

ELASTICITY ANALYSIS OF THE GRAZING AND DETRITAL PATHWAYS IN A SHALLOW PHILIPPINE SEAGRASS MEADOW

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ABSTRACT

Ecotrophic efficiency (*EE*) is an estimate of the proportion of production that is utilized by the next trophic level through direct predation or fishing or exported out of the ecosystem. In seagrass systems, analysis of *EE* provides crucial information on how biomass, when used or lost in biological functioning, affects the higher trophic levels via death or grazing relative to the energy lost via decomposition (i.e., Flow to the detritus, *FTD*) and exports to another ecosystem (i.e., Sum of all exports, *SAE*). In this study, projections on the effect of change in the *EE* of functional groups in seagrass systems due to the alteration of biomass were established heuristically using Elasticity Analysis. Using a previously constructed Ecopath model for a shallow Philippine seagrass meadow, the simulations of altering the biomass of seagrasses and their grazers were done to determine the change in *EE*, *FTD*, and *SAE*, thereby generating information on the dynamics of the grazing and detrital pathways in the seagrass ecosystem. Results showed the effects of biomass increase and decrease of grazers (herbivorous gastropods, *Triploneustes gratilla*, and polychaetes). If the grazers' biomass increases, their *EE* tends to decrease, and biomass accumulation tends to increase. This implies that a fraction of their production used in the system is reduced even if their predators' density and feeding rate are still constant. In addition, the *EE* of seagrasses tends to increase, leading to a decrease in biomass accumulation at the primary producers' trophic level. Lastly, the *EE* of detritus decreased because the *FTD* and *SAE* of its major contributors (the seagrasses) had also decreased. The findings contribute to the ongoing analysis of the role of herbivores versus detritivores in the energetics of seagrass habitats.

Keywords: biomass elasticity, ecotrophic efficiency, flow to detritus, grazing, seagrass, trophic

INTRODUCTION

The two major food chains in any ecosystem, namely, grazing and detrital or decomposer food chains, vary primarily in terms of energy source: autotrophs and living plant materials for the former and the detritus or dead organic matter for the latter. Furthermore, the directional flow of net primary production characterizes the grazing pathway (Attayde and Ripa, 2008). In contrast with the grazing pathway, the detrital pathway has a unidirectional flow that dominates, wherein the recycling of detritus eventually results in inputs at the food chain (Smith and Smith, 2009). Odum (1956) first presented the y-shaped model in which the

energy flow in the grazing and detritus food chain are sharply separated. Lindeman and Lindeman (2007), in a comprehensive trophic and energy flow model of ecosystems, presented an integrated ecological interaction of the grazing and detrital pathways. In seagrasses, the detrital food chain relies on input from waste materials and decaying matter from the grazing food chain. The two food chains are also linked via the process of predation. Aside from the breaking down of dead organic matter, decomposer organisms are also food for numerous other animals (Hearne *et al.* 2019; Johnson *et al.* 2019; Breithaupt *et al.* 2019; Boncagni *et al.* 2019; Johnson *et al.* 2020).

Quantifying the flux of energy through the seagrass ecosystem requires evaluating the consumption, ingestion, assimilation, respiration, and production at each trophic level

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(Du *et al.* 2020). Within the food webs in the seagrass system, the trophic level represents seagrasses and their consumers' position. Seagrass biomass enters the second trophic level by either secondary production through grazing, recycling biomass by the detrital loops, and feeding on phytoplankton by certain species as early-stage larvae. Biomass outputs happen at all trophic levels involving predation and mortalities (Blomberg *et al.* 2014; Gloeckner and Luczkovich, 2008).

Following Lindeman's (1942), and Lindeman and Lindeman (2007) tropho-dynamics concept, this study aims to examine the trophic levels of the seagrasses and their consumers and how they are leveraged by the various scenarios of increasing and decreasing biomass. Using a previously constructed model by Clores and

Cuesta (2019), such a model was subjected to elasticity analysis by focusing on the

seagrasses (producers) and the benthic invertebrates (consumers). The model's scope reflects the total size of the ecosystem, thereby reflecting the properties of the system, particularly the extent of the trophic structure (Gascuel 2005; Heyman *et al.* 2014). The modeling outputs are the Ecotrophic Efficiency (EE) and Flow to Detritus. The model subjected to elasticity analysis concentrated on the grazing effects on the seagrasses by the invertebrates and almost trifling recreational fisheries.

MATERIALS AND METHODS

The study site is Sabitang-Laya Island located at Maqueda Channel, Caramoan Peninsula, Philippines (13051'56.22" N, 123057'35.20" E) (Fig 1).

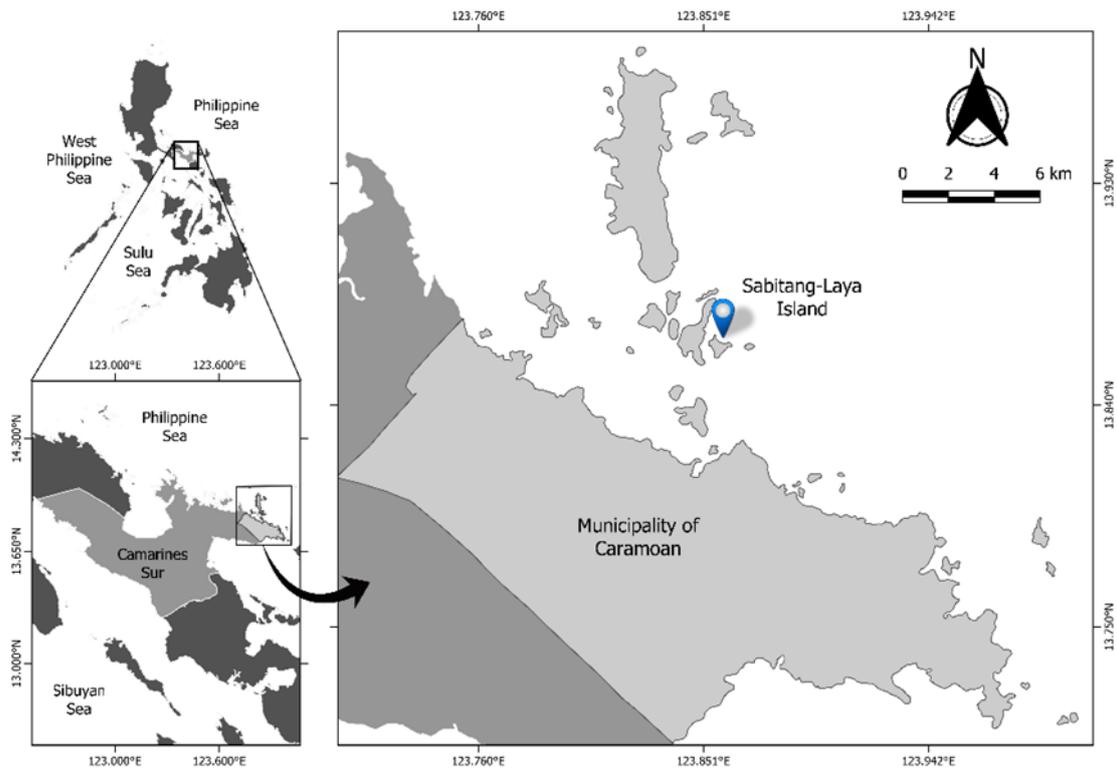


Figure 1 Study area in Maqueda Channel, Caramoan Peninsula, Philippines

A trophic model for the seagrass meadow of this island was constructed using Ecopath with Ecosim (*EwE*) version 6.6.3 (Christensen, Waters, and Pauly, 2000) and was already reported by Clores and Cuesta, 2019. The model used an estimate of 22 functional groups' biomass to construct a food web model that described the trophic structure and linkages, and energy flows in the seagrass system (Clore and Cuesta, 2019) (Table 1 and Figure 2). *EwE* required the following: Biomass (*B*) of functional groups, ratios of Productivity:

Biomass (P/B), Consumption: Biomass (Q/B), proportion of unconsumed food, or other collective variables (e.g., Gross food conversion Efficiency (GE as PB/QB) (Christensen *et al.* 2000). Ecotrophic Efficiency (EE), estimated with *EwE*, is the proportion of any of the functional groups' production assimilated inside the, and is the proportion of production taken by the predators or are transported out from the system (Ullah *et al.* 2012). In this study, the EE was subjected to elasticity analysis.

Table 1 Basic inputs and estimated outputs (bold) of the Sabitang-Laya Is., Maqueda Channel) seagrass system model

| Group name | TL | B (t km ⁻²) | P/B (yr ⁻¹) | Q/B (yr ⁻¹) | EE | P/Q | Predat Mort | Other mort | Flow to detritus |
|----------------------------|-------------|----------------------------|----------------------------|----------------------------|-------------|-------------|----------------|---------------|------------------------|
| 1 Carnivorous gastropods | 3.04 | 2.35 | 2.80 | 5.60 | 0.96 | 0.50 | 2.69 | 0.12 | 1.45 |
| 2 <i>P. nodosus</i> | 3.02 | 12.89 | 0.52 | 2.60 | 0.31 | 0.20 | 0.16 | 0.36 | 5.67 |
| 3 Crustaceans | 2.96 | 1.85 | 8.40 | 28.00 | 0.99 | 0.30 | 8.37 | 0.03 | 5.21 |
| 4 <i>Diadema spp.</i> | 2.86 | 0.99 | 7.51 | 25.00 | 0.95 | 0.30 | 7.13 | 0.38 | 2.67 |
| 5 Sand dollar | 2.60 | 0.27 | 10.00 | 50.00 | 0.87 | 0.20 | 8.86 | 1.14 | 1.50 |
| 6 Nematodes | 2.47 | 2.94 | 10.00 | 50.00 | 0.79 | 0.20 | 7.85 | 2.15 | 17.86 |
| 7 Ophiuroids | 2.46 | 0.80 | 8.63 | 34.52 | 0.97 | 0.25 | 8.36 | 0.27 | 2.87 |
| 8 Pelecypods | 2.26 | 25.03 | 2.06 | 6.86 | 0.99 | 0.30 | 2.04 | 0.02 | 17.46 |
| 9 Polychaetes | 2.33 | 4.20 | 1.63 | 12.46 | 0.54 | 0.13 | 0.89 | 0.74 | 6.80 |
| 10 <i>S. maculata</i> | 2.22 | 2.09 | 4.45 | 22.25 | 0.55 | 0.20 | 2.44 | 2.02 | 6.76 |
| 11 Other <i>Holothuria</i> | 2.22 | 0.30 | 4.45 | 22.25 | 0.74 | 0.20 | 3.30 | 1.15 | 0.84 |
| 12 Zooplankton | 2.11 | 2.87 | 67.00 | 192.0 | 0.68 | 0.35 | 45.69 | 21.31 | 85.68 |
| 13 Herbivorous gastropods | 2.00 | 3.11 | 2.80 | 5.60 | 0.90 | 0.50 | 2.51 | 0.29 | 2.19 |
| 14 <i>T. gratilla</i> | 2.00 | 3.77 | 4.47 | 25.00 | 0.33 | 0.18 | 1.50 | 2.98 | 15.03 |
| 15 <i>S. isoetifolium</i> | 1.00 | 178.5 | 8.43 | --- | 0.07 | --- | 0.06 | 8.37 | 747.1 |
| 16 <i>H. uninervis</i> | 1.00 | 262.3 | 8.43 | --- | 0.01 | --- | 0.05 | 8.38 | 1099 |
| 17 <i>H. minor</i> | 1.00 | 10.24 | 8.43 | --- | 0.15 | --- | 1.30 | 7.13 | 36.51 |
| 18 <i>C. serrulata</i> | 1.00 | 1424 | 8.43 | --- | 0.01 | --- | 0.03 | 8.40 | 5983 |
| 19 <i>C. rotundata</i> | 1.00 | 269.6 | 8.43 | --- | 0.01 | --- | 0.08 | 8.35 | 1125 |
| 20 <i>E. acoroides</i> | 1.00 | 5501 | 8.43 | --- | 0.01 | --- | 0.00 | 8.43 | 23181 |
| 21 Phytoplankton | 1.00 | 48.00 | 30.42 | --- | 0.38 | --- | 11.79 | 18.63 | 447.0 |
| 22 Detritus | 1.00 | 19.80 | --- | --- | 0.01 | --- | --- | --- | --- |

Notes: TL = trophic level; B = biomass (t wet weight (WW) km⁻²); P/B = production/biomass ratio or the instantaneous rate of total mortality (Z) (yr⁻¹); Q/B = consumption/biomass ratio or consumption rate (yr⁻¹); EE = ecotrophic efficiency, P/Q = production/consumption ratio or gross efficiency; Predat = predator; mort = mortality; Flow to detritus in t WW km⁻² yr⁻¹.

Elasticity analysis (Caswell, 2001) of the Ecopath model, a form of sensitivity analysis, was done to determine the effects of biomass alterations of functional groups in seagrass systems. The analysis allowed the simulation of various forms of disturbances by using small proportional changes in the parameter values. Elasticity is defined by Barbeau and Caswell (1999) as:

$$E_p (\%) 100 = \frac{X_p - X_o}{X_o}$$

where:

- $E_p (\%)$ = elasticity of the yield to % rise of parameter p
- X_o = yield of the original model
- X_p = yield of the model with a change in parameter p

RESULTS AND DISCUSSION

The Sabitang-laya seagrass model identified three functional groups in the seagrass system to be subjected to elasticity analysis: important grazers, *Triploneustes gratilla*, herbivorous gastropods, and polychaetes. The seagrass system's impacts were explored by conducting

an elasticity analysis that entailed altering (i.e., increasing and decreasing) their biomass.

The results of the elasticity analysis done on the seagrass model showed that much of the flows to detritus were contributed by the seagrasses (Figure 2). But in general, if the biomass of grazers increased, the flow to detritus also decreased, suggesting that much of the seagrass material goes to the grazing pathway. An overall result of elasticity analysis was shown in Figure 3. If the density and biomass of grazers: *T. gratilla*, herbivorous gastropods, and polychaetes increased, their *EE* decreased. This observation indicates that a fraction of their production used in the system reduces, this is despite that their predators' density and feeding rate are still constant. Also, there is increased biomass accumulation at the grazers' trophic level. When grazing is intense, the *EE* of seagrasses increased because of the high consumption of their production in the system due to grazing. This eventually decreases the biomass accumulation at the primary producers' trophic level. Furthermore, since much of the seagrass materials goes to the grazing pathway, the *FTD* from them decreased. Lastly, the *EE* of detritus decreased because the flow into the detrital pool of its major contributors (the seagrasses) had also decreased.

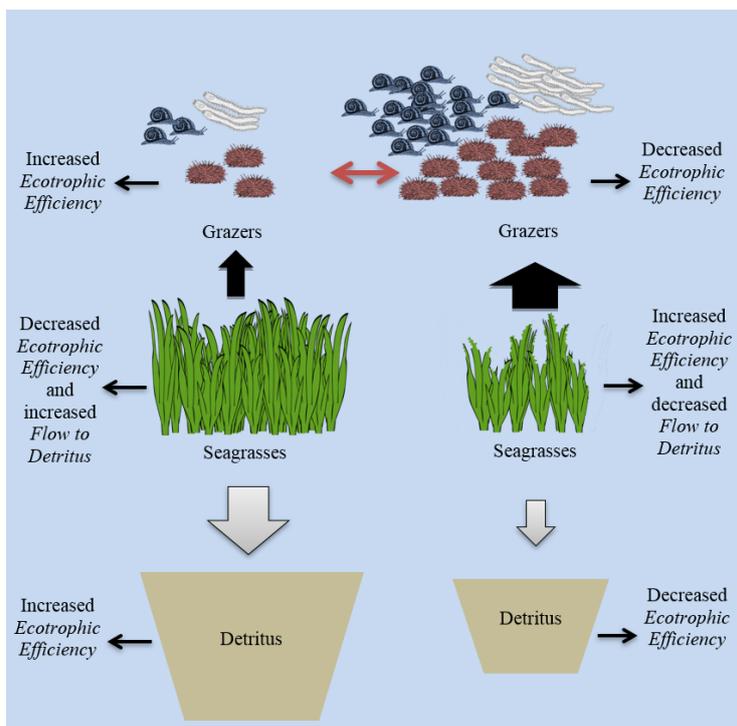


Figure 2 Simplified representation of the grazing scenarios effects of biomass increase and decrease of grazers (herbivorous gastropods, *Triploneustes gratilla* and polychaetes) on a shallow Philippine seagrass systems

Projections showed that if the biomass of grazers (polychaetes, herbivorous gastropods, *Tripneustes gratilla*) increased under steady-state assumptions, their Ecotrophic Efficiency (*EE*) decreased, and flow to detritus (*FTD*) increased. For example, if the biomass of *T. gratilla* decreased by 99%, their *EE* increased by almost 30% while their ‘flow to detritus’ (*FTD*) increased to about 60 tons/km²/year. This finding means that when grazers become abundant in the seagrass system, their biomass accumulates and enters the detrital pool when they die (Figures 3).

Furthermore, if the biomass of grazers (polychaetes, herbivorous gastropods, and *T. gratilla*) in the seagrass system increased, the *EE*

of seagrasses had relatively increased also, suggesting that a fraction of the production of seagrass was used in the system or passed up the food web (Fig 4). However, the *FTD* from the seagrasses almost remains unchanged, indicating that their biomass goes to the grazing pathway (Fig 5). Grazers also tend to consume the seagrasses *Cymodocea serrulata*, *Syringodium isoetifolium*, *Halodule uninervis* and *C. rotundata*, suggesting intense utilization of these seagrasses through grazing. The low *EE* of *E. acoroides*, despite the increasing biomass of grazers, suggests that this seagrass group was underexploited or not favored by the grazers; hence their supply exceeded demand, and much of this excess production went to detritus (Fig 4).

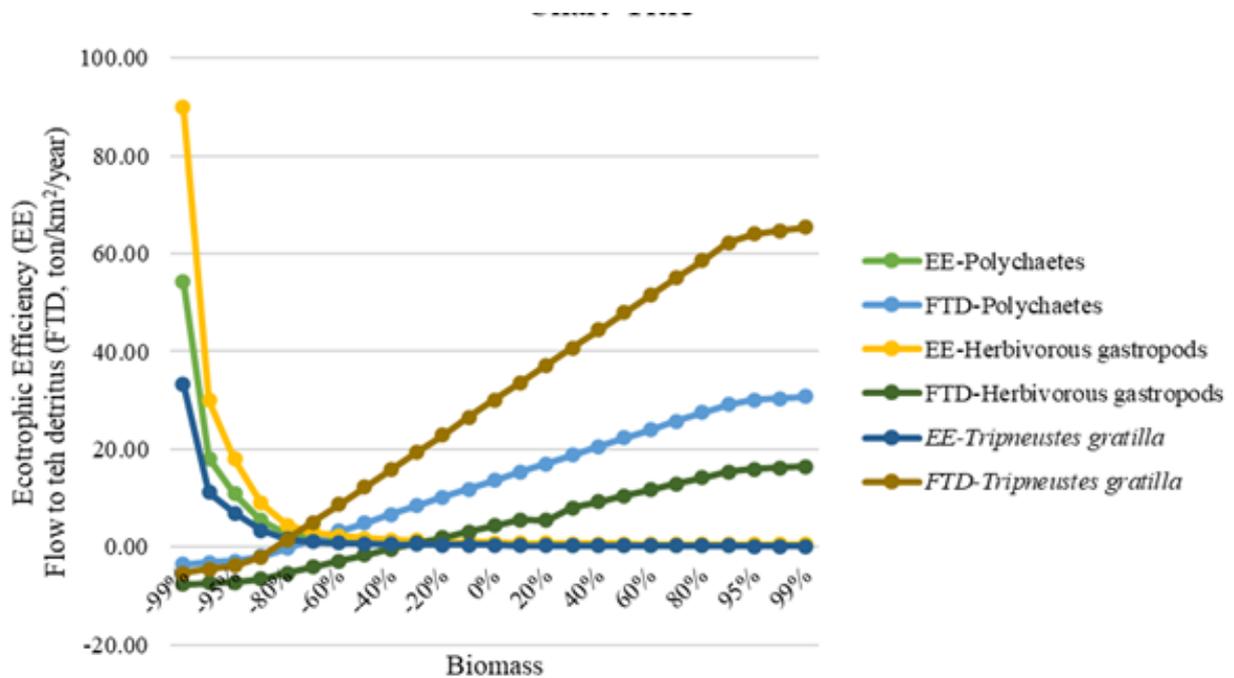


Figure 3 Projected Ecotrophic Efficiency (*EE*) and ‘flow to detritus’ (*FTD*, ton/km²/year) of the seagrass grazers as their biomass decrease or increase

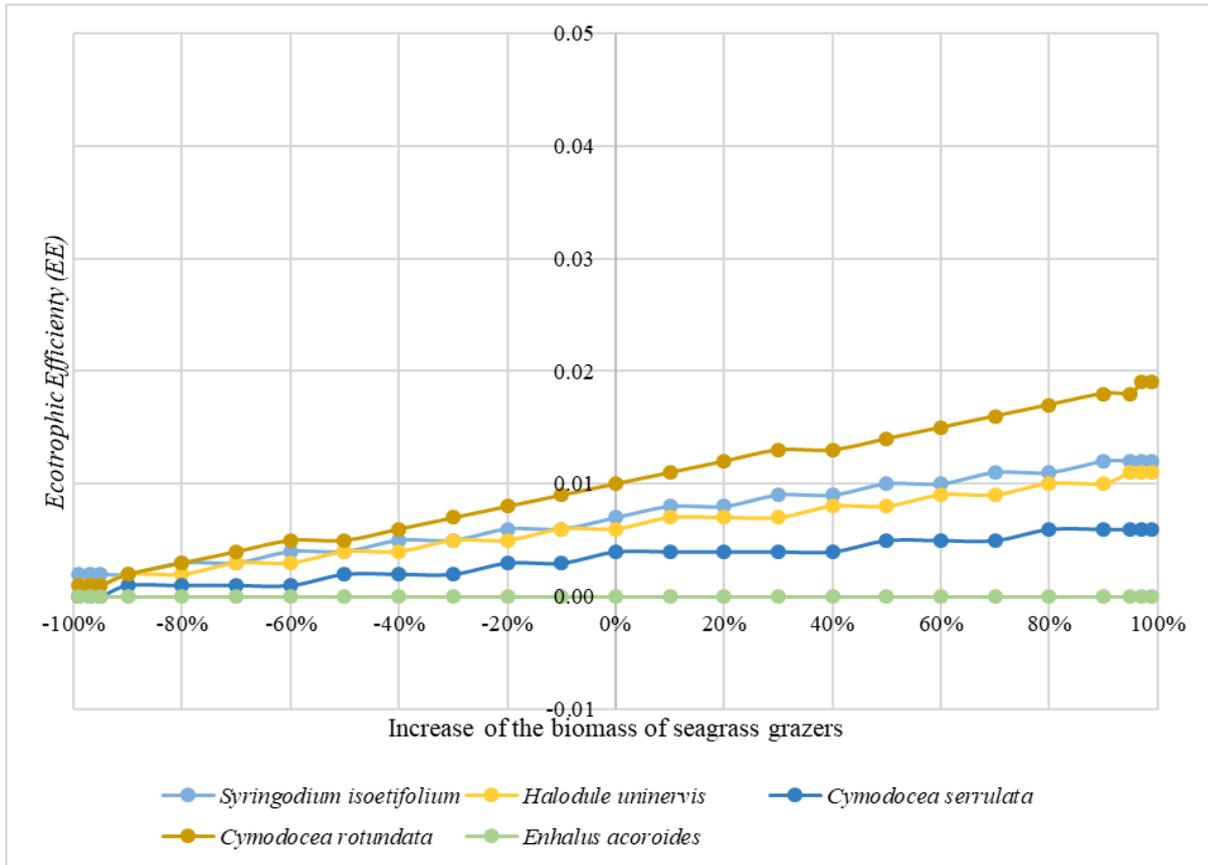


Figure 4 Projected change in the Ecotrophic Efficiency (EE) of seagrasses as the biomass of their grazers (Polychaetes, herbivorous gastropods, and *Tripneustes gratilla*) is decreased or increased

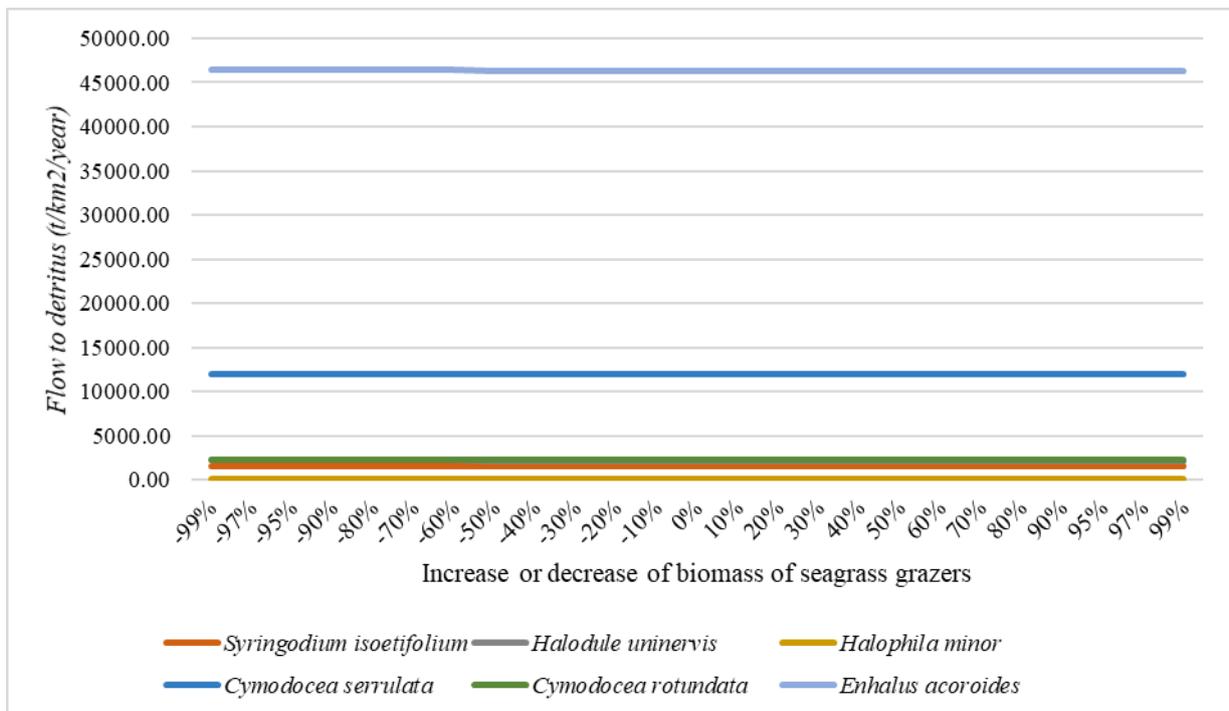


Figure 5 Projected change in the Flow to the detritus (FTD, %) of seagrasses as the biomass of their grazers (Polychaetes, herbivorous gastropods, and *Tripneustes gratilla*) is decreased or increased

It was also revealed that, as the biomass of grazers increased, the *EE* of phytoplankton slightly increased, and their *FTD* remain unchanged. For instance, an increase in the biomass of grazers by 90% resulted in an increase of their *EE* by 0.20 (Figure 6).

The ‘sum of all exports’ (*SAE*) decreased as the biomasses of grazers increased. This means that an increase in grazer biomass leads to the consumption of all biomass that otherwise will be exported from the seagrass systems (Figure 7).

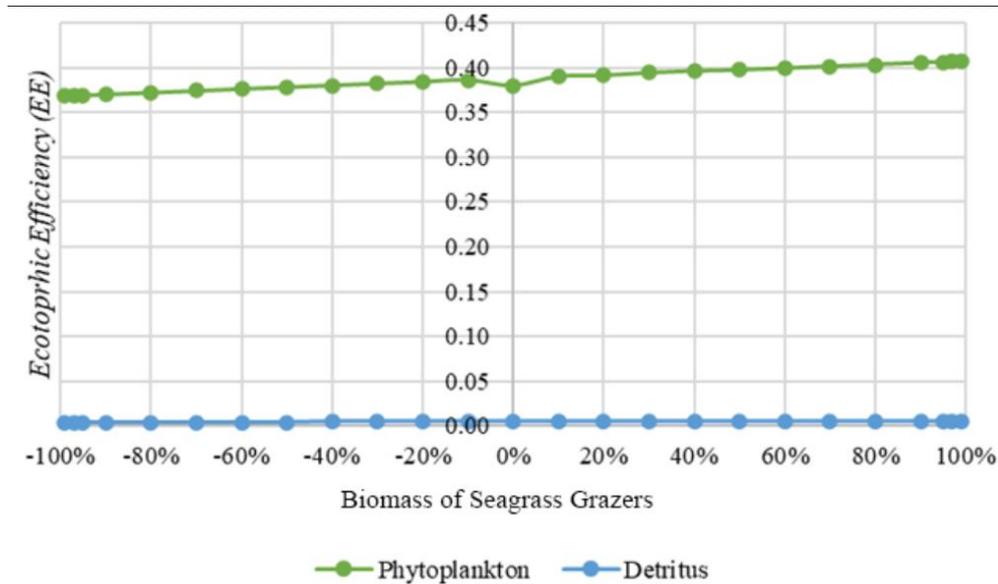


Figure 6 Projected change in the Ecotrophic Efficiency (*EE*) of phytoplankton and detritus as the biomass of seagrass grazers (polychaetes, herbivorous gastropods, and *Tripneustes gratilla*) decreased or increased

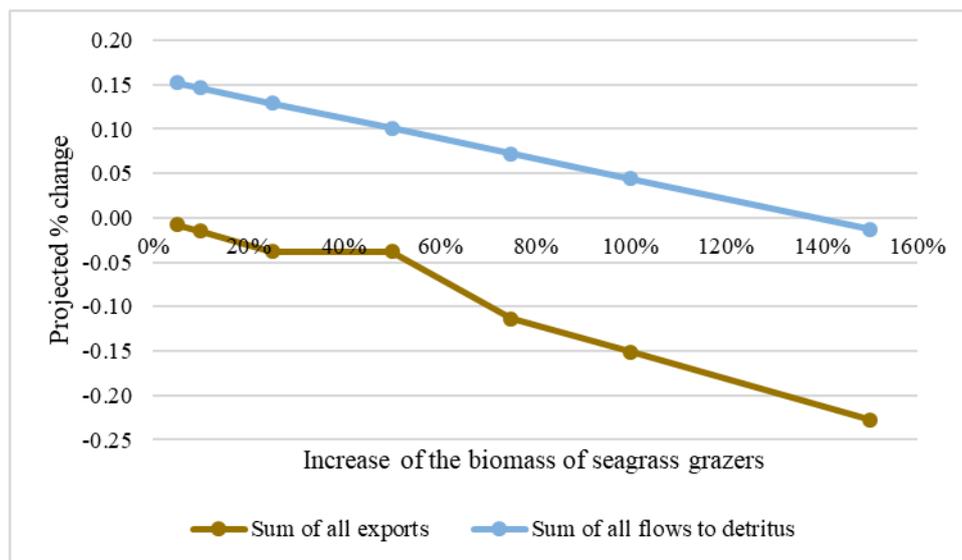


Figure 7 Projected change in the ‘Sum of all Exports’ (t/km²/year) and ‘Sum of All Flows into Detritus’ (t/km²/year) if the biomass of grazers is increased in the seagrass system.

Elasticity analysis of the seagrass model in Sabitang-Laya Island, Maqueda Channel, Caramoan Peninsula, a shallow seagrass meadow in the Philippines, was useful in predicting the impacts on the seagrass systems' energy flows. Fluctuations of the *EE* fractions and the *FTD* from the seagrasses as their grazers' biomass change was used to make projections. The projections showed that the seagrasses' energy/biomass proceeds to either the grazing or detrital pathways; It is expected that the energy/biomass of seagrasses will proceed to either the grazing or detrital pathways. However, if there are possible disturbances brought by overgrazing or overharvesting of grazers, the result is a restraint of these routes, or rerouting of the energy/biomass in the system. The overall flows in the system remain constant. It is expected that if an increase in the biomass of grazers (e.g., *T. gratilla*) happens, a large amount of energy/biomass from the seagrasses flows directly into the grazing pathway. This data indicates that grazers have a critical role in consuming seagrass material and biomass disposal due to grazing, which ultimately ends up in detrital food webs.

Projections also revealed that the seagrass that was discarded or not consumed by grazing might be exported from the seagrass systems. This could be through wave action and water currents. This export of biomass/energy to other ecosystems means that grazing on seagrass systems has an important role in seagrass beds' connectivity with other habitats like coral reefs and mangrove forests.

Elasticity analysis of the seagrass model in Bageing Bay, Sabitang-Laya Island showed increasing the biomass of seagrass grazers *T. gratilla*, polychaetes, and herbivorous gastropods in shallow Philippine seagrass meadows could lead to significant over-exploitation for resources of low trophic levels. The model became imbalanced as grazers' biomass decreased, hence the collapse of biomass affecting the functional biodiversity that may have substantial consequences, particularly on ecosystem resilience. In effect, the model simulations provided relevant theoretical bases to explain the distribution of biomass per trophic level and the impact of grazing on biomass distribution. Consequently, real observations should be compared with the

model results to validate virtual ecological modeled ecosystems.

The interactions of the essential components of the shallow Philippine seagrass systems, as shown by this seagrass meadow at Maqueda Channel, Caramoan Peninsula, and their influence in regulating the ecosystem are manifested by the steady-state models and elaborated by the Elasticity Analysis done in this study. The links from the seagrasses as producers to the invertebrates as intermediate consumers portrayed by the results contribute to a better understanding of how the ecosystem functions. The results of the elasticity analysis proved to be a practical tool for diagnosing and forecasting the impacts of overgrazing in seagrass systems commonly reported in the literature (Burnel *et al.* 2013; Yeager and Layman, 2011; Fourqurean *et al.* 2010) and the mechanistic interactions between predators and prey in seagrass meadows (Clore and Cuesta, 2019; Archer, Stoner, and Layman, 2015; Clores, Conde and Perez, 2020).

CONCLUSION

The findings of the current study contribute to the ongoing reevaluation of the role of herbivores and detritivores in the energetics of seagrass habitats. Clearly, when in steady-state conditions, as shown by the shallow Philippine seagrass meadow in this study, seagrass systems significantly contribute their seagrass production to the detrital pool. This result of the elasticity analysis of the seagrass trophic model analysis showed that when grazers become abundant, much of this production proceeds to the herbivory pathway. This research provides robust elasticity models of the dynamics of a seagrass system that offer relevant insights into the seagrass structure's energy dynamics. Analysis of this study's data showed that interactions are strong between the functional groups at the lower trophic levels in seagrass systems. In the context of conservation programs for seagrasses, top-down (detrital pathway) and bottom-up (grazing pathway) factors that control seagrass ecosystem structure and function should be considered. For instance, when grazing rates could surpass the seagrass growth rates (i.e., overgrazing), the

possible detrimental threats on the seagrass-associated ecosystem services should be mitigated.

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