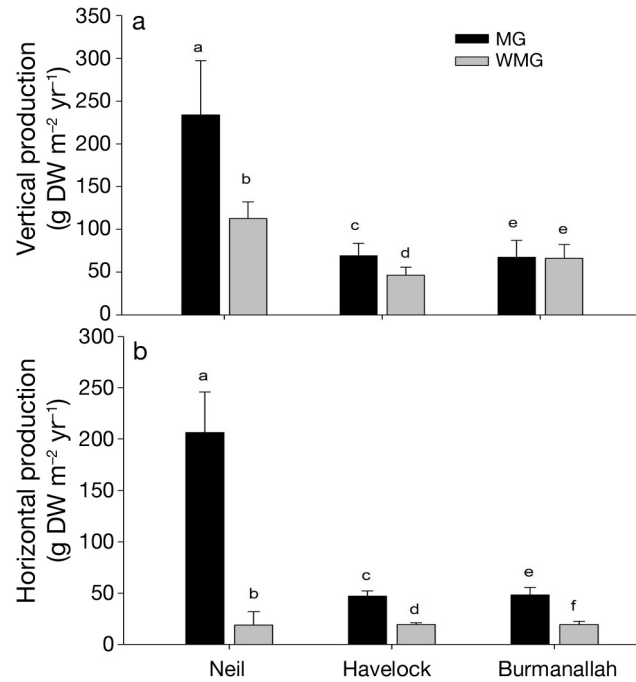


Fig. 5. (a) Vertical and (b) horizontal rhizome production of *Thalassia hemprichii* at the Neil Island, Havelock Island and Burmanallah locations associated with mangroves (MG) and without mangroves (WMG). Error bars: SE. Lowercase letters: significant differences ( $p < 0.001$ ) between the 2 sites (MG and WMG) derived from 2-way ANOVA results with sites as fixed factors

The recruitment ( $R_0$ ) rate of the *T. hemprichii* population sampled for 2019 was higher than  $R$  at the MG sites, except at the WMG site of Burmanallah. The  $R_0$  at the MG site of Havelock Island was 1.2-fold higher than that of its WMG site. Higher  $R_0$  than  $R$  indicates positive growth of the *T. hemprichii* population. The only exception was the WMG site of Burmanallah, where the population showed a negative growth rate. Although the MG sites at all 3 locations showed positive growth rates, the differences between  $R$  and  $R_0$  were higher at the WMG sites at all locations. The current growth rate of the MG site of Havelock Island was 7-fold lower than that of the WMG site, whereas that of Neil Island was 4-fold lower. Though lower in current growth rate, the plants associated with mangroves had increased fitness, supported by the age frequency distribution of *T. hemprichii*, which showed a higher number of younger plants at the MG sites ( $n = 167$ , 107 and 67 individuals of age class 1) of Neil, Havelock and Burmanallah when compared to their WMG sites ( $n = 100$ , 73 and 42 individuals of age class 1), respectively (Fig. 7).

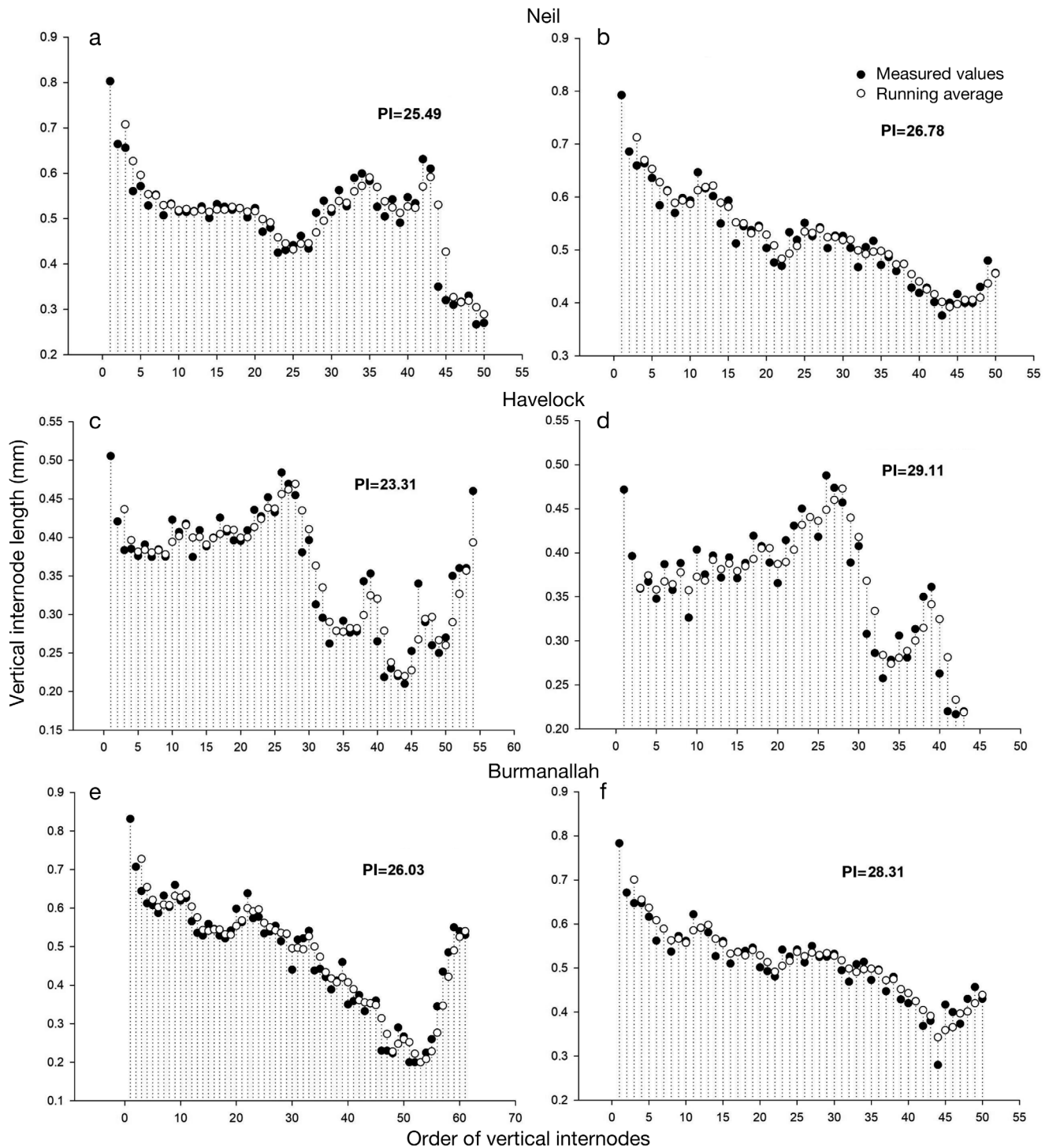


Fig. 6. Plastochrone interval (PI) of *Thalassia hemprichii* population for (a,b) Neil Island, (c,d) Havelock Island and (e,f) Burmanallah locations associated with mangroves (MG; a,c,e) and without mangroves (WMG; b,d,f) derived from average internodal length of 10 quadrats. A running average was plotted against the original internode values to filter short-term seasonal variability

#### 4. DISCUSSION AND CONCLUSIONS

The ecological connectivity/association between seagrass and mangrove ecosystems is a multifaceted process that is beneficial to both systems, and plays

an important role in maintaining the wide mosaic of ecological functions of coastal seascapes (Dorenbosch et al. 2007, Medina-Gómez et al. 2016). Consistent with previous studies (Poovachiranon & Chansang 1994, Mendoza et al. 2019), we observed a significant

Table 3. Age structure and population dynamics of *Thalassia hemprichii* associated with mangroves (MG) and without mangroves (WMG) at the Neil Island, Havelock Island and Burmanallah locations. Mean  $\pm$  SE are presented for the shoot age. Lowercase and capital superscript letters: significant differences between sites (MG and WMG) and locations (A: Neil vs. Havelock; B: Neil vs. Burmanallah; C: Havelock vs. Burmanallah; X: no difference), respectively. The exponential coefficient  $\pm$  SE of the exponential decay regression is presented for the long-term average recruitment rate ( $R$ ). Different letters indicate significant differences between MG and WMG only for  $R$ , ns: not significant. **Bold** highlights the negative growth rate at Burmanallah (WMG site)

	Neil MG	Neil WMG	Havelock MG	Havelock WMG	Burmanallah MG	Burmanallah WMG
<b>Age structure</b>						
Shoot longevity (yr)	4.39	2.84	4.73	2.95	3.34	2.37
Shoot age (yr)	$0.95 \pm 0.04^{ABa}$	$0.88 \pm 0.04^{ABb}$	$1.22 \pm 0.05^{AXc}$	$1.29 \pm 0.05^{AXd}$	$1.14 \pm 0.06^{BXe}$	$1.09 \pm 0.06^{BXf}$
<b>Population dynamics</b>						
Long term avg. recruitment ( $R$ , $yr^{-1}$ )	$1.08 \pm 0.16^{ns}$	$0.85 \pm 0.29^{ns}$	$0.62 \pm 0.16^{ns}$	$0.32 \pm 0.28^{ns}$	$0.64 \pm 0.23^{ns}$	$0.62 \pm 0.30^{ns}$
Present recruitment rate ( $R_0$ , $yr^{-1}$ )	1.11	0.97	0.65	0.53	0.69	0.57
Population growth rate ( $r$ , $yr^{-1}$ )	0.03	0.12	0.03	0.21	0.05	<b>-0.05</b>

and positive influence of mangrove (*Rhizophora apiculata*) ecosystem association on the population dynamics of seagrass (*Thalassia hemprichii*), resulting in enhanced meadow traits, recruitment rates and longevity of plants at 3 locations (Neil, Havelock and Burmanallah) in an island ecosystem of ANI.

#### 4.1. Sediment characteristics

*T. hemprichii* prefers sandy habitat (80–90 % sand), and the presence of >80 % sand at both the MG and WMG sites indicates a suitable habitat (Tussenbroek et al. 2006, Ragavan et al. 2016) for seagrass populations of ANI. The higher silt content at the MG sites indicates that the influx of fine grain size fractions from the mangrove ecosystem during daily receding tides (Kathiresan & Alikunhi 2011) is filtered by seagrass leaves (higher canopy height = better filtration) and retained in the seagrass meadows (Short et al. 2007, Potouroglou et al. 2017). High shoot density of *T. hemprichii* at the MG sites can also facilitate the retention and deposition of incoming fine particles in the meadows (Bos et al. 2007, Fonseca et al. 2019). A similar phenomenon of sediment retention has been observed for *T. hemprichii* in Southeast Asia (Miyajima et al. 2015) and other seagrasses like *Posidonia oceanica* (Gacia & Duarte 2001), *Zostera marina* (Miyajima et al. 2015, Fonseca et al. 2019), *Halodule uninervis* (Christianen et al. 2013) and *Cymodocea serrulata* (Gangal et al. 2012). The percentage of sand (82–99 %) content in the sediment at both sites (MG and WMG)

was within a similar range, whereas the silt (27.8 % at Neil island) content was 1.7-fold and 2-fold higher (silt, 0.98–15.9 %) than previously reported for Neil Island (Nobi et al. 2010) and for ANI (Savurirajan et al. 2018), respectively. Interestingly, the silt content (10.55 %) was 2.7-fold higher than previously reported for Burmanallah (Savurirajan et al. 2018). These differences in silt content between our results and those reported by previous authors differ due to the selection of sediment sampling sites. We sampled the seagrass sediments associated with mangroves, whereas the other authors selected non-mangrove locations. Similarly, the silt content at all 3 of our study locations was similar to grain-size fractions in *T. hemprichii* meadows along the coast of Thailand in the Andaman Sea (Rattanachot et al. 2018).

#### 4.2. Meadow traits

Seagrass density and biomass are dependent on the morphometric features of the plant. These morphometric features were influenced by the presence or absence of mangroves and mangrove-associated benefits. *T. hemprichii* plants at the MG sites were also successful in overcoming the stress associated with the 3 most important abiotic factors, such as hydrodynamics, temperature and nutrient limitation.

Being present in close proximity to mangrove ecosystems, the MG sites were able to avoid the daily wave-breaking and hydrodynamic stress. *T. hemprichii* meadows under sheltered conditions at the MG

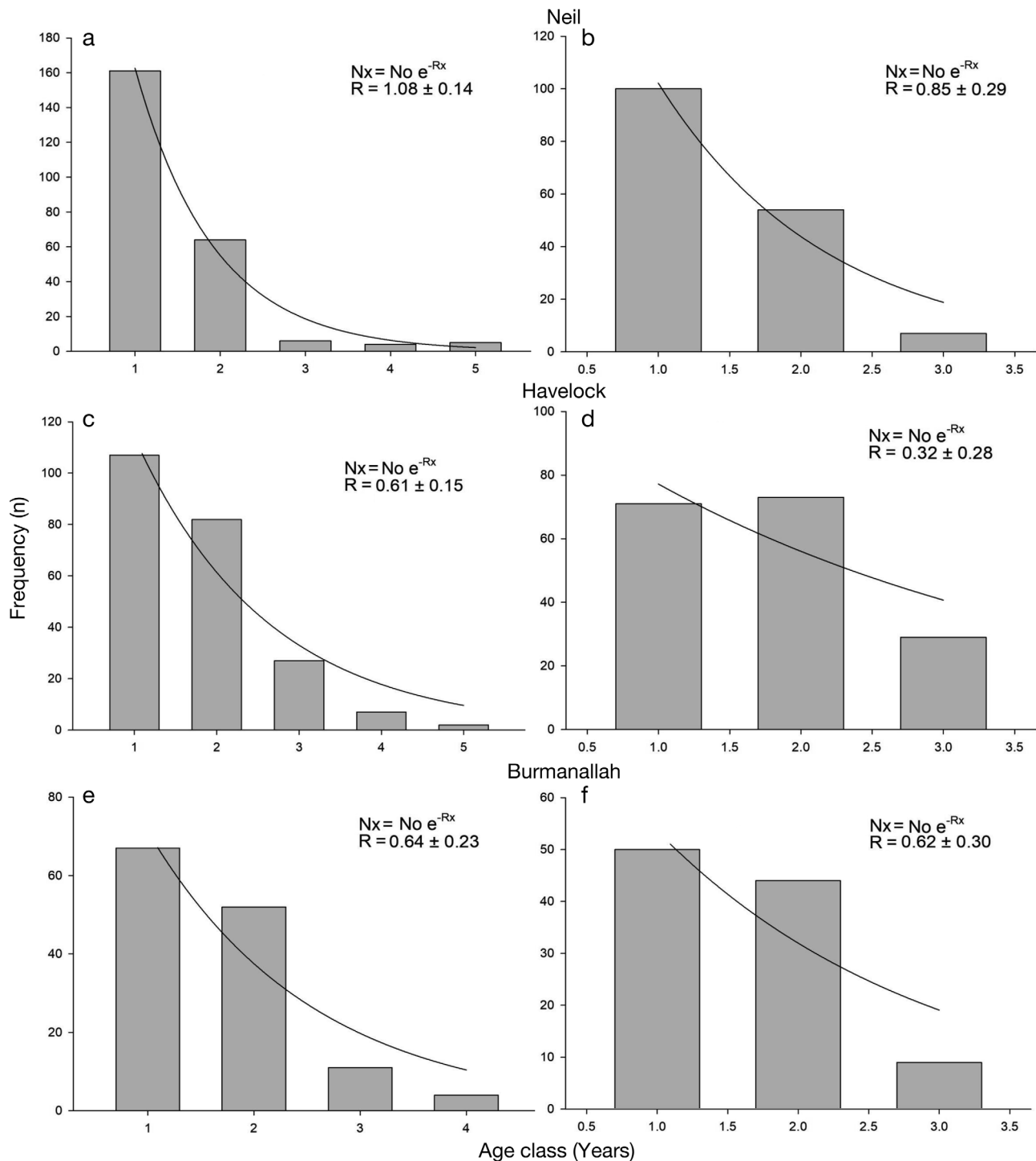


Fig. 7. Age frequency distribution of *Thalassia hemprichii* population of the (a,b) Neil Island, (c,d) Havelock Island and (e,f) Burmanallah locations associated with mangroves (MG; a,c,e) and without mangroves (WMG; b,d,f). The long-term average recruitment rate ( $R$ ) was estimated from the exponential decay regression line fitted to age frequency distribution

sites were less prone to physical damage with respect to the plant morphometric traits, such as leaves, fruits and shoots (Saenger et al. 2013), eventually resulting in higher shoot density, reproductive density and biomass. The higher reproductive density (no. of

fruits per quadrat) at the MG sites coincided with the current sampling season (March 2019) that was favourable for fruit production in *T. hemprichii* (Tongkok et al. 2017). Higher number of leaves per shoot and the number of leaves produced per year

(derived from the PI) contributed directly to the higher above-ground biomass of *T. hemprichii* at the MG sites. Presence of soft sediments (silt) adjacent to mangrove areas (at the MG sites) and higher horizontal growth rate may have helped in greater spatial migration of the *T. hemprichii* meadow resulting in increasing below-ground biomass. The high silt content of the MG sites also provided requisite nutrients other than nutrient outflow from mangroves to adjacent *T. hemprichii* meadows (Gillis et al. 2017, Mishra & Kumar 2020, authors' unpubl. data). The epiphytic microbial communities of *T. hemprichii* under favourable and sheltered conditions also played a significant role in nutrient cycling (Mishra & Mohanraju 2018), providing essential nutrients for *T. hemprichii* growth. Other than the above-mentioned factors, land run-off is also an important factor (in island ecosystems) that determines the nutrient inflow into these coastal ecosystems. Contrastingly, our sampling was carried out in the dry season of ANI, when there was land run-off only at Burmanallah and not at Neil and Havelock Islands.

*T. hemprichii* morphometric features at Neil and Havelock Islands (MG and WMG sites) are reported for the first time, whereas the morphometric features of *T. hemprichii* at the Burmanallah WMG site have been previously reported (Savurirajan et al. 2018). The total density of *T. hemprichii* at Neil (2-fold) and Burmanallah (1.5-fold) was higher and that of Havelock Island (1-fold) was lower than the density values previously reported from the Philippine coast in the Andaman Sea (Rollon et al. 2001). The pattern of below- and above-ground biomass of *T. hemprichii* in our findings was similar to the pattern observed at ANI (Savurirajan et al. 2018), on the coast of Thailand (Poovachiranon & Chansang 1994) and in mixed meadows of *T. hemprichii* and *Cymodocea rotundata* along the Thai coast in the Andaman Sea (Pattarach et al. 2018).

The lower density of *T. hemprichii* at the WMG sites may be due to the presence of seagrass meadows close to the wave-breaking zone (Fig. 2), resulting in shoot damage (Cabaço et al. 2008, Saunders et al. 2017). In a similar instance, low density of *T. hemprichii* was observed in areas susceptible to sand wave burial in the Philippines in the Andaman Sea (Duarte et al. 1997). The exposure of *T. hemprichii* meadows to higher temperature during receding tides may also have led to the loss of AG structures and consequent loss of AG biomass at the WMG sites. This loss of biomass under the influence of increased temperature has been observed for *T. hemprichii* in both *in situ* (Stapel et al. 1997, Pedersen et

al. 2016) and *ex situ* (Collier & Waycott 2014, George et al. 2018) studies.

To avoid being buried and to compensate for the breakage of leaves, *T. hemprichii* increased its vertical growth rate of leaves, resulting in higher leaf elongation and growth rates at the WMG sites. Supporting this vertical growth, the morphological features of *T. hemprichii*, such as vertical rhizomes per shoot, vertical rhizome length, vertical internodal length and vertical elongation rates, were higher at the WMG sites. Similar increases in vertical rhizomes of *T. hemprichii* to avoid hydrodynamic stress have been observed for *T. hemprichii* meadows worldwide (Cabaço et al. 2008), including off the coast of the Philippines in the Andaman Sea (Olesen et al. 2004) and off the coast of Taiwan (Kuo & Lin 2010), and also for other seagrass species like *C. rotundata* of the Gulf of Mannar in India (Gangal et al. 2012).

Intertidal stress and tidal waves play a significant role in the spatial migration of seagrass meadows (Koch 2001, Infantes et al. 2009, Pereda-Briones et al. 2018). Higher horizontal rhizome length at the WMG sites indicates the need for spatial migration towards a more suitable habitat away from the breaking waves. However, this meadow migration was not supported by plant morphometric traits, such as higher apex densities or higher horizontal rhizome growth rates. Substratum type (such as sandy or rocky habitats) also influences seagrass meadow migration by facilitating or restricting BG rhizome and root growth (Koch et al. 2010, Alagna et al. 2013, Pereda-Briones et al. 2018). Although *T. hemprichii* meadows were present in sandy habitats, they were surrounded by dead coral patches at the WMG sites of Neil and Havelock Islands (Fig. 2) and by the rocky intertidal at Burmanallah, which may have restricted the spatial migration of the plant. Positive correlation between habitat disturbance and spatial migration of meadows for colonizing new areas has been recorded for *T. hemprichii*, *H. uninervis*, *C. rotundata* and *Enhalus acoroides* on the Philippine coast (Olesen et al. 2004, Rollon et al. 2003).

### 4.3. Population traits

Population traits were influenced by seagrass meadow traits, as the population growth rates are directly correlated with plant morphometrics. Nitrate and phosphate outflow from mangroves into the surrounding coastal waters (Holmer & Olsen 2002, Mishra & Kumar 2020, authors' unpubl. data) provided the requisite nutrient levels for leaf formation



of *T. hemprichii*. As a result, the PIs for *T. hemprichii* at the MG sites of Neil (25.49 d leaf<sup>-1</sup>), Havelock (23.31 d leaf<sup>-1</sup>) and Burmanallah (26.03 d leaf<sup>-1</sup>) for *T. hemprichii* were lower than at the sites without mangroves. However, in our results, the PIs of *T. hemprichii* were lower than previously observed for *T. hemprichii* (9.2 d leaf<sup>-1</sup>) on the Philippine coast (Rollon et al. 2001). Consequently, the *T. hemprichii* population of the ANI required more days to produce a single leaf compared to global data of *Thalassia* spp. (10.9–21.9 d leaf<sup>-1</sup>) reported by Short & Duarte (2001). The lower PIs can also be the result of seasonal and temperature influence (i.e. sampling in the summer season), when the plant allocates more energy towards reproductive processes than to plant productivity (Tongkok et al. 2017).

The shoot longevity of the *T. hemprichii* population was higher at the MG sites, which suggests that association with mangroves could aid the *T. hemprichii* population to survive longer by 4 or 5 yr. From the age frequency data, we observed that the association of *T. hemprichii* meadows with mangroves resulted in having higher numbers of younger plants (<1 yr old) when compared to those at the WMG sites (MG, n = 161, 107 and 67 vs. WMG, n = 100, 73 and 42 at Neil, Havelock and Burmanallah, respectively; Fig. 7). This reduction in the number of younger plants at the WMG sites can be the direct impact of unfavourable environmental conditions in shallow waters (Duarte et al. 1997, Olesen et al. 2004, Cabaço et al. 2008).

The present recruitment ( $R_0$ ) at MG sites was higher than the long-term average recruitment ( $R$ ) for *T. hemprichii* at all locations except Burmanallah, where  $R_0$  was lower at the WMG site (Table 3). Higher  $R_0$  indicates that the population is growing in these islands, while lower  $R_0$  indicates a declining population. This decline of *T. hemprichii* at the WMG site of Burmanallah may be due to domestic wastewater discharge, aquaculture expansion and agricultural input leading to high levels of cadmium and lead that can be toxic to plant physiological processes (Mishra & Kumar 2020). Although  $R_0$  was lower at the WMG sites than at the MG sites, the rate of growth ( $r$ ) was higher for the seagrass population under environmental stress at the WMG sites of Neil and Havelock Islands when compared to the steady state of growth at their MG sites. Higher  $R_0$  and  $r$  of the WMG sites indicates that the seagrasses are efficient ecosystem engineers (Rietkerk et al. 2004, Gangal et al. 2012) and can stimulate the growth of their leaves and rhizomes (Cardoso et al. 2004, McMahon et al. 2017) to avoid being buried. This higher growth rate can be correlated with higher reproductive effort at the WMG sites of Neil (4.7%), Havelock (16.3%) and

Burmanallah (10.4%). Although this positive response of *T. hemprichii* is an indication of short-term plant resilience to local environmental stress, over the long term, this stress can lead to the loss of seagrass meadows from these unique island habitats.

Therefore, in the context of declining seagrass ecosystems of Southeast Asian bioregions, the growing *T. hemprichii* population (at Neil and Havelock Islands) provides a positive scenario. Our results agree with the findings of Short et al. (2011) that cataloguing global population dynamics of seagrass ecosystems is necessary to determine their current status. Growing *T. hemprichii* populations would ensure various ecosystem services, including feeding grounds for green sea turtles (Christianen et al. 2017) at Neil and Havelock Islands, along with providing suitable nurseries for marine fishes (Unsworth et al. 2019). However, the declining seagrass population at Burmanallah reflects the influences of various anthropogenic disturbances on *T. hemprichii* meadows and requires the attention of environmental management agencies, as well as suitable intervention from the local government.

#### 4.4. Conclusions

Our results represent an early assessment of *T. hemprichii* population and meadow traits from 3 locations in ANI in India using reconstruction techniques. Our findings indicate a positive response of seagrass population dynamics in association with mangroves. We agree with previous findings that ecological connectivity between coastal seascapes structures the population dynamics of the embedded ecosystems. Our results provide a clear picture of the increase in population longevity and meadow traits of *T. hemprichii* when associated with mangroves. We further emphasize the need for more research on the subject to better explore and quantify the various complex ecological processes that help in the functioning of these coastal ecosystems along the Indian coast. We believe that ecological connectivity/association between seagrass and mangroves can increase the resilience of these coastal seascapes in the event of natural or anthropogenic disturbances and climate change scenarios. This increased resilience can play a vital role in conservation and management of these coastal seascapes and their associated biodiversity.

**Acknowledgements.** We are grateful to the PCCF, Wildlife of Andaman and Nicobar Islands for providing the required official help during the sampling programme. We are thankful to P. M. Ishaq and Sumantha Narayana for help during

field work and to M. R. Maithreyi for English language editing of earlier drafts of the manuscript. We are also grateful to the 2 anonymous reviewers whose comments/suggestions improved the manuscript. A pre-print of this manuscript is archived in bioRxiv.

## LITERATURE CITED

- Alagna A, Vega-Fernández T, Terlizzi A, Badalamenti F (2013) Influence of microhabitat on seedling survival and growth of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile. *Estuar Coast Shelf Sci* 119:119–125
- Bayraktarov E, Saunders MI, Abdullah S, Mills M and others (2016) The cost and feasibility of marine coastal restoration. *Ecol Appl* 26:1055–1074
- Berkström C, Jörgensen TL, Hellström M (2013) Ecological connectivity and niche differentiation between two closely related fish species in the mangrove-seagrass-coral reef continuum. *Mar Ecol Prog Ser* 477:201–215
- Bos AR, Bouma TJ, de Kort GLJ, van Katwijk MM (2007) Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. *Estuar Coast Shelf Sci* 74:344–348
- Cabaço S, Santos R, Duarte CM (2008) The impact of sediment burial and erosion on seagrasses: a review. *Estuar Coast Shelf Sci* 79:354–366
- Campbell SJ, Kartawijaya T, Sabarini EK (2011) Connectivity in reef fish assemblages between seagrass and coral reef habitats. *Aquat Biol* 13:65–77
- Cardoso PG, Pardal MA, Lillebo AI, Ferreira MD, Marques JC (2004) Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *J Exp Mar Biol Ecol* 302:233–248
- Christianen MJA, Belzen JV, Herman PMJ, van Katwijk MM, Lamers LPM, van Leent PJM, Bouma PMJ (2013) Low-canopy seagrass beds still provide important coastal protection services. *PLOS ONE* 8:e62413
- Christiansen F, Esteban N, Mortimer JA, Dujon AM, Hays GC (2017) Diel and seasonal patterns in activity and home range size of green turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. *Mar Biol* 164:10
- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Velde G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuar Coast Shelf Sci* 55:309–321
- Collier CJ, Waycott M (2014) Temperature extremes reduce seagrass growth and induce mortality. *Mar Pollut Bull* 83:483–490
- Costanza R, de Groot R, Sutton P, van der Ploeg S and others (2014) Changes in the global value of ecosystem services. *Glob Environ Change* 26:152–158
- Crook DA, Lowe WH, Allendorf FW, Eros T and others (2015) Human effects on ecological connectivity in aquatic ecosystems: integrating scientific approaches to support management and mitigation. *Sci Total Environ* 534:52–64
- Cullen-Unsworth LC, Nordlund LM, Paddock J, Baker S, McKenzie LJ, Unsworth RKF (2014) Seagrass meadows globally as a coupled social-ecological system: implications for human wellbeing. *Mar Pollut Bull* 83:387–397
- Cunha AH, Duarte CM (2005) Population age structure and rhizome growth of *Cymodocea nodosa* in the Ria Formosa (southern Portugal). *Mar Biol* 146:841–847
- Das HS (1996) Status of seagrass habitats of Andaman and Nicobar coast. Tech Rep 4. SACON, Coimbatore
- Dorenbosch M, Verberk WCEP, Nagelkerken I, van der Velde G (2007) Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. *Mar Ecol Prog Ser* 334:103–116
- Duarte CM, Marbá N, Agawin N, Cebrián J and others (1994) Reconstruction of seagrass dynamics: age determinations and associated tools for the seagrass ecologist. *Mar Ecol Prog Ser* 107:195–209
- Duarte CM, Terrados J, Agawin NSR, Fortes MD, Bach S, Kenworthy WJ (1997) Response of a mixed Philippine seagrass meadow to experimental burial. *Mar Ecol Prog Ser* 147:285–294
- Duarte CM, Kennedy H, Marba N, Hendriks I (2013) Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies. *Ocean Coast Manag* 83:32–38
- Fonseca MS, Fourqurean JW, Koehl MAR (2019) Effect of seagrass on current speed: importance of flexibility vs. shoot density. *Front Mar Sci* 6:376
- Fourqurean WJ, Duarte CM, Marba N (2003) Elucidating seagrass population dynamics: theory, constraints and practice. *Limnol Oceanogr* 48:2070–2074
- Gacia E, Duarte CM (2001) Sediment retention by a Mediterranean *Posidonia oceanica* meadow: the balance between deposition and resuspension. *Estuar Coast Shelf Sci* 52:505–514
- Gangal M, Arthur R, Alcoverro T (2012) Structure and dynamics of South East Indian seagrass meadows across a sediment gradient. *Aquat Bot* 98:34–39
- George R, Gullström M, Mangora MM, Mtolera MSP, Björk M (2018) High midday temperature stress has stronger effects on biomass than on photosynthesis: a mesocosm experiment on four tropical seagrass species. *Ecol Evol* 8:4508–4517
- Gillis LG, Bouma TJ, Jones CG, van Katwijk MM and others (2014) Potential for landscape-scale positive interactions among tropical marine ecosystems. *Mar Ecol Prog Ser* 503:289–303
- Gillis LG, Jones CG, Ziegler AD, van der Wal D, Breckwoldt A, Bouma TJ (2017) Opportunities for protecting and restoring tropical coastal ecosystems by utilizing a physical connectivity approach. *Front Mar Sci* 4:374
- Guannel G, Arkema K, Ruggiero P, Verutes G (2016) The power of three: Coral reefs, seagrasses and mangroves protect coastal regions and increase their resilience. *PLOS ONE* 11:e0158094
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hemminga MA, Duarte CM (2000) Seagrass ecology. Cambridge University Press, Cambridge
- Holmer M, Bachmann Olsen A (2002) Role of decomposition of mangrove and seagrass detritus in sediment carbon and nitrogen cycling in a tropical mangrove forest. *Mar Ecol Prog Ser* 230:87–101
- Howard J, Hoyt S, Isensee K, Telszewski M, Pidgeon E (eds) (2014) Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature, Arlington, VA
- Huxham M, Whitlock D, Githaiga M, Dencer-Brown A (2018) Carbon in the coastal seascape: how interactions between

- mangrove forests, seagrass meadows and tidal marshes influence carbon storage. *Curr For Rep* 4:101–110
- ✦ Infantes E, Terrados J, Orfila A, Cañellas T, Álvarez-Ellacuría A (2009) Wave energy and the upper depth limit distribution of *Posidonia oceanica*. *Bot Mar* 52: 419–427
- ✦ Jagtap TG (1991) Distribution of seagrasses along the Indian coast. *Aquat Bot* 40:379–386
- ✦ Jagtap TG, Komarpant DS, Rodrigues RS (2003) Status of a seagrass ecosystem: an ecologically sensitive wetland habitat from India. *Wetlands* 23:161–170
- ✦ Kathiresan K, Alikunhi NM (2011) Tropical coastal ecosystems: rarely explored for their interaction! *Ecología (Madr)* 1:1–22
- ✦ Koch EW (2001) Beyond light: physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries* 24:1–17
- ✦ Koch EW, Ailstock MS, Booth DM, Shafer DJ, Magoun AD (2010) The role of currents and waves in the dispersal of submersed angiosperm seeds and seedlings. *Restor Ecol* 18:584–595
- ✦ Kristensen E, Bouillon S, Dittmar T, Marchand C (2008) Organic carbon dynamics in mangrove ecosystems: a review. *Aquat Bot* 89:201–219
- ✦ Kuo YM, Lin HJ (2010) Dynamic factor analysis of long-term growth trends of the intertidal seagrass *Thalassia hemprichii* in southern Taiwan. *Estuar Coast Shelf Sci* 86: 225–236
- ✦ Lirman D, Cropper WP (2003) The influence of salinity on seagrass growth, survivorship, and distribution within Biscayne Bay, Florida: field, experimental, and modelling studies. *Estuaries* 26:131–141
- McKenzie LJ, Campbell SJ (2002) Seagrass-watch: manual for community (citizen) monitoring for seagrass habitat. Western Pacific Edition. QFS, NFC, Cairns
- ✦ McMahon KM, Evans RD, van Dijk K, Hernawan U and others (2017) Disturbance is an important driver of clonal richness in tropical seagrasses. *Front Plant Sci* 8:2026
- ✦ Medina-Gómez I, Madden CJ, Herrera-Silveira J, Kjerfve B (2016) Response of *Thalassia testudinum* morphometry and distribution to environmental drivers in a pristine tropical lagoon. *PLOS ONE* 11:e0164014
- Mendoza ARR, Patalinghung JMR, Divinagracia JY (2019) The benefit of one cannot replace the other: seagrass and mangrove ecosystems at Santa Fe, Bantayan Island. *J Ecol Environ* 43:18
- Mishra AK, Kumar M (2020) Mangrove sediments act as source of nutrients and sink of heavy metals of coastal Andaman Sea. *Indian J Geo-Mar Sci* 49:156–166
- Mishra AK, Mohanraju R (2018) Epiphytic bacterial communities in seagrass meadows of oligotrophic waters of Andaman Sea. *Open Access Libr J* 5:e4388
- ✦ Miyajima T, Hori M, Hamaguchi M, Shimabukuro H, Adachi H, Yamano H, Nakaoka M (2015) Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. *Global Biogeochem Cycles* 29:397–415
- ✦ Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Mar Ecol Prog Ser* 202:175–192
- ✦ Nagelkerken I, Blaber SJM, Bouillon S, Green P and others (2008) The habitat function of mangroves for terrestrial and marine fauna: a review. *Aquat Bot* 89:155–185
- ✦ Nobi EP, Dilipan E, Thangaradjou T, Sivakumar K, Kannan L (2010) Geochemical and geo-statistical assessment of heavy metal concentration in the sediments of different coastal ecosystems of Andaman Islands, India. *Estuar Coast Shelf Sci* 87:253–264
- ✦ Nordlund LM, Koch EW, Barbier EB, Creed JC (2016) Seagrass ecosystem services and their variability across genera and geographical regions. *PLOS ONE* 11:e0163091
- ✦ Nordlund LM, Jackson EL, Nakaoka M, Samper-Villarreal J, Beca-Carretero P, Creed JC (2018) Seagrass ecosystem services - What's next? *Mar Pollut Bull* 134:145–151
- ✦ Olesen B, Marba N, Duarte CM, Savelle RS, Fortes MD (2004) Recolonization dynamics in a mixed seagrass meadow: the role of clonal versus sexual processes. *Estuaries* 27:770–780
- ✦ Ondiviola B, Losada IJ, Lara JL, Maza M, Galvan C, Bouma TJ, Belzen J (2014) The role of seagrasses in coastal protection in a changing climate. *Coast Eng* 87:158–168
- Pattarach K, Titioatchasai J, Darakrai A, Mayakun J (2018) Effects of wave exposure and shore level on seagrass abundance and distribution in the intertidal community. *Songklanakarin J Sci Technol* 40:1446–1450
- ✦ Pedersen O, Colmer TD, Borum J, Zavala-Perez A, Kendrick GA (2016) Heat stress of two tropical seagrass species during low tides - impacts on underwater net photosynthesis, dark respiration and diel *in situ* aeration. *New Phytol* 210:1207–1218
- ✦ Pendleton L, Donata MC, Murray BC, Crooks S and others (2012) Estimating global 'blue carbon' emissions from conversion and degradation of vegetated coastal ecosystems. *PLOS ONE* 7:e43542
- ✦ Pereda-Briones L, Infantes E, Orfila A, Tomas F, Terrados J (2018) Dispersal of seagrass propagules: interaction between hydrodynamics and substratum type. *Mar Ecol Prog Ser* 593:47–59
- Poovachiranon S, Chansang H (1994) Community structure and biomass of seagrass beds in the Andaman Sea. I. Mangrove-associated seagrass beds. *Phuket Mar Biol Cent Res Bull* 59:53–64
- ✦ Potouroglou M, Bull JC, Krauss KW, Kennedy HA and others (2017) Measuring the role of seagrasses in regulating sediment surface elevation. *Sci Rep* 7:11917
- Ragavan P, Saxena A, Mohan PM, Coomar T, Ragavan A (2014) Leaf reddening in seagrasses of Andaman and Nicobar Islands. *Trop Ecol* 54:269–273
- Ragavan P, Jayaraj RSC, Muruganantham M, Jeeva C, Ubare VV, Saxena A, Mohan PM (2016) Species composition and distribution of seagrasses of the Andaman and Nicobar Islands. *Vegetos* 29:78–87
- Rattanachot E, Stankovis M, Aongsara S, Prathep A (2018) Ten years of conservation efforts enhance seagrass cover and carbon storage in Thailand. *Aquat Bot* 61:441–451
- ✦ Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J (2004) Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305:1926–1929
- ✦ Rollon R, Cayabyab NM, Fortes M (2001) Vegetative dynamics and sexual reproduction of monospecific *Thalassia hemprichii* meadows in the Kalayaan Island group. *Aquat Bot* 71:239–246
- ✦ Rollon RN, de Ruyter van Steveninck ED, van Vierssen W (2003) Spatio-temporal variation in sexual reproduction of the tropical seagrass *Enhalus acoroides* (L.f.) Royle in Cape Bolinao, NW Philippines. *Aquat Bot* 76:339–354
- Saenger P, Gartside D, Funge-Smith S (2013) A review of mangrove and seagrass ecosystems and their linkage to

- fisheries and fisheries management. RAP Publ 2013/09. FAO Regional Office for Asia and the Pacific, Bangkok
- ✦ Saunders MI, Atkinson S, Klein CJ, Weber T, Possingham HP (2017) Increased sediment loads can cause non-linear decrease in seagrass suitable habitat extent. PLOS ONE 12:e0187284
- Savurirajan M, Lakra RK, Equbal J, Ganesh KST (2018) A note on morphometric, shoot density and biomass of *Thalassia hemprichii* from the south Andaman coast, Andaman and Nicobar Islands, India. Indian J Geo-Mar Sci 47:1222–1227
- Saxena A, Ragavan P, Ambika R (2010) Assessment of status and diversity of seagrasses in Andaman and Nicobar Islands. In: Proc National Seminar on Tropical Ecosystems: structure, function and services. IFGTB, Coimbatore, p 31–38
- ✦ Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. Mar Ecol Prog Ser 391: 107–115
- Short FT, Duarte CM (2001) Methods for the measurement of seagrass growth and production. In: Short FT, Coles RG (eds) Global seagrass research methods. Elsevier Science, Amsterdam, p 155–182
- ✦ Short FT, Carruthers T, Dennison W, Waycott M (2007) Global seagrass distribution and diversity: a bioregion model. J Exp Mar Biol Ecol 350:3–20
- ✦ Short FT, Polidoro B, Livingstone SR, Carpenter KE and others (2011) Extinction risk assessment of the world's seagrass species. Biol Conserv 144:1961–1971
- Sokal RR, Rohlf FJ (2012) Biometry: the principles and practice of statistics in biological research, 4<sup>th</sup> edn. W. H. Freeman and Co., New York, NY
- Spalding MD, Taylor ML, Ravilious C, Short F, Green E (2003) Global overview: the distribution and status of seagrasses. In: Green E, Short FT (eds) World atlas of seagrasses. University of California Press, Berkeley, CA, p 5–26
- ✦ Stapel J, Manuntun R, Hemminga MA (1997) Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass bed following seasonal low tide exposure during daylight. Mar Ecol Prog Ser 148:251–262
- Swapna A, Santhosh RB, Sasidharan V (2016) Fish diversity and distribution in Carbyns Cove mangrove habitat along the south Andaman coast in relation to environmental variables. Res Rev Res J Biol 4:28–37
- ✦ Thangaradjou T, Bhatt JR (2018) Status of seagrass ecosystems in India. Ocean Coast Manag 159:7–15
- Thangaradjou T, Nobi EP, Dilipan E, Sivakumar K, Kannan L (2009) Threats to seagrass ecosystems of India. Seagrass Watch 39:20–21
- ✦ Tongkok P, Kaewsuralikhit C, Kermanee P (2017) Reproductive organ characteristics and phenology of a seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson in the Andaman Sea, Thailand. Taiwan 62:168–174
- Tussenbroek BI, Vonk JA, Stapel J, Erftemeijer PLA, Middleburg JJ, Ziemann JC (2006) The biology of *Thalassia*: paradigms and recent advances in research. In: Larkum AWD, Orth RJ, Duarte C (eds) Seagrasses: biology, ecology and conservation. Springer, Dordrecht, p 409–439
- ✦ Unsworth RKF, Nordlund LM, Cullen-Unsworth LC (2019) Seagrass meadows support global fisheries production. Conserv Lett 12:e12566
- ✦ Valdez SR, Zhang YS, van der Heide T, Vanderklift MA, Tarquinio F, Orth RJ, Silliman BR (2020) Positive ecological interactions and the success of seagrass restoration. Front Mar Sci 7:91
- ✦ Waycott M, Duarte CM, Carruthers TJB, Orth RJ and others (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381

Editorial responsibility: Mirta Teichberg,  
Bremen, Germany

Submitted: November 14, 2019; Accepted: April 23, 2020  
Proofs received from author(s): June 13, 2020