



ORIGINAL RESEARCH

Effects of fish herbivory on seagrass meadows of Guang-guang, Mati City, Philippines

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ABSTRACT. This study provides information on the effects of fish grazing on a seagrass bed that was dominated by *Thalassia hemprichii* in Guang-guang, Dahican, Mati City, Davao Oriental, Philippines. We tested the assumption that herbivore exclusion keeps the growth of seagrass shoots up to a minimum length. Fish visual census was used to count the abundance of fish in the area during high tide at a distance of 5 m away from the treatment cages with a 15 m transect length. Among all species, *Siganus fuscescens* was the most abundant (499) followed by *S. guttatus* (153), while *Thalassoma janseni* was the less abundant (13). The result of the weekly fish count in the seagrass bed showed highly significant variations in the number and census of species present in the area ($df = 11$, $MS = 2.88$, $F = 30.10$, $p < 0.001$). Analysis of shoot length measurement in treatment cages also exhibited highly significant differences throughout the sampling period ($df = 11$, $MS = 726.71$, $F = 1,633.10$, $p < 0.001$). Comparison between initial and final shoot counts also showed significant differences, with a higher shoot count in the full cage ($X^2 = 8$, $df = 2$, $p = 0.018$; $FC > PC > OP$). This study raises clear evidence to support the assumption that herbivore exclusion positively influences the growth of *T. hemprichii* in this area.

Key words: Davao Oriental, fish grazing, herbivore exclusion, plant-herbivory interactions, *Siganus fuscescens*, *Thalassia hemprichii*.



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Efectos de la herbivoría de peces sobre las praderas marinas de Guang-guang, ciudad de Mati, Filipinas

RESUMEN. Este estudio proporciona información sobre los efectos del forrajeo de peces en un lecho de pastos marinos dominado por *Thalassia hemprichii* en Guang-guang, Dahican, ciudad de Mati, Davao Oriental, Filipinas. Se probó la suposición de que la exclusión de herbívoros mantiene el crecimiento de los brotes de pastos marinos hasta una longitud mínima. Se utilizó el censo visual de peces para contar la abundancia de peces en el área durante la marea alta a una distancia de 5 m de las jaulas de tratamiento con una longitud de transectas de 15 m. Entre todas las especies, *Siganus fuscescens* fue la más abundante (499) seguida de *S. guttatus* (153), mientras que *Thalassoma janseni* fue la menos abundante (13). El resultado del conteo semanal de peces en el lecho de fanerógamas marinas mostró variaciones altamente significativas en el número y censo de especies presentes en el área ($df = 11$, $MS = 2,88$, $F = 30,10$, $p < 0.001$). El análisis de la medición de la longitud de los brotes en las jaulas de tratamiento también mostró diferencias muy significativas a lo largo del período de muestreo ($df = 11$, $MS = 726,71$, $F = 1.633,10$, $p < 0,001$). La comparación entre el conteo de brotes inicial y final también mostró diferencias significativas, con un mayor conteo de brotes en la jaula completa ($X^2 = 8$, $df = 2$, $p = 0,018$; $FC > PC > OP$). Este

estudio presenta evidencia clara para apoyar la suposición de que la exclusión de herbívoros influye positivamente en el crecimiento de *T. hemprichii* en esta área.

Palabras clave: Davao Oriental, forrajeo de peces, exclusión de herbívoros, interacciones planta-herbívoro, *Siganus fuscescens*, *Thalassia hemprichii*.

INTRODUCTION

Shallow tropical and subtropical coastal areas contain seagrass beds considered as one of the most biodiverse, productive, and economically important ecosystems in the world (Fortes 2004; Macusi et al. 2011). Seagrass beds are known to host visitors and resident species such as sea turtles, dugongs, sea cucumbers, sea urchins, clams and shellfish, as well as adult and juvenile fish that take advantage of the productive ecosystem found in seagrass beds (Abreo et al. 2018). It also provides ecological services such as filtering debris, stabilizing sediment, reducing coastal erosion, and protecting the shoreline from extreme storm events (Koch 2001; Bjork et al. 2008a; Macusi and Tipudan 2020). In addition, seagrass beds also store large quantities of organic carbon, which is crucial for fighting climate change (Duarte and Hemminga 2000). Excess carbon produced by seagrass is buried under sediments, helping in biological carbon sequestration (Duarte et al. 2005). Its proximity to other habitat engineers, such as mangroves and coral reefs, allows for the trophic transfer of energy essential to maintaining the abundance of mangrove and reef fish species (Valentine and Heck 2005). Seagrass beds are also economically critical for the livelihood of coastal communities as they function as gleaned areas and ecotourism sites (Maynawang and Macusi 2023). While these are all essential features of seagrass beds, one neglected connection is how the trophic transfer occurs from producers to consumers, such as herbivores.

Sea urchins and fish have replaced historically dominant mega-grazers like sirenians and turtles

in tropical areas and waterfowl in temperate areas as primary grazers in current seagrass beds (Heck and Valentine 2006). Moreover, sea urchins are crucial to managing damaged aquatic vegetation and recycling nutrients (Shears and Babcock 2002; Vonk et al. 2008). One commonly found seagrass ecosystem resident is the rabbitfish of Genus *Siganus* with 28 species (Randall and Kulbicki 2005). These are found in the Red Sea and the Mediterranean in great abundance causing overgrazing along the marine ecosystem in various locations (Pickholtz et al. 2018). Although individual species of the Siganid family can dominate the herbivore biomass within seagrass beds and estuarine habitats (Campos et al. 1994; Solomon et al. 2008), siganids tend to be found in lower abundance on reefs (Wilson et al. 2003; Cheal et al. 2012). Herbivores usually leave patches of seagrasses, i.e. they are not completely overgrazed; somehow, seagrass shoots are only clipped. Grazing by fish and invertebrates in seagrass beds has a long history of being studied in Africa, South America, Australia, and Europe (McGlathery 1995; Valentine and Heck 1999; Smulders et al. 2022). Grazing animals usually forage on seagrasses to gain nourishment. However, there are cases when fish and invertebrates may be construed as directly grazing on seagrass leaves when this may not be the case. Instead, they are found grazing on epiphytes attached to the seaweed or plant.

There are documented studies showing that rabbitfish usually eat macrophytes not just for plant leaves but also for its epiphytes and other associated small invertebrates that are ingested accidentally (von Westernhagen 1973; Fox and Bellwood 2008; Hoey et al. 2013). Their diets consist primarily of macrophytes with low lipid

content, probably resulting in sub-optimum growth and inconsistent production (Bariche 2006). As a matter of fact, the gut content analysis of rabbitfish from Mediterranean coastal habitats showed that the macroalga *Dictyota* spp. was the main food item, followed by *Cystoseira* spp., *Sargassum* spp., and *Caulerpa racemose* (Bariche 2006; Serio et al. 2006). This finding was also similar to that of Azzurro et al. (2007), where the most represented food items included *Sargassum* spp., *Cystoseira* spp., and *Dictyota* spp. This highlights the wide range of herbivory by rabbitfish and emphasizes the importance of its seagrass habitat. Sea urchins, on the other hand, graze on seagrasses to gain energy for their physiological function as well as reproduction. Few studies have been conducted in the Philippines to observe or investigate the influence of herbivore exclusion on the growth of marine plants like seagrasses. In general, herbivores (such as rabbitfish and sea urchins) are widely acknowledged as critical components that determine the structure and resilience of marine ecosystems (Teresa and Simone 2002; Burkepille and Hay 2006). Herbivores facilitate healthy seagrass meadows and nutrient recycling by grazing (Duarte 2002) and can strongly influence ecosystem organization and functioning (Steneck and Dethier 1994; Vinueza et al. 2006; Macusi 2012). Plant-herbivore interactions have substantial ecological and evolutionary consequences but have traditionally been overlooked in marine higher plants (Verges et al. 2007). Investigations of plant-herbivore relationships, such as fish grazing, are essential for understanding the interconnectivity of different ecosystems. This study aimed to investigate how herbivore exclusion influences the growth and abundance of seagrass, particularly *Thalassia hemprichii* in Guang-guang, Davao Oriental, Philippines. No previous studies have been conducted on fish grazing in this location. Therefore, it is important to carry out this assessment as it will serve as baseline information for further ecological studies related to fish grazing.

MATERIALS AND METHODS

Description of the study area

The study was conducted from March to May 2018 in Guang-guang, Dahican, Mati City, Davao Oriental, Philippines, where natural mangrove forests and rehabilitated mangroves can be found (Figure 1). The current mangrove area planted in the study site covers 77 ha, with its wide intertidal area covered by seagrass beds, sandy and rocky substrate (Nallos and Macusi 2023). Seagrass species found in the area include *Cymodocea rotundata*, *Cymodocea serrulata*, *Enhalus acoroides*, *Halodule pinifolia*, *Halodule univervis*, *Halophila minor*, *Halophila ovalis*, *Syringodium isoetifolium* and *T. hemprichii*. Seagrass species *T. hemprichii* and *C. rotundata* are predominant in the current study site (De Troch et al. 2008; Jimenez 2016; Terayama et al. 2022). This study was established in a pre-selected seagrass bed of *T. hemprichii* to better understand the ecology of this vital ecosystem in a controlled manner in Guang-guang mangrove sanctuary, which is part of a Marine Protected Area (MPA) in Davao Oriental (6° 54' 59" N-126° 15' 10" E). This area was chosen because of its gently sloping seagrass cover known for its abundance of siganids. Moreover, this area is undisturbed by fishermen or gleaners and supports a rich diversity of marine flora and fauna, including various species of mangrove trees and seagrass beds (Abreo et al. 2020).

Exclusion experiment

This study used caging experiments to determine the effect of herbivore exclusion on seagrass. Cages measuring 0.5 × 0.5 m were placed in the sampling site using a plastic chicken net with a mesh size of 1 cm in diameter. The full cage (FC) treatment was overlaid with a wire mesh roof tied with a cable tie on top of the

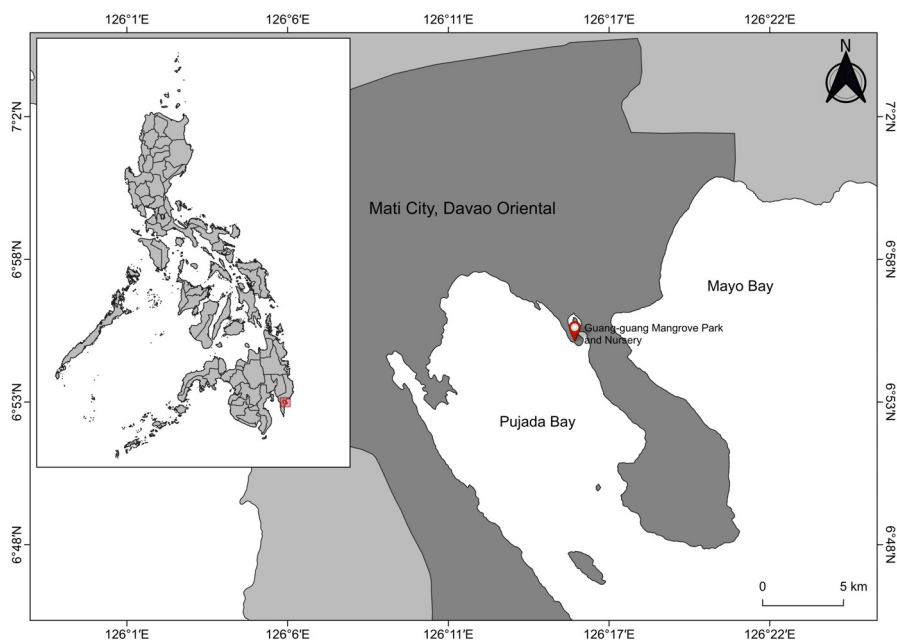


Figure 1. Study area in Guang-guang, Dahican, Mati City, Philippines, indicating the location of caging experiments.

fenced area. In this treatment, it was expected that *T. hemprichii* would be free from grazing effects of large fishes, except for juvenile fish, which can enter the mesh size (< 1 cm in diameter). The partial cage (PC) has an open top portion, which constitutes a procedural control that allows rabbitfish and other juvenile fishes to feed from *T. hemprichii* found inside the fenced area. The open cage (OC) was distinguished from the two other cages by using a pegged stick with marker flags anchored to the substrate ground floor of *T. hemprichii* bed to allow all herbivores, including sea urchins and rabbitfish, to feed on the shoots of *T. hemprichii*. Four replicates of each treatment (12 replicates in total), were randomly distributed on the seagrass bed and arranged close to each other with two-meter intervals (Figure 2).

Fish visual census

In order to quantify the abundance of rabbitfish and other fish species in the study site, fish visual census (FVC) was used. A visual census was per-

formed only when the water was clear and with a minimum distance of 5 m from the treatment cages with a 15 m transect length. To do this, researchers counted and identified the fish abundance over the 15 m transect line to determine the density of rabbitfish and other fish species found in the area during high tide. By using a slate, names and sizes (cm) of fish species were recorded, including the time of starting and finishing diving. This was performed during high tide near *T. hemprichii* bed of the study area. The FVC lasted from 15-20 min per transect. There were two perpendicular transect lines during each sampling period.

Shoots of *T. hemprichii* were initially tagged during the first sampling using a colored thread and then measured using a tape measure for counting and length measurement. A total of 120 shoots of *T. hemprichii* were monitored and measured in all cages. To quantify the effects of herbivore exclusion on seagrass, the number of shoots was counted, and shoot length was measured separately for the tagged shoots of *T.*

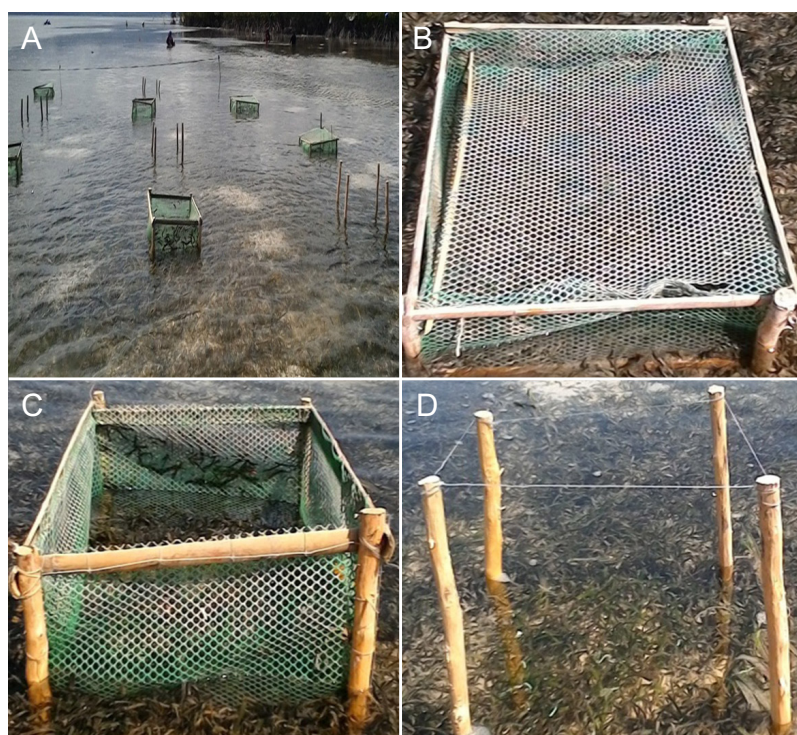


Figure 2. Different caging treatments in the study site (A), full cage (B), partial cage (C), and open cage (D).

hemprichii in the full cage, partial cage, and open cage, respectively. Initial shoot counts for *T. hemprichii* were determined during the first sampling, and final cover was counted during the last sampling. These data were later used to compare different treatments in terms of the number of shoots, but no attempt to statistically compare the data was done because of the sparse number of unit observations. Tagged individual shoots of *T. hemprichii* in each treatment were measured repeatedly during the weekly monitoring to the study site. Initial and final shoot length measurements were noted and compared in all treatments. Seagrass counting and measurement of shoots were done during the low tide period. During data collection, observations on the abundance and density of rabbitfish and other fish species found in the sampling site were performed during high tide using FVC. On the other hand, counting and measuring of leaf shoots happened during low

tide. The observation started during the daytime cycles of high and low tide, usually from 6:00 am to 5:00 pm.

Taxonomic identification of fishes

Fishing nets were used to collect individual fish samples, which were subsequently photographed and identified based on their morphological characteristics, such as color, size or length, eyes, fin size, fin color, tail size, tail color, and other bodily markings according to Lieske and Myers (2002) and (Froese and Pauly 2020).

Data analysis

The standard formula to calculate the relative abundance of taxa was applied to rabbitfish and other herbivorous fishes in the sampling site. Relative abundance (%RA) was calculated as:

$$\%RA = \frac{\text{Number of individuals per species}}{\text{Number of individuals of all species}} \times 100$$

Fish density was calculated by getting the number of individuals per unit area = n_i/A , where n_i is the total number of individuals of a species found in the transect, and A is the total length of two transects times (15×15 m) the width of vision (5 m) of the researcher during the FVC. The area was calculated based on the transect used, and the width of the area swam by the researcher from one end to the other.

The relative density was quantified using the number of individuals of a given species over the total density of all species. To analyze the relative density of rabbitfish and other herbivorous fish in the study area, the formula $D_i/\Sigma D$ was applied, where D_i is the density of a species A and ΣD is the density of all species

Minimum and maximum fish lengths for each species were estimated through observation during the FVC, with a minimum size set to 1 cm total length. Average length was used to estimate a biomass index (kg) of all species according to $B_i = L_i N_i / 1,000$ g (Taquet et al. 2007), where L_i is the mean length of the species i (in cm), N_i is the number of fish counted for the species i , and 1,000 is for the conversion of g to kg.

ANOVA was used to find differences in total weekly abundance during the 12 weeks of FVC and to compare shoot number length among treatments (full, partial, and open cages). Data were checked for the assumptions of ANOVA. Non-transformed data were checked for normality and Kolmogorov-Smirnov (KS) test for equal variance. When this violated the assumptions of ANOVA, data were fourth-root transformed and again checked for its normality. The FVC count data were also analyzed using one-way ANOVA to compare the abundance of the species during the 12 weeks of observation. When data showed significant differences, this was further explored by using *post hoc* Tukey test and Fisher's LSD.

Means that differed and those grouped together according to their means were recorded. A one-way ANOVA was also used to compare treatments and determine if there was variation between shoot length growths. Shoot length data were first explored and then check for violations of ANOVA assumptions. Then, if this did not satisfy the assumptions of ANOVA, a data transformation was used (e.g. fourth root transformation, \log_{10} transformation, or square root transformation). Furthermore, when data transformation did not work out, untransformed data were used because ANOVA can be robust to violations of the assumptions of ANOVA given large sample sizes (Quinn and Keough 2002).

In addition, initial and final shoot length measurements from treatments were also compared to determine differences using one-way ANOVA. Mood's median test was also used owing to the small number of replicates per treatment and two instances of counting, initial versus final. All statistical analyses were performed using Minitab version 17 (Minitab Inc., Pennsylvania, USA).

RESULTS

Species composition

A total of 13 fish species were found in the sampling site. These species were categorized into 6 families, namely: Siganidae (2), Labridae (4), Acanthuridae (1), Pomacentridae (3), Chaetodontidae (2), and Apogonidae (1).

First-level carnivores consuming benthic invertebrates

The feeding levels of the 13 species were classified based on their feeding habit. *Siganus fuscescens* (Siganidae), *Siganus guttatus* (Siganidae), and *Acanthurus triostegus* (Acanthuridae) grazed mainly on algal turfs and seagrasses. There were five other fish species classified as

omnivores: *Chaetodon auriga* (Chaetodontidae), *C. kleinii* (Chaetodontidae), *Plectroglyphidodon leucozonus* (Pomacentridae), *P. dickii* (Pomacentridae), and *Abudefduf vaigiensis* (Pomacentridae) which fed on algal turfs, benthic seaweeds, crustaceans, zooplanktons and finfish.

Second-level carnivores consuming fish

Halichoeres margaritaceus (Labridae), *H. hortulanus* (Labridae), *Thalassoma janseni* (Labridae), *Stethojulis bandanensis* (Labridae), and *Pristiapogon kallopterus* (Apogonidae) were classified as zooplanktivores mainly feeding on crustaceans, zooplanktons and zoobenthos.

Relative abundance and density of fishes

Among different fish species observed in the study site, *S. fuscescens* was the most abundant, with 499 individuals (mean = 41.76), followed by *S. guttatus* with 153 individuals (mean = 12.8), then *A. triostegus* with 127 individuals (mean = 10.63). Compared to all other fish species found in the study site, *T. janseni* was the least abundant fish species with only 13 individuals. These species were recorded for their feeding levels, whether an herbivore, carnivore or omnivore (Table 1).

The ANOVA result of the total weekly abundance of fish density in the study area showed no significant differences. However, a comparison of fish count in terms of the abundance of various fish species showed highly significant differences ($df = 12$, $MS = 2.88$, $F = 30.10$, $p < 0.001$). The *post hoc* analysis showed different means: *S. fuscescens* had the highest mean count (40.97) compared to all the other species, followed by *S. guttatus* (12.49), *A. triostegus*, and *P. kallopterus* (10.27 and 7.41), *A. vaigiensis* (5.92), *H. margaritaceus* (5.34), *P. leucozonus* (4.30), *C. auriga* (2.22), *P. dickii* (1.57), and *S. bandanensis* (1.31). Three species had similar fish count means: *H. hortulanus* (0.63), *C. kleinii* (0.52), and *T. janseni* (0.43).

Fish length and biomass index of fishes

The estimated fish length ranged from 5 to 12 cm. *H. hortulanus* and *S. bandanensis* had the highest estimated length (12 cm), followed by *S. fuscescens*, *S. guttatus*, *H. margaritaceus*, and *T. janseni* (10 cm) while *C. kleinii*, *P. leucozonus*, *P. dickii*, and *P. kallopterus* were the smallest (5 cm). The mean length of fish species was derived from the computation of minimum and maximum fish length with a range of 3.0 to 6.5 cm. In terms of their biomass index, *S. fuscescens* recorded the highest biomass with 2.47 kg, followed by *S. guttatus* with 0.84 kg, while *C. kleinii* had the lowest biomass obtained from their feeding activity with 0.05 kg.

Seagrass (*Thalassia hemprichii*) cover and shoot data

In the full cage, all shoot counts in each replicate increased in number from five to ten individual shoots. Some of these new individual shoots were shorter than the others in this treatment. In the second treatment, the partial cage, replicates one and two also increased in the number of shoots in the final counts, while replicates three and four decreased in the number of individual shoots in the final counts. However, in the open cage treatment, all individual shoot counts decreased in their number from five to ten individuals in the final count. The test showed that initial counts were not different between treatments as shown by Mood's median test: $X^2 = 2$, $df = 2$, $p = 0.368$; $FC = PC = OP$, but the final shoot counts showed significant differences ($X^2 = 8$, $df = 2$, $p = 0.018$; $FC > PC > OP$). Median values showed highest final shoot counts in the full cage (170 shoots) compared to the partial cage (156 shoots) and the open cage (38 shoots) (Figure 3 A). By using these median values, it was estimated that fish predation damage comparing full and partial cages was about 8%, while using average values this figure could be 10%. Although full and

Table 1. Relative abundance, density, relative density, fish length, biomass and trophic and feeding levels of fish species found in the study area.

Species	Relative abundance	Density (n/A)	Relative density ($D_i/\Sigma D$)	Fish length			Biomass index (kg)	Trophic level*	Feeding level*
				Mean	Max.	Min.			
<i>Siganus fuscescens</i>	41.76	83.17	0.42	5.5	10	1	2.47	2	Herbivore
<i>Siganus guttatus</i>	12.80	25.5	0.13	5.5	10	1	0.84	2	Herbivore
<i>Halichoeres margaritaceus</i>	5.61	11.17	0.06	5.5	10	1	0.37	> 3	Omnivore
<i>Halichoeres hortulanus</i>	1.51	3.00	0.02	6.5	12	1	0.12	> 3	Omnivore
<i>Thalassoma janseni</i>	1.09	2.17	0.01	5.5	10	1	0.07	3.1	Omnivore
<i>Stethojulis bandanensis</i>	1.84	3.67	0.02	6.5	12	1	0.14	3.2	Omnivore
<i>Acanthurus triostegus</i>	10.63	21.17	0.11	3.5	6	1	0.44	2	Herbivore
<i>Chaetodon auriga</i>	2.34	4.67	0.02	3.5	6	1	0.10	3.7	Omnivore
<i>Chaetodon kleinii</i>	1.34	2.67	0.01	3.0	5	1	0.05	3.5	Omnivore
<i>Plectroglyphidodon leucozonus</i>	4.52	9.00	0.05	3.0	5	1	0.16	2	Omnivore
<i>Plectroglyphidodon dickii</i>	2.18	4.33	0.02	3.0	5	1	0.08	3.7	Omnivore
<i>Abudefduf vaigiensis</i>	6.78	13.50	0.07	4.5	8	1	0.36	2.6	Omnivore
<i>Pristiapogon kallopterus</i>	7.62	15.17	0.08	3.0	5	1	0.27	3.6	Planktivore

*Taken from Froese and Pauly 2020.

open cages can be compared, there is a high probability that predation in the open cage is not only carried out by fish, but also by other invertebrates. Nonetheless, comparison values between the full cage and open cage using the median count will put that to 77%, while if average values are used, that number could be 22%.

Among mean shoot length treatments, the full cage recorded the highest mean length (16.75 cm), followed by the partial cage treatment (11.81 cm), and the open cage with the shortest length (8.86 cm). In terms of replicates, full cage replicate two registered the longest length at 16.86 cm, followed by replicate one with a length of 16.82 cm, and then replicate four with a length of 16.76 cm and followed by replicate three with the shortest length measured at 16.54 cm. In the partial cage, replicate two was the longest, measured at

12.13 cm, followed by replicate four at 11.88 cm, then replicate one with a length of 11.68 cm, while replicate three recorded the shortest length, measured at 11.57 cm. In the open cage, replicate four was the longest (8.96 cm), followed by replicate one (8.92 cm), then replicate three (8.88 cm), and last was replicate four (8.71 cm) (Figure 3 B).

Highly significant ($p < 0.001$) results from weekly shoot length of *T. hemprichii* from the full, partial and open cages were observed. The shoot length measured in the full and partial cages exhibited a weekly increased since the initial week. The open cage recorded the opposite, and the plotted chart showed a decreasing trend in growth.

Comparison of the initial shoot length of *T. hemprichii* among treatments showed differences, with the full cage recording initial mean

values of 9.97 cm, followed by the open cage with a value of 9.93 cm and the partial cage with 9.74 cm. The *post hoc* Fisher's pairwise compar-

ison revealed that shoot lengths in the full and open cages were similar but the partial cage was lower, e.g. OP = FC > PC (df = 2, MS = 0.6, $F = 3.41$, $p = 0.036$) (Table 2).

Results of the final assessment of shoot length of *T. hemprichii* in all cages were highly significant. The *post hoc* analysis using Fisher's pairwise comparison showed that the full cage treatment obtained the highest shoot length (22.24 cm) compared to the partial (13.49 cm) and open cages (7.24 cm), e.g. FC > PC > OP (df = 2, MS = 2271.54, $F = 3476.46$, $p < 0.001$) (Table 2).

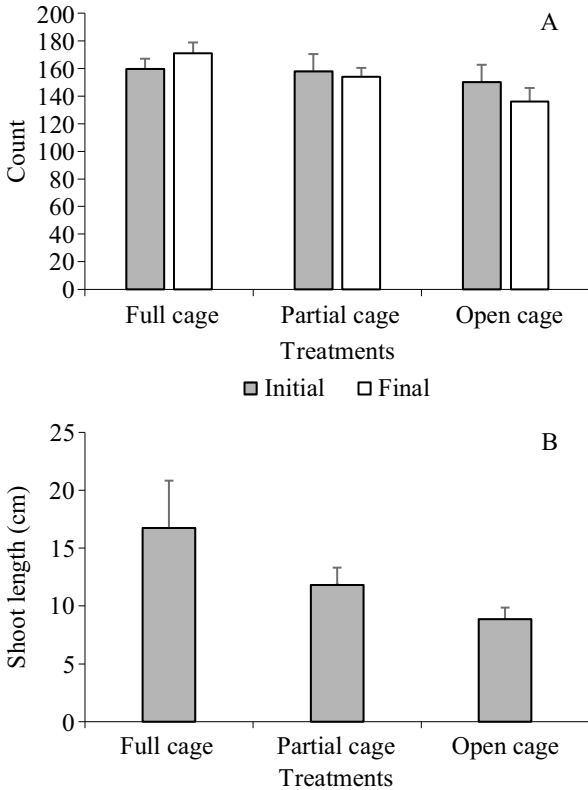


Figure 3. Initial and final mean shoot counts of seagrass (A) and mean shoot length measurements of *Thalassia hemprichii* under different treatments (B).

DISCUSSION

A total of 13 marine fish species belonging to six families were observed in the area. Fish species commonly occur in seagrass beds in the Philippines (Salita et al. 2003). Many of these fish species use the seagrass beds either throughout their life (residents) or only as a nursery for younger individuals of the species (Nagelkerken et al. 2000). Members of the Family Labridae and Siganidae are frequently observed in seagrass beds not only in the local area but also in other parts of the country (Salita et al. 2003). The Genus *Siganus* is herbivorous and considered resident of seagrass beds (Randall and Kulbicki

Table 2. ANOVA results on weekly shoot length increase of *Thalassia hemprichii* in full cage, partial cage, open cage, and for all treatments.

	Full cage			Partial cage		Open cage		All treatments				
	df	MS	F^*	MS	F^*	MS	F^*	df	MS	F^{**}	MS	F^*
Weeks	11	726.71	1,633.1	96.85	140.28	42.80	181.99	2	0.60	3.41	2,271.54	3,476.46
Error	468	0.45		0.69		0.24		117	0.18		0.65	
Total	479							119				

* $p < 0.01$; ** $p < 0.5$.

2005; Jumawan-Nanual and Metillo 2008; Metillo et al. 2016) which explain its high density. Herbivores may play an essential role in mitigating impacts of increased N_2 as nutrient by interacting with primary productivity (Gruner et al. 2008). Furthermore, herbivores can positively impact on seagrass by consuming nutrient-rich algae (McSkimming et al. 2015). A frequent natural disturbance in seagrass meadows is herbivory, which shows that grazing generally reduces seagrass growth (Hughes et al. 2004). Intensive grazers can severely reduce seagrass production and distribution to the point of degradation in meadows, often known as overgrazing event (Peterson et al. 2002).

Rabbitfish in the area is a crucial species in determining the structure and resilience of seagrass aquatic ecosystems (Burkepile and Hay 2007). Understanding and quantifying the impact of herbivores on the ecosystem is, therefore, fundamental to our ability to devise strategies for protecting these ecosystems (Mumby et al. 2006). The most abundant fish species in this study were *S. guttatus* and *S. fuscescens*. Significant differences in length and number of *T. hemprichii* shoots in the full cage and open cage set-ups were attributable to lesser grazing pressure due to protection offered by the cage from herbivores. Restricting the access of herbivorous fish in the full cage allowed the seagrass to increase in shoot number and length. Alcoverro and Mariani (2000) observed lesser fish grazing in seagrass beds with fewer herbivorous fish, a scenario in which the full cage treatment emulates. Significant differences in *T. hemprichii* shoot count and length measurement from week 1 to 12 showed evidence of high grazing intensity of rabbitfish in all replicates of treatment cages in the sampling area. This grazing was observed closely in the slow growth of *T. hemprichii* particularly in partial and open cages.

While the importance of grazing in algal-dominated communities is well documented (Macusi 2010), the premise that ingesting living seagrass

biomass is infrequent and inconsequential remains a central tenet of current food web theory (Cebrian 2002). This idea has been so widely accepted that it is found in most marine ecology textbooks in North America. As an example, Levinton (2001) asserts in his widely used marine biology textbook that ‘one of the most interesting aspects of seagrasses is their apparent unpalatability to grazers’. Our observation of the impact of rabbitfish grazing, which affected the growth and cover of *T. hemprichii* in the control treatment (partial cage) and the open cage (marked grazing plot) compared to the full cage, contradicts this statement. The result of higher shoot count and longer shoots found in the full cage supports the hypothesis that the higher density of rabbitfish in the area potentially reduced the chance for higher growth of *T. hemprichii* in the partial and open cages.

In Inner Ambon Bay, white-spotted rabbitfish *Siganus canaliculatus* correlates with available seagrass meadows (Latuconsina et al. 2013; 2020a). This fish matures at six months of age, has a high exploitation and mortality rate (Latuconsina et al. 2020b), and gives a high grazing pressure on seagrasses (Irawan and Nganro 2016; Noya et al. 2016). *S. canaliculatus* also affects seagrass vegetation, as it is necessary for its growth and reproductive biology (Madduppa et al. 2019). Rabbitfishes are tropical herbivorous fish species and highly dependent on benthic algae and seagrasses (Simora et al. 2015).

CONCLUSIONS

This study contributes to the rising evidence that grazing activity of rabbitfish on seagrass beds strongly influences the growth of *T. hemprichii*. Of the various fish species found in the study area, two species of rabbitfish (*S. fuscescence* and *S. guttatus*) were the most abundant. These species were observed engaging in intense grazing activity, which strongly influenced the growth of sea-

grass. The hypothesis that rabbitfish grazing on *T. hemprichii* beds is a significant cause of decreased shoot cover and length in the study area is strongly supported by our findings.

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