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Trophic Models of Seagrass Ecosystems in Maqueda Channel, Caramoan Peninsula, Philippines

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Abstract

Steady-state trophic models were constructed using the Ecopath with Ecosim software to examine the general status, development trends, and functional integrity of three extensive seagrass meadows located in Maqueda Channel of Caramoan Peninsula, Southern Luzon Island, Philippines. The results show that the ecosystems are composed of 23-24 functional groups with effective trophic levels extending from 1.00 to 3.76. Mixed trophic impacts show that decrease in the biomass of grazers *Tripneustes gratilla* (collector urchin) had a positive impact on the biomass of seagrasses. On the other hand, a positive effect on the benthic groups is expected with an assumed decrease in the biomass of detritus and phytoplankton. Analysis of the flow network of organic matter and trophic efficiencies showed that flows were generally low for higher TLs but high for lower TLs (i.e., from TL 1 to IV. The ecosystems were found to be in mature and stable state based on the system statistics.

Keywords: Trophic models; Dynamic models; Seagrass systems; Caramoan Peninsula; Philippines

Introduction

Seagrass meadows, mangroves and coral reefs are ranked almost equally in terms of productivity [1-3] and provide numerous ecological goods and services [4]. These marine ecosystems are highly connected and support each other [5-6].

The seagrasses are important food source, habitats and refuges. Many populations of fish and invertebrates rely on seagrass meadows are their nursery grounds. Seagrass beds protect coastal habitats from extreme wave action, filters contaminants, and prevents sedimentation [1]. Seagrasses are classified as pioneer or

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climax species based on the successional series along with the ranges of disturbance. For instance, *Enhalus acoroides* (tape or broad blade seagrass) is the South-East Asian species that best survive heavy siltation [7] while the small pioneer species are the first to recolonize barren areas [8].

Tropical and subtropical waters are often characterized by mixed-species meadows. Co-existing seagrass species likely show strong interactions because of their similar architecture and resource requirements. The mixed communities represent steady-state communities in the tropics caused by small-scale disturbance and positive interactions. Recurrent disturbance appears to be a common feature essential to maintenance of many seagrass beds [8]. Sedimentary processes like sand waves [9] or biotic disturbance including grazing result in local perturbation that allows maintenance of fast-growing species to dominate [10-11].

The positive interactions observed in seagrass meadows involve the activity of species that modify the environment resulting in more suitable habitat to support plant life and growth of other species. For example, when several species are eliminated as a consequence of problematic resource use, as observed in many Philippine mixed seagrass meadows, the dominant species tend to facilitate the development of denser populations of the co-existing species [8]. This is due to the oxygenation of sediments preventing accumulation of toxins that cause seagrass mortality [7]. Moreover, moderate disturbance also allows maintenance of complex and diverse communities and spatial patterns, but intense disturbance drastically reduce the meadows [8].

It has been established that the increased level of abundance and diversity of animals found in seagrasses are due to the productivity of seagrasses, intricacy of food webs, and complexity of the physical structure of the meadows [12, 6]. Experiments showed that a large quantity of aboveground biomass of seagrass are consumed by grazers [13] yet most food webs of seagrass systems depicted that only a small amount of seagrass material are assimilated [14]. This could be explained by the high rate of excretion but low rate of assimilation of consumed seagrass material [15] as well as the temporal and spatial variability in the abundance and biomass of the seagrass-dwelling organisms [16].

Marine ecologists are still grappling with the unresolved knowledge issues about the energy flow depicted in seagrass food webs. There is still a need to examine how much of the production of seagrasses are incorporated into coastal food webs. Doing so could help understand better the seagrass ecosystem structure and the linkages that regulate the component processes that are crucial for effective management of marine resources [17]. Thus, a study that will elucidate through modelling tools the energy fluxes within the food web in seagrass systems is very timely. Such studies could provide a benchmark for future work on the ecosystem-based management approach and the basic knowledge about the key ecosystem metrics required in predicting ecosystem change to less sustainable and imbalanced state.

Unresolved critical gaps of knowledge between the contribution to seagrasses incorporated in into coastal food webs call for research using modelling approaches that when confirmed by future studies, would have insightful implications for our appreciation and understanding of ecosystem functioning and required ecosystem-based management thereto.

The objective of this study was to use trophic modelling as tool, specifically the Ecopath with Ecosim and Ecospace (EwE) modelling approach [18] to express and simulate trophic flows between various groups present in the seagrass system to answer the question:

What are the characteristics of the seagrass ecosystem structure (i.e., components, links, and transfer efficiencies) and the flows of energy and biomass in seagrass ecosystems? The models were utilized to examine the seagrass ecosystem structure and were used in analysing impacts on the biomass of organisms on the whole ecosystem. The results of the study provided information as basis for formulating management goals for seagrass systems. Policy makers, particularly the local government of Caramoan, may act on the research output to commence possible options for sustainable ecosystem interventions.

This study specifically aimed to estimate the basic building blocks of Ecopath models such as biomass, production, consumption rates, and diet for each defined functional group within a defined model area and time, to describe the impact of components, and to determine the level of development and state of maturity of the ecosystems.

Materials and methods

1) Research design and approach

Extensive computer-based work to run mass-balanced trophic modelling aided by the Ecopath with EwE software [19] was done to examine the trophic structure and development trends of the Caramoan seagrass ecosystems. This involved the estimation of the basic building blocks of Ecopath models such as biomass, production, consumption rates, and diet for each defined functional group. Field work was done to conduct standard sampling strategies on the functional groups in the seagrass ecosystems in three sampling locations.

2) Sample sites

Three locations at the Maqueda Channel, Caramoan Peninsula, Southern Luzon Island, Philippines where extensive seagrass beds exist were selected for the study. In each location, a seagrass meadow was selected as study site (Site 1: Cagbanilad Bay, 13038’14”N 123053’27”E, Site 2: Sabitang-laya Island, 13052’00”N 123051’32”E, and Site 3: Nipa Bay, 13057’51”N 123050’07”E) (Figure 1). Data collection was conducted from June 2017 to March 2018.

3) Sampling design

A 20-cm corer was used in estimating the biomass of seagrasses and seagrass-associated macroinvertebrates. The corer collected seagrasses with their substrate from an area of 0.031 m^2. In Site 1: Cagbanilad Bay, the samples were collected at five (5) transects oriented perpendicular to the shoreline extending to about 25 m offshore across the seagrass meadow. In Site 2: Sabitang Laya Island and Site 3: Nipa Bay, ten (10) 50-m transects were established in each of the two sites.

A total of 115 core samples (15 samples in Site 1, 50 samples each in Site 2 and 3) were collected from a point-to-point distance of ~5 m for Site and ~10 m for Sites 2 and 3, perpendicular to the shoreline during each sampling time. Collection of samples was done during the lowest tidal level for accuracy and ease of sampling, from at least 20-30 m starting from the landwards edge of the seagrass bed.

A fine mesh bag (0.5 to 1.0 mm mesh) was used to sieve the core samples while still in the field. After sorting the seagrass and fauna, these were identified to the lowest taxon, and then counted. Before obtaining the wet weights (g ww m^{-2}) of the seagrasses, these were scraped using a razor blade to remove the epiphytes. The sturdy beam trawl sampler that provided a sampling area of 50 m^2 was used to collect epifauna (Raz-Guzman and Grizzle, 2001). Ten sampling efforts were done at daytime for diurnal fauna and another ten at night time for nocturnal fauna. The total wet weight biomass in g ww m^{-2} of each sample was converted to t km^{-2}.

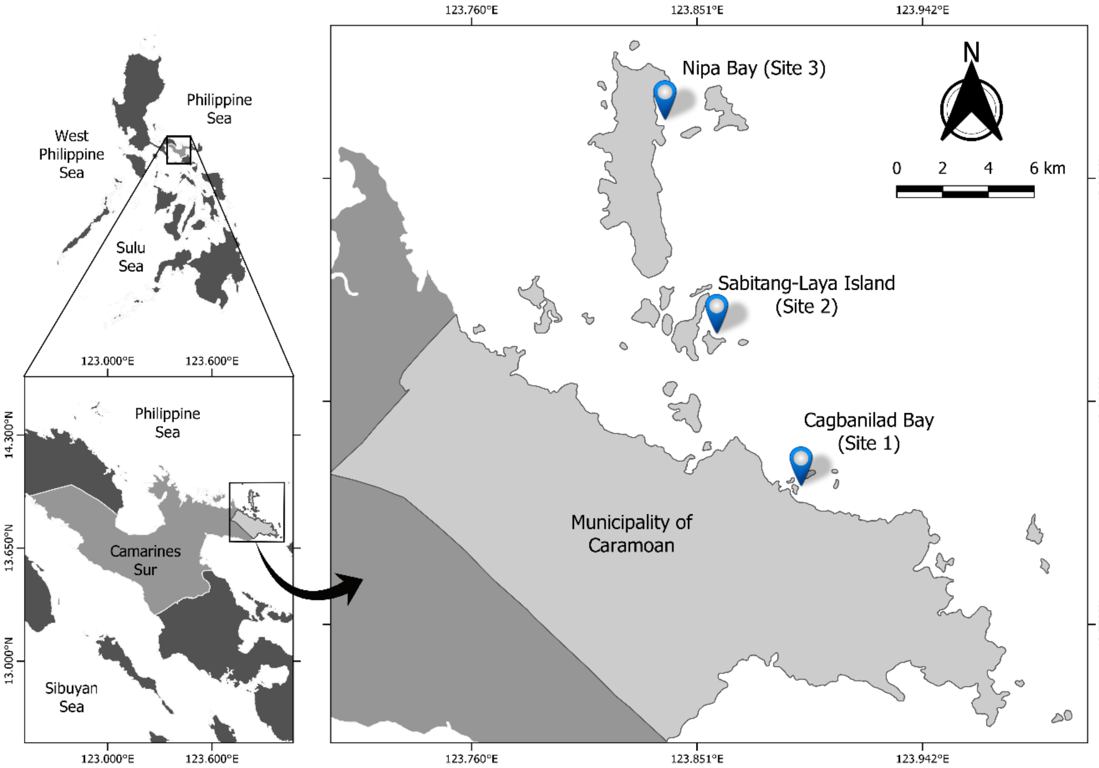

Figure 1 Sampling sites: Cagbanilad Bay (Site 1), Sabitang-Laya Island (Site 2) and Nipa Bay (Site 3) in Maqueda Channel, Caramoan Peninsula.

4) Modelling approach

The models for the three seagrass meadows were constructed using Ecopath with EwE version 6.2 [19]. The Ecopath food web models were constructed with biomass estimations of 23 to 24 trophic groups and their prey and predators to determine an instantaneous mass balance description of the seagrass food web structure and linkages.

No data on the diet of invertebrates in the study sites was available, hence diet items of these functional groups were based on the literature [20-22]. Diet compositions were estimated based on the relative abundance of each prey in the study area. Moreover, if reasonably applicable, the P/B (production/ biomass ratio for functional group) and Q/B (the ratio of the consumption to biomass for predator) of certain marine organisms were derived from values reported from various coastal ecosystems [23-27] (see Supplementary Material 1).

Estimates of Biomass (B) per compartment were from actual field data, but most of the value of other parameters such as Productivity: Biomass (P/B), Consumption: Biomass (Q/B), fraction of unassimilated food, and/or some combined variable (e.g. Gross food conversion Efficiency (GE as PB/QB), were based on published literature. Biomass and P/B of phytoplankton were based on Campos' [29] derivation of initial estimates for phytoplankton using mean primary rates for Pacific shelf areas (=0.52 g C m^{-2} d^{-1}, Mann, 1982). P/B ratio of seagrasses was based on Aliño et al.'s [23] initial estimates for seagrasses utilizing estimates of Fortes [30] of seagrass biomass (61.7 g organic matter m^{-2}) and productivity (1.4 g C m^{-2} d^{-2}). This is consistent with the notion that P/B ratio provides a better indication of energy transfer between trophic levels than instantaneous measures of biomass. Populations of large, long-lived seagrass have a greater biomass but lower production than the plankton, hence P/B ratio is relatively low for seagrasses (low production, high biomass) and high for phytoplankton (high production, low biomass).

Probable diet and life history characteristics were used as bases for the living compartments of taxa. For instance, for gastropod families known to be coral, algae and seagrass-eaters [31], their diet was estimated to be composed of 10% of each of the seagrass species.

Gut content analysis was done to determine the diet composition of sea urchin *T. gratilla* [32]. The diet of asteroid *Proteroaster nodosus* (horned sea star or chocolate chip sea star) was estimated based on literature that they prey on polychaetes, bivalves, gastropods, and other large invertebrates [33]. Other trophic models and literature [34] were used for the diet composition of other invertebrate groups.

Biomass, P/B, Q/B ratios, and diet composition were entered as basic inputs to EwE while biomass accumulation was set as zero. P/Q ratio and Ecotrophic Efficiency (EE) were estimated by the software. EE is the portion of the production of a group that is consumed within the system and is the portion of production exported or consumed by predators [35]. Trophic levels are part of the calculated results. The diet compositions of groups were checked if the outputs differ from the anticipated level.

Initial models were not balanced because the EEs of some functional were higher than 1 suggesting that their demand was very high [35-36]. Manual adjustments of the input parameters, such as biomass and diet composition were done to ensure that EE is less than 1 to balance the model. This is to ensure that at the end of one year there is excess biomass that could accrue or transfer from the system or lose by mortality [36]. Trophic models were finally balanced after integrating all the basic inputs and manual adjustments of biomass.

The functional groups which showed EEs greater than 1 were suspected to have underestimated biomass using the beam trawl net sampling tool, hence their biomasses were adjusted based on available literature (Table 1). In the succeeding model runs, the EEs of some functional groups, such as *P. nodosus*, *Diadema* spp. (long-spined sea urchins), pelecypods, *Synapta maculata* (spotted worm sea cucumber), and other holothurians, were still more than 1. The models were still imbalanced, thus their P/Bs were adjusted, and as a final step, their biomasses were instead manually adjusted by gradually increasing or decreasing the values until the EE is less than 1.

5) Data analysis

The first set of analysis for the Ecopath models of the seagrass systems is the structural analysis of the food webs which is based on all flows and biomasses that can be depicted in a single flow diagram constructed by Ecopath. The size of the circles is relative to biomass for each group. Circles are placed on the Y-axis based on the trophic level. The figure shows the aggregation of the functional groups represented as discrete trophic levels, and the estimation of the distribution of biomass and transfer efficiencies among trophic levels. The figure can indicate the following: (i) main paths in the ecosystem, (ii) the degree of importance of detrital and grazing food chains in the ecosystem, (iii) main sources for flow to detritus, and (iv) where most a functional group was a main food source leading to the occurrence of most of flow the in the trophic web.

The second analysis on the Ecopath models of the seagrass systems was done by using mixed trophic impact (MTI) routine [37]. MTI allows measurement of the impact of one functional group in the seagrass system on all the other groups after a short period of variation. Hence it can be considered as a form of sensitivity analysis for the seagrass models' input parameters. Network flows and ecosystem attributes based on the seagrass system models were used to compare the status of seagrass ecosystems and to characterize their scale, stability and maturity status. For instance, to characterize the ecosystem size and how proportion of matter that the system processes, as reflected by the respiratory flows, flows to detritus, sum of consumption, and exports, the Total System Throughput (TST) index was used [38]. An index of ecosystem maturity is the Total Biomass:TST ratio (B:TST) which is based on the fraction of biomass necessary to maintain one unit of flow. Two other indices of ecosystem maturity are the Net Primary Production: Respiration ratio (P:R) and the Net Primary Production:Total Biomass ratio (P:B) To describe the maturity and intricacy of the links inside the seagrass ecosystems, the values computed by Ecopth for System Omnivory Index (SOI) and Connectance Index (CI), which is anticipated to be higher in mature ecosystems was used. Overhead Index (OI) was used to identify which ecosystems is more stable and can recover faster after unexpected disturbances [40]. Cycling of matter that regulate the magnitude of flows in the seagrass systems was also analysed based on the Finn Cycling Index (FCI) [40-41]. Trophic transfer efficiency (TE) across trophic levels based on the proportion of the organic matter input was summarized the complex food web into a linear food chain using the Lindeman trophic analysis [41].

Results and discussion

1) The input and output parameters

Tables 1-3 show the basic parameterization results for seagrass models for the three study sites. The feeding matrices can be shown in Supplementary Material 2. The food web models provided the basic and informative descriptions of seagrass community showing their feeding relationships. The three seagrass systems in Maqueda Channel, Caramoan Peninsula are composed of 23-24 functional groups with effective trophic levels extending from 1.00 to 3.76. Thus, the seagrass system models were relatively similar in terms of the number of compartments or functional groups with other ecosystems: 18 in the fringing reefs in Nanwan Bay (Taiwan) [42], 17 in the seagrass-benthic ecosystems in Tongoy Bay (Chile) [43], 26 in the Pearl River (China) [25] and 24 in the coral reef flat ecosystems in Bolinao (Philippines) [23]. The effective trophic values are also close to the reported in the literature [23, 25, 42-43].

Producers such as phytoplankton and seagrasses, and the detritus are assigned to trophic level TL = 1; the invertebrate groups are placed in the second and/or third levels. Syngnathidae are in the maximum TL (TL = 3.76 for Cagbanilad Bay and 3.75 for Sabitang-Laya and Nipa bays), crustaceans (TL = 3.46 for Cagbanilad Bay and 3.45 for Sabitang-Laya and Nipa bays), constitute the top predators in the three seagrass systems. This assignment of trophic levels to the functional groups did not differ from the those described in the seagrass model reported in Laguna Alvarado, western Gulf of Mexico [44], wherein fish and invertebrate groups were placed in the third and second trophic levels.

The total living biomass was 1165 tWW km^2 a^{-1}, 1430 tWW km^2 a^{-1}, and 1330 tWW km^2 a^{-1} in Seagrass Models for Cagbanilad Bay, Sabitang Laya Island and Nipa Bay, respectively. The most dominant group composing the 30% of the total biomass in Cagbanilad Bay, 41% in Sabitang-Laya Island, and 36% in Nipa Bay seagrass models, respectively, are the seagrasses. Fish comprised 1.7% to 2.6% of the total biomass in the three models. When compared to the smaller scale models for the seagrass models of Maqueda Channel, Caramoan Peninsula, the larger scale models developed by by other researchers [42-43] showed almost similar values in terms of total biomass for primary producers.

Table 1 Basic inputs and estimated outputs (bold) of Cagbanilad (coastal inlet of Tinago in Minalahos Island) seagrass system model

Group name		TL	B (t km^{-2})	P/B (a^{-1})	Q/B (a^{-1})	EE	P/Q	NE	OI	Resp	Predat mort	Other mort	Flow to detritus
1	Syngnathidae	**3.76**	5.06	9.75	39.06	0.95	**0.25**	**0.31**	**0.50**	**108.8**	**20.89**	**0.18**	**42.0**
2	Crustaceans	**3.46**	65.50	4.93	14.50	0.95	**0.34**	**0.43**	**0.75**	**436.9**	**5.74**	**0.25**	**206.1**
3	Jellyfish	**3.34**	36.20	5.01	25.00	**0.99**	**0.20**	**0.25**	**0.65**	**524.6**	**4.98**	**0.03**	**181.9**
4	*Proteroaster nodosus*	**3.09**	44.90	0.52	2.60	0.95	**0.20**	**0.25**	**0.60**	**70.04**	**3.20**	**0.03**	**24.52**
5	Omnivorous fish	**3.04**	89.50	1.78	13.05	**0.67**	**0.14**	**0.170**	**0.79**	**775.1**	**1.20**	**0.58**	**285.5**
6	Pelecypods	**3.02**	87.50	2.06	6.86	**0.97**	**0.30**	**0.76**	**1.13**	**300.0**	**2.00**	**0.06**	**125.1**
7	Other benthic feeding fish	**2.76**	25.60	4.00	15.00	0.95	**0.27**	**0.33**	**0.82**	**204.8**	**2.60**	**1.40**	**81.92**
8	Nematodes	**2.63**	16.30	3.80	12.50	0.95	**0.30**	**0.38**	**0.68**	**101.1**	**13.50**	**0.19**	**43.85**
9	Other Holothuria	**2.34**	30.80	2.80	5.60	0.95	**0.50**	**0.63**	**0.42**	**51.74**	**4.46**	**0.14**	**38.81**
10	Gastropods	**2.32**	46.60	4.45	22.25	0.95	**0.20**	**0.25**	**0.27**	**622.1**	**31.67**	**0.22**	**217.7**
11	Ophiuroids	**2.32**	33.90	3.08	16.35	0.95	**0.19**	**0.24**	**0.44**	**339.0**	**4.05**	**0.15**	**116.1**
12	*Synapta maculata*	**2.27**	33.40	4.45	22.25	**0.95**	**0.20**	**0.25**	**0.29**	**512.6**	**4.20**	**0.25**	**180.3**
13	Zooplankton	**2.13**	15.17	67.00	192.0	**0.79**	**0.35**	**0.44**	**0.16**	**1314**	**43.85**	**23.15**	**799.6**
14	Polychaetes	**2.00**	15.50	1.63	12.46	0.95	**0.13**	**0.16**	**0.03**	**129.2**	**13.58**	**0.08**	**39.89**
15	*Tripneustes gratilla*	**2.00**	66.30	4.47	25.00	**0.52**	**0.18**	**0.22**	**--**	**1030**	**3.34**	**2.58**	**472.6**
16	*Cymodocea serrulata*	**1.00**	88.30	8.42	--	**0.65**	--	**--**	**--**	--	**5.48**	**2.95**	**260.3**
17	*Cymodocea rotundata*	**1.00**	72.10	8.43	--	**0.77**	--	**--**	**--**	--	**6.48**	**1.95**	**140.3**
18	*Halophila ovalis*	**1.00**	48.80	8.43	--	**0.77**	--	**--**	**--**	--	**6.61**	**1.82**	**88.96**
19	*Halodule univervis*	**1.00**	63.30	8.43	--	**0.62**	--	**--**	**--**	--	**5.19**	**3.24**	**205.2**
20	*Thalassia hemprichii*	**1.00**	76.20	8.43	--	**0.61**	--	**--**	**--**	--	**5.17**	**3.26**	**248.5**
21	Phytoplankton	**1.00**	184.1	30.42	--	**0.61**	--	**--**	**--**	--	**17.45**	**12.97**	**2206**
22	Detritus	**1.00**	19.80	--	--	**0.41**	--	**--**	**0.70**	--	--	--	--

Table 2 Basic inputs and estimated outputs (bold) of Sabitang Laya seagrass system model

Group name		TL	B (t km^{-2})	P/B (a^{-1})	Q/B (a^{-1})	EE	P/Q	NE	OI	Resp	Predat mort	Other mort	Flow to detritus
1	Syngnathidae	**3.75**	6.10	9.75	39.06	0.95	**0.25**	**0.31**	**0.49**	**131**	**16.0**	**0.49**	**50.6**
2	Crustaceans	**3.45**	46.7	4.93	14.50	0.95	**0.34**	**0.43**	**0.74**	**311**	**8.16**	**0.25**	**147**
3	Jellyfish	**3.34**	31.2	5.01	25.00	0.95	**0.20**	**0.25**	**0.64**	**468**	**5.15**	**0.25**	**164**
4	*Proteroaster nodosus*	**3.08**	59.3	0.52	2.60	0.95	**0.20**	**0.25**	**0.60**	**92.5**	**2.10**	**0.03**	**32.4**
5	Omnivorous fish	**3.04**	95.4	1.78	13.05	**0.57**	**0.14**	**0.17**	**0.78**	**826**	**1.01**	**0.77**	**323**
6	Pelecypods	**3.02**	83.1	2.06	6.86	**0.99**	**0.30**	**0.38**	**1.12**	**285**	**2.05**	**0.01**	**115**
7	Other benthic feeding fish	**2.72**	30.5	4.00	15.00	0.95	**0.27**	**0.33**	**0.83**	**244**	**1.55**	**2.45**	**97.6**
8	Nematodes	**2.63**	15.7	3.80	12.50	0.95	**0.30**	**0.38**	**0.68**	**97.3**	**13.9**	**0.19**	**42.2**
9	Other Holothuria	**2.34**	43.8	2.80	5.60	0.95	**0.20**	**0.25**	**0.27**	**585**	**31.0**	**0.22**	**205**
10	Gastropods	**2.33**	79.3	4.45	22.25	**0.64**	**0.50**	**0.63**	**0.37**	**133**	**1.79**	**1.01**	**169**
11	Ophiuroids	**2.32**	32.1	3.08	16.35	0.95	**0.19**	**0.24**	**0.44**	**321**	**4.42**	**0.15**	**110**
12	*Synapta maculata*	**2.27**	37.3	4.45	22.25	**0.88**	**0.20**	**0.25**	**0.29**	**498**	**3.90**	**0.55**	**186**
13	Zooplankton	**2.13**	15.2	67.0	192.0	**0.58**	**0.35**	**0.44**	**0.16**	**1314**	**39.0**	**28.0**	**852**
14	Polychaetes	**2.00**	26.4	1.63	12.46	0.95	**0.13**	**0.16**	**0.03**	**220**	**6.80**	**0.08**	**67.9**
15	*Tripneustes gratilla*	**2.00**	42.7	4.47	25.00	**0.82**	**0.18**	**0.22**	**--**	**663**	**3.68**	**0.79**	**247**
16	*Cymodocea serrulata*	**1.00**	79.9	8.43	--	**0.59**	--	**--**	**--**	--	**5.00**	**3.43**	**274**
17	*Cymodocea rotundata*	**1.00**	69.0	8.43	--	**0.69**	--	**--**	**--**	--	**5.79**	**2.64**	**182**
18	*Halophila ovalis*	**1.00**	38.2	8.43	--	**0.95**	--	**--**	**--**	--	**8.03**	**0.40**	**15.2**
19	*Halodule univervis*	**1.00**	36.7	8.43	--	**0.92**	--	**--**	**--**	--	**7.76**	**0.67**	**24.6**
20	*Syringidium isoetifolium*	**1.00**	67.3	8.43		**0.43**					**3.65**	**4.78**	**322**
21	*Enhalus acoroides*	**1.00**	290.0	8.43	--	**0.10**	--	**--**	**--**	--	**0.85**	**7.58**	**2199**
22	Phytoplankton	**1.00**	184.1	30.42	--	**0.58**	--	**--**	**--**	--	**17.45**	**13.6**	**2355**
23	Detritus	**1.00**	19.80	--	--	**0.29**	--	**--**	**0.70**	--	--	--	--

Table 3 Basic inputs and estimated outputs (bold) of Nipa seagrass system model

Group name		TL	B (t km^{-2})	P/B (a^{-1})	Q/B (a^{-1})	EE	P/Q	NE	OI	Resp	Predat mort	Other mort	Flow to detritus
1	Syngnathidae	**3.75**	7.3	9.75	39.06	**0.95**	**0.25**	**0.31**	**0.49**	**156.94**	**9.28**	**0.47**	**60.49**
2	Crustaceans	**3.45**	30.4	4.93	14.50	0.95	**0.34**	**0.43**	**0.74**	**202.77**	**18.47**	**0.25**	**95.65**
3	Jellyfish	**3.34**	32.1	5.01	25.00	**0.69**	**0.20**	**0.25**	**0.64**	**481.18**	**3.47**	**1.54**	**209.88**
4	*Proteroaster nodosus*	**3.08**	120	0.52	2.6.00	0.95	**0.20**	**0.25**	**0.60**	**187.20**	**0.71**	**0.03**	**65.52**
5	Omnivorous fish	**3.04**	74.3	1.78	13.05	**0.49**	**0.14**	**0.17**	**0.78**	**643.44**	**0.87**	**0.90**	**261.46**
6	Pelecypods	**3.02**	90.5	2.06	6.86	**0.99**	**0.30**	**0.38**	**1.12**	**310.23**	**2.04**	**0.02**	**125.97**
7	Other benthic feeding fish	**2.72**	15.3	4.00	15.00	0.95	**0.27**	**0.33**	**0.83**	**122.40**	**12.51**	**0.20**	**48.96**
8	Nematodes	**2.63**	20.4	3.80	12.50	0.95	**0.30**	**0.38**	**0.68**	**126.48**	**10.32**	**0.20**	**54.88**
9	Other Holothuria	**2.34**	65.3	2.80	22.25	0.95	**0.20**	**0.25**	**0.27**	**871.76**	**10.41**	**0.22**	**305.11**
10	Gastropods	**2.33**	44.2	4.45	5.60	**0.93**	**0.50**	**0.63**	**0.37**	**74.26**	**2.62**	**0.18**	**57.57**
11	Ophiuroids	**2.32**	38.9	3.08	16.35	**0.97**	**0.19**	**0.24**	**0.44**	**389.00**	**2.974**	**0.11**	**131.32**
12	*Synapta maculata*	**2.27**	32.4	4.45	22.25	**0.84**	**0.20**	**0.25**	**0.29**	**432.54**	**3.76**	**0.69**	**166.53**
13	Zooplankton	**2.13**	15.17	67.0	192.00	**0.87**	**0.35**	**0.44**	**0.16**	**1313.72**	**58.41**	**8.59**	**712.79**
14	Polychaetes	**2.00**	13.6	1.63	12.46	0.95	**0.13**	**0.16**	**0.03**	**113.40**	**11.47**	**0.08**	**35.00**
15	*Tripneustes gratilla*	**2.00**	46.9	4.47	25.00	**0.76**	**0.18**	**0.22**	**--**	**728.36**	**3.41**	**1.06**	**284.27**
16	*Cymodocea serrulata*	**1.00**	113.3	8.43	--	**0.36**	--	**--**	**--**	--	**3.07**	**5.36**	**607.53**
17	*Cymodocea rotundata*	**1.00**	93.3	8.43	--	**0.44**	--	**--**	**--**	--	**3.73**	**4.70**	**438.93**
18	*Halophila ovalis*	**1.00**	29.2	8.43	--	**0.97**	--	**--**	**--**	--	**8.15**	**0.28**	**8.19**
19	*Halodule univervis*	**1.00**	46.6	8.43	--	**0.66**	--	**--**	**--**	--	**5.52**	**2.90**	**135.47**
20	*Syringidium isoetifolium*	**1.00**	24.8	8.43		**0.99**	--	**--**	**--**	--	**8.32**	**0.11**	**2.70**
21	*Thalassia hemprichii*	**1.00**	49.2	8.43	--	**0.50**					**4.19**	**4.24**	**208**
22	*Enhalus acoroides*	**1.00**	123	8.43	--	**0.00**	--	**--**	**--**	--	**--**	**8.43**	**1037**
23	Phytoplankton	**1.00**	184	30.42	--	**0.61**	--	**--**	**--**	--	**18.53**	**11.9**	**2190**
24	Detritus	**1.00**	19.9	--	--	**0.34**	--	**--**	**0.63**	--	**--**	**--**	--

In Cagbanilad Bay seagrass model, the EE of jellyfish, pelecypods, and *S. maculata* have high EE values which suggests the important role they play in the trophic web and that they face high predation mortality. The EE of phytoplankton, detritus, omnivorous fish, and *T. gratilla*) are lower compared to most other functional groups, implying that these groups are not fully consumed. The values of EE of the predators estimated in the seagrass models ranked within the limits commonly described in the literature [23, 43]. In the Sabitang-Laya Island seagrass model, the EE of pelecypods and *Halophila ovalis* (paddle weed, spoon grass or dugong grass) are high which suggests their importance in the food web and high predation mortality. The EE of detritus, phytoplankton, and *E. acoroides* are lower compared to most other functional groups, implying that these groups are not fully consumed. A comparison with EE values of other seagrass ecosystem model, particularly, that by Ortiz and Wolff (2002), despite the heterogeneity in terms of biomass of the compartments, the same was concluded in terms of the fate of the production. Furthermore, the similarity of the present models in terms of the EE of detritus compared with other models [25, 42] can be explained by almost similar proportion of the detritus in the diet compositions of the epifauna. In Nipa Bay seagrass model, the EE of *E. acoroides*, *Cymodocea serrrulata* (serrated ribbon seagrass), *C. rotundata* (smooth ribbon seagrass) and omnivorous fish are lower compared to most other functional groups, implying that these groups are not fully consumed. The EE of Syngnathidae, pelecypods, ophiuroids, and *H. ovalis* have high values indicating their food web importance and high level of predation mortality. These EEs of the functional groups, particularly for the invertebrates in the seagrass meadows are comparable even with other ecosystems such as the fringing reefs [42].

2) Analysis of the trophic flow interactions

Figures 2-4 depict the flow diagrams constructed using EwE for the three seagrass ecosystems. Biomass of functional groups are relative to the size of the circles and are structured along the vertical axis based on their trophic level. Lines link prey sources to predators. Color of the lines indicates the magnitude of the flow of materials (t km^{-2} a^{-1}) from prey to predator.

Seagrasses, phytoplankton and detritus are the three main paths in the seagrass ecosystems. More biomass was moving towards the detrital group than was moving away from the seagrass systems. This indicates that much of the production of seagrasses is unconsumed and proceeds to detritus to be accumulated. The flows from phytoplankton and seagrasses indicate that grazing food chains is as important as the flows from detritus. Benthic groups, including pelecypods and ophiuroids prey upon the phytoplankton hence the biomass of such group passed up the food web.

3) Analysis of the Mixed Trophic Impacts (MTI) of the functional groups

Mixed Trophic Impact (MTI) analyses for the seagrasses system in the three sites (Figures 5-7) simply quantified all the direct and indirect trophic impacts and can also be considered as a sensitivity analysis [37, 46]. In the modelled seagrass systems, an assumed decrease in the biomass of grazers *T. gratilla* had a positive impact on the biomass of seagrasses. On the other and, a positive effect on the benthic groups is expected with an assumed decrease in the biomass of detritus and phytoplankton.

The MTI matrix in the seagrass system models indicated that functional groups in Maqueda Channel are closely interconnected. This findings is opposed to Nanwan Bay (Taiwan) [42] wherein large biomasses of macrophytes and detritus were little affected by changes in other groups hence low fraction of flows utilized by the fish community led extremely low TE in the bay.

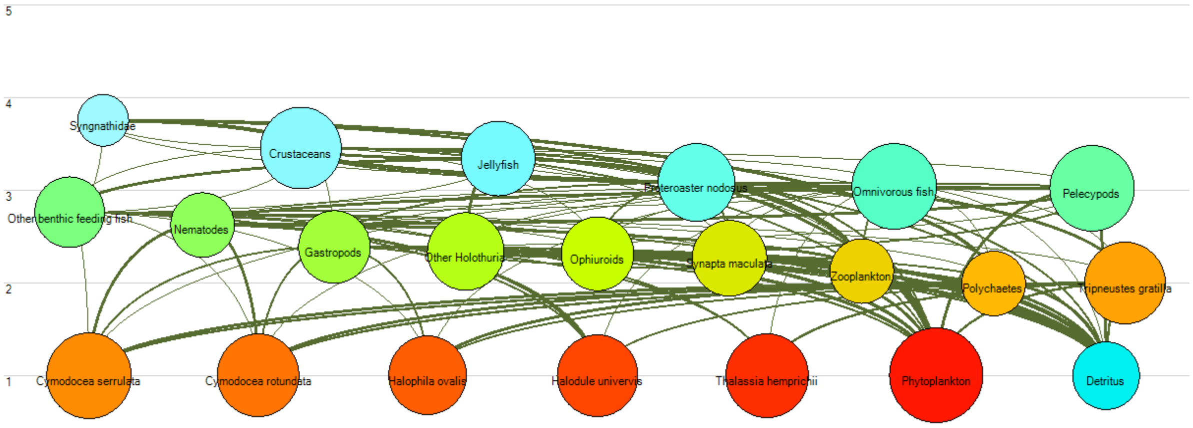

Figure 2 Diagram showing the trophic flow interaction in the Cagbanilad (coastal inlet of Tinago in Minalahos Island) seagrass system where the node indicates biomass, curved lines show food connectivity and arch lines showing trophic levels. All flows are expressed in t km^{-2} a^{-1}.

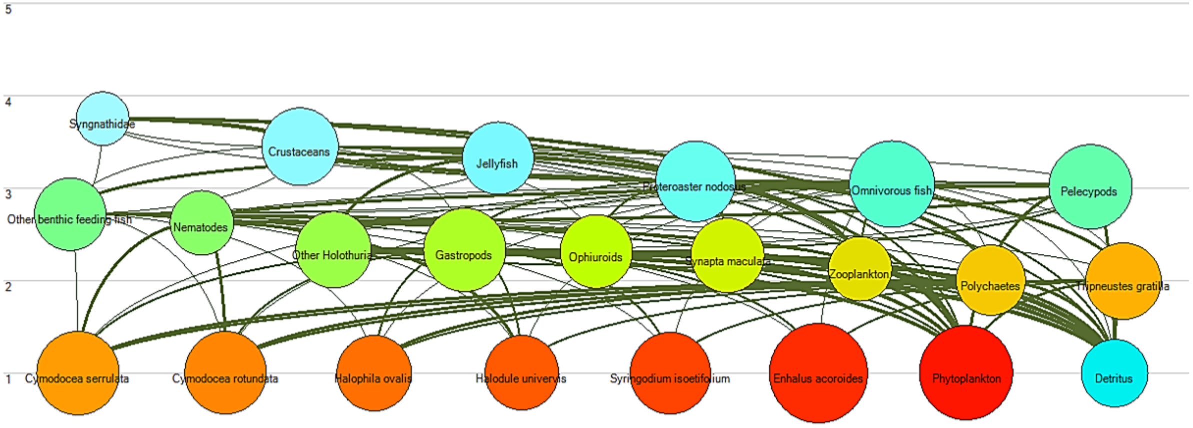

Figure 3 Diagram showing the trophic flow interaction in the Sabitang-Laya seagrass system where the node indicates biomass, curved lines show food connectivity and arch lines showing trophic levels. All flows are expressed in t km^{-2} a^{-1}.

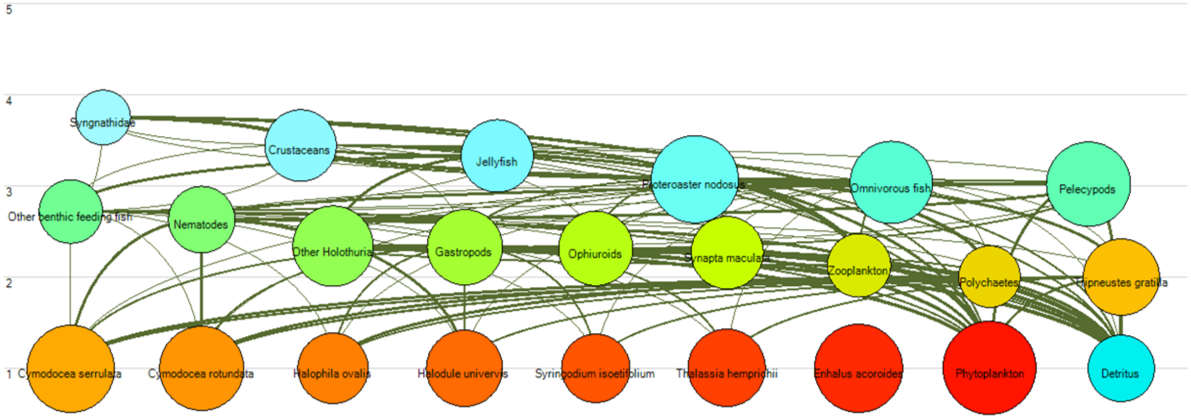

Figure 4 Diagram showing the trophic flow interaction in the Nipa seagrass system where the node indicates biomass, curved lines show food connectivity and arch lines showing trophic levels. All flows are expressed in t km^{-2} a^{-1}.

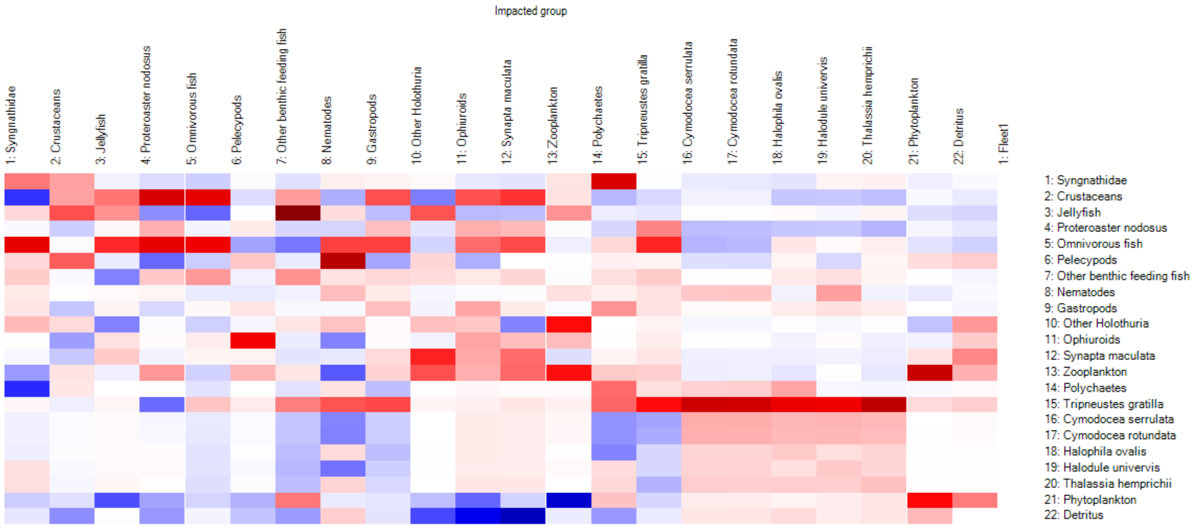

Figure 5 Combined direct and indirect trophic impacts of the functional groups in the Cagbanilad (coastal inlet of Tinago in Minalahos Island) seagrass system model. Blue rectangles indicate positive impacts and red rectangles negative impacts.

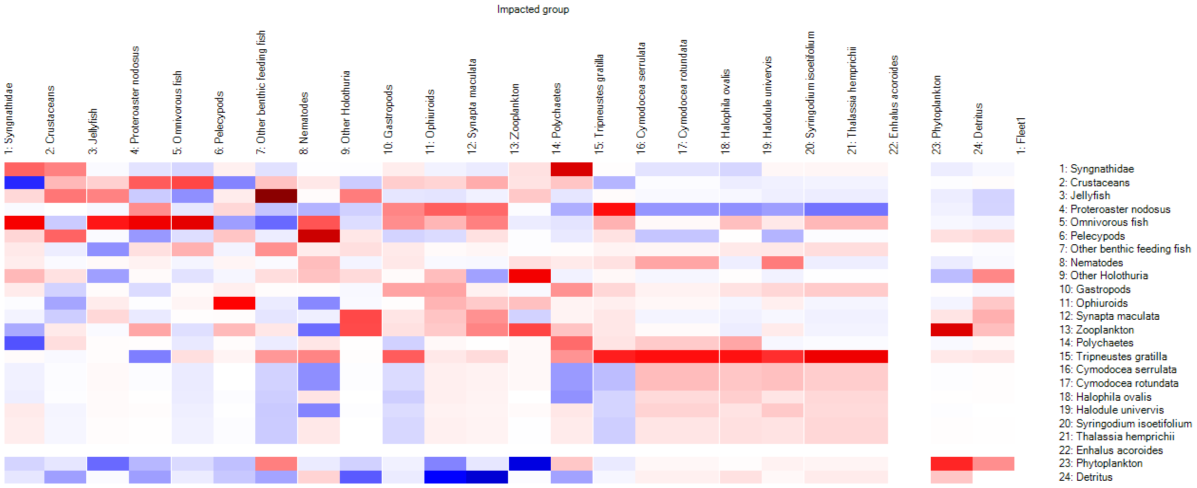

Figure 6 Combined direct and indirect trophic impacts of the functional groups in the Sabitang-Laya seagrass system model. Black circles indicate positive impacts and white circles negative impacts.

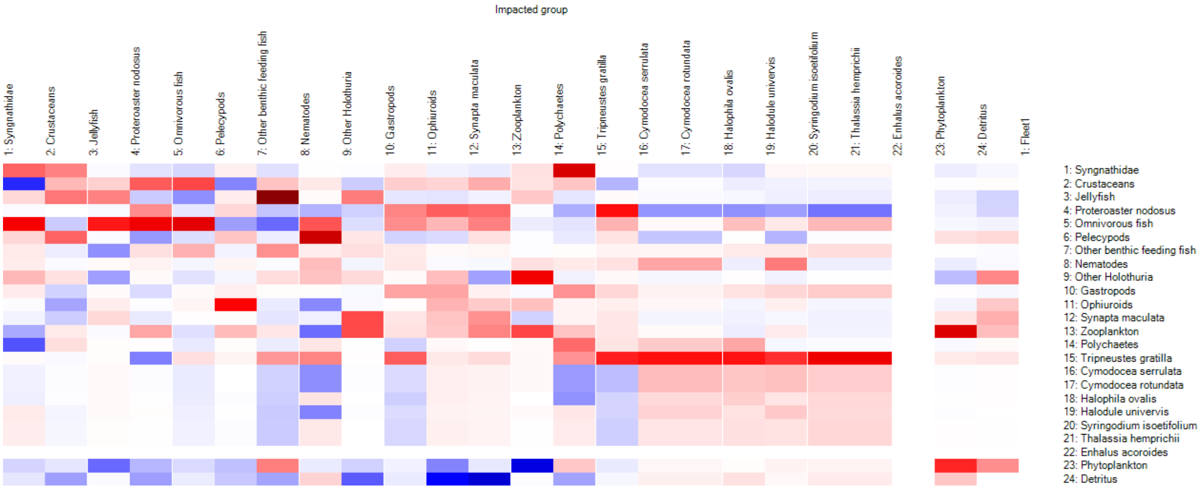

Figure 7 Combined direct and indirect trophic impacts of the functional groups in the Nipa seagrass system model. Black circles indicate positive impacts and white circles negative impacts.

4) Analysis of the flow network of organic matter and trophic efficiencies

Flows of the seagrass systems of Cagbanilad Bay, Sabitang-laya Island and Nipa Bay as depicted in the Lindeman spine were organized by integer trophic levels (TL), in the form of a Lindeman spine as shown in Supplementary Material 3. In order to further examine Trophic Level I, it was separated into detritus (D) and primary producers (P). It is shown that flows were generally low for higher TLs but high for lower TLs (i.e., from TL I to IV). Consumption by TL II on detritus and the flows from zooplankton and benthic invertebrates (TL II to IV) were high.

In Cagbanilad Bay, TL I and TL II had very high %TST (54.2% and 33.08%, respectively). In Sabitang-Laya Island, the %TST was also very high (61.19%) followed by TL II (27.87%). The same was observed in Nipa bay, wherein %TST was also very high for TL I (58.33%) followed by TL II (29.15%). The observed greater flows occurring from the higher TLs to lower TLs was reported also in other ecosystems [25, 42] wherein flows originate from primary producers and detritus and TE drop significantly from level I to II; and thereafter continued decreasing. The seagrass system models therefore provided a vivid indication of the sustainability of living aquatic resources in the seagrass ecosystems, which are mainly based on the trophic structure and flows of biomass through species interactions.

Further analysis showed that the primary production is a limiting factor in Cagbanilad Bay seagrass ecosystem based on the TE related to primary production (22.82%) which is higher than the TE related to detritus (22.48%). In contrast, TE related to detritus in Sabitang-Laya and Nipa (24.06% and 24.49%, respectively) were higher than the TE related to primary producers (23.45% and 24.30%, respectively) indicating that detritus is the limiting factor for these ecosystems. Lastly, mean TE (24.34%) for Nipa Bay was also higher than the mean TE values for the bays of Cagbanilad Bay (23.04%) and Sabitang-Laya Island (23.65%). Thus, in two of the three seagrass models (e.g., Sabitang-laya and Nipa Bay), the TE for primary producers was higher than for detritus. This finding is opposed with those found for other systems [45-47] which indicate that detritus is the main pathway to support the biological communities in the ecosystem.

5) Flow network of organic matter and trophic efficiencies in the seagrass systems

Several statistics were calculated in Ecopath to analyse the status of the seagrass ecosystems and to characterize their scale, maturity and stability status (see Supplementary Material 4). The total system throughput (TST) was highest in Sabitang-laya Island, 31596 t km^{-2} a^{-1}, of which 36.1% of the total flows constitute the internal consumption, 19.59% constitute the respiration, and 25.89 constitute the detritus. Total system throughput (TST) was lowest in Cagbanilad Bay, 27996 t km^{-2} a^{-1}, of which 42.53% of the total flows represent the internal consumption, 23.35% represent the respiration, and 21.45%, the detritus. In contrast, the TST of the in the current models are higher than the averages reported in the literature, particularly in Nanwan Bay (China) [42] and Pearl River Delta coastal ecosystem [25].

An index of maturity of an ecosystem is the ratio between total primary production and total respiration (TPP/TR). An index value close to 1.0 indicates that an ecosystem is nearing a “mature” stage; higher than 1 means the ecosystem is in the early developmental stage, and lower than 1 means an ecosystem is under pressure (for example, organic pollution). Hence, all the three seagrass systems are in early developmental stage and the Cagbanilad seagrass appeared to be the most mature system while Sabitang-Laya Island appeared to be the most immature. The findings support previous report

[48] that majority of aquatic ecosystems have a TPP/TPR ratios between 0.8 and 3.2.

The intensity of recycling and efficiency of retaining particular matter measured by Finn's cycling index (FCI, % of total throughput) showed that the seagrass system found in Cagbanilad Bay was the most highly recycling system (FCI = 4.726) and Sabitang-Laya Island was the least (FCI = 3.790). These FCI values also showed that the positive feedbacks in the two seagrass systems had contributed to their stability. In comparison, the FCI in the seagrass systsme are relatively similar with the FCI in Nanwan Bay (3.5) [42].

The Connectance Index (CI) and System Omnivory Index (SOI) indicate the complexity of the inner linkage within the ecosystem, hence its maturity. Based on the CI and SOI values, Cagbanilad Bay seagrass system model has the most complex inner linkage compared with the other three seagrass systems. The CI for Cagbanilad Bay (0.252), Sabitang-laya Island (0.28) and Nipa Bay (0.217) are relatively the same with the Pearl River Delta coastal ecosystem (0.235) [25] but lower than Laguna Alvarado in western Gulf of Mexico (0.3) [44]. In contrast, the SOI for the three seagrass models (0.469, 0.453, 0.449, respectively) in the current study are higher than Pearl River Delta (0.328) [25] and Laguna Alvarado (0.25) [44]. This is indicative of the similarity the modelled ecosystems in terms of ecosystem complexity but not in variety in terms of existing food links.

Overhead (Ø, flowbits), a measure of the power or ascendancy of a system to recover from stress and the system maturity, showed that among the three seagrass systems, the most stable is the Cagbanilad Bay seagrass systems. In contrast, the Sabitang-Laya Island seagrass system is more predisposed to perturbation-induced ecosystem changes and recover longer from unforeseen disturbances. The relative overhead of the seagrasses systems in the current study ranges from 76% to 78%, which are relatively higher compared with the Pearl River Delta (China) (67%) [25], which indicates that the latter is more prone to changes brought by perturbations.

Conclusion

The trophic models of the seagrass systems of Cagbanilad Bay, Sabitang-Laya Island and Nipa Bay provide a summary of the knowledge of the biomass, consumption, production, food web and trophic structure of these ecosystems, and are comparable to other ecosystems [23, 42-48] elsewhere in the world. The models provide tools to quantitatively investigate the trophic state of the ecosystem by describing how matter and energy propagate through the food web. Therefore, it is possible to obtain a more holistic understanding of structure and functioning of the ecosystems. The modelling results indicate that the seagrass ecosystems had three main trophic circulation pathways and most of the activities in terms of flow occurred in the lower part of the trophic web. All the attributes of ecosystem maturity and stability indicate explicitly that the seagrass systems of Caramoan Peninsula are mature aquatic ecosystems that require peculiar management and conservation strategies. The models can be useful tools for policy development and basis for hypothesis to be tested in the future.

Many functional groups in the trophic model of the three seagrass systems are known to be dependent on seagrass material. The crustaceans, holothurid *S. maculata* and the herbivorous fish assimilate material originating from seagrasses, mainly seagrass carbon [50]. The seagrass material can be incorporated directly by the herbivores or omnivores indirectly through predation and detrivores as detritus. Many small crustaceans, such as copepods, isopods and amphipods graze on seagrasses [51-52] thus incorporate seagrass carbon in their tissue and form a substantial portion of the diet for seagrass-associated fish assemblages [53-54]. Thus, the food web models constructed for the seagrass systems included in the current study can be useful in redefining the importance of seagrass material for the food web especially that there is lack of information on the combines number of fish and invertebrate species that directly use seagrass material and secondary consumers that depend on them.

Based on the trophic models of the three Caramoan seagrass ecosystems, the following implications on how to manage seagrass systems can be derived. Foremost, the presence of mesoherbivores and small invertebrates, including sea urchins, crustaceans, gastropod, and holothuroids in the seagrass systems indicate how important seagrass as nursery ground and habitat refuge for these animals. The trophic models, the results of mixed trophic impact analysis and statistics derived from network analysis provided a clear static, mass-balanced snapshot of the seagrass systems in Caramoan Peninsula. The models identified and quantified major energy flows in the ecosystems. Through the models, the ecosystem resources and the interactions among species were described and the ecosystem effects of fishing or environmental change were evaluated. The major energy flows in an ecosystem were also identified and quantified. The seagrass ecosystem resources and their interactions among species were also described using the trophic models. All the information can be used by ecosystem managers and stakeholders as basis for prioritizing which seagrass systems must be given more attention when it comes to conservation.

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References

[1] Guannel, G., Arkema, K., Ruggiero, P., Verutes, G. The power of three: Coral reefs, seagrasses and mangroves protect coastal regions and increase their resilience. PLoS ONE, 2016, 11(7), e0158094. doi: 10.1371/journal.pone.0158094.

[2] Paillon, C., Wantiez, L., Kulbicki, M., Labonne, M., Vigliola, L. Extent of mangrove nursery habitats determines the geographic distribution of a coral reef fish in a South-Pacific Archipelago. PLos ONE, 2014, 9(8), e105158. Doi:10.1371/ journal.pone.0105158.

[3] Gretch, A., Chartrand-Miller, K., Erftemeijer, P., Fonseca, M., McKenzie, L., Rasheed, M., ..., Coles, R. A comparison of threats, vulnerabilities, and management approaches in global seagrass bioregions. Environmental Research Letters, 2012, 7(2), 1-8.

[4] Pogoreutz, C., Kneer, D. Litaay, M. Asmus H., Ahnelt, H. The influence of canopy structure and tidal level on fish assemblages in tropical Southeast Asian seagrass meadow. Estuarine, Coastal and Shelf Science, 2012, 107(107), 58-68.

[5] Mumby, P.J., Dahlgren, C.P., Harbornel, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., …, Gill, A.B. Fishing, Trophic Cascades, and the Process of Grazing on Coral Reefs. Science, 2006, 311(5757), 98-101.

[6] Short, F.T., Coles, R.G. Global Seagrass Research Methods. Elsevier Science B.V. 2001, 1-506.

[7] Terrados, J., Duarte, CM., Kamp-Nielsen, L., Agawin, N.S.R., Gacia, E., Lacap, D., …, Greve, T. Are seagrass growth and survival affected by reducing conditions in the sediment? Aquatic Botany, 1999, 65(1-4), 175-98.

[8] Hemminga, M.A., Duarte, C.M. Seagrass ecology. UK: Cambridge University Press, 2000, 1-298.

[9] Marbá, N., Duarte, C.M. Coupling of seagrass (Cymodocea nodosus) patch dynamics to subsequeous dune migration. Journal of Ecology, 1995, 83(3), 381-389.

[10] Dahl, M., Deyanova, D., Lyimo, L.D., Näslund, J., Samuelsson, G.S., Mtolera, M.S.P., ..., Gullström, M. Effects of shading and simulated grazing on carbon sequestration in a tropical seagrass meadow. Journal of Ecology, 2016, 104(3), 654-664.

[11] Nakaoka, M., Aioi, K. Growth of the seagrass Halophila ovalis at dugong trails compared to existing within-patch variation in a Thailand intertidal flat. Marine Ecology Progress Series, 1999, 184, 97-103.

[12] Moncreiff, C.A., Sullivan, M.J. Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. Marine Ecology Progress Series, 2001, 215, 93-106.

[13] Heck, K.L. Jr., Valentine, J.F. Plant-herbivore interactions in seagrass meadows. Journal of Experimental Marine Biology and Ecology, 2006, 330(1), 420-436.

[14] Smit, A.J., Brearley, A., Hyndes, G.A., Lavery, P.S., Walker, D.I. $\delta^{15}N$ and $\delta^{13}C$ analysis of a Posidonia sinuosa seagrass bed. Aquatic Botany, 2006, 84(3), 277-282.

[15] Mateo, M.A., Cebria ́n, J., Dunton, K.H., Mutchler, T. Carbon fluxes in seagrass ecosystems. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, 2006, 159-192.

[16] Avila, E., Avila-Garcia, A.K., Cruz-Barraza, J.A. Temporal and small-scale spatial variations in abundance and biomass of seagrass-dwelling sponges in a tropical estuarine system. Marine Ecology, 2015, 36(3), 623-636.

[17] Coll, M., Libralato, S. Contribution of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish and Fisheries, 2012, 13(1), 60-88.

[18] Christensen, V., Walters, C. Ecopath with Ecosim: Methods, capabilities, and limitations. Ecological Modelling, 2004, 172(2-4), 109-139.

[19] Ecopath.org. Ecopath with Ecosim - Ecopath with Ecosim food web modeling approach. [Online] Available from: http://ecopath.org/ [Accessed 7 Oct. 2018].

[20] Bozec Y.M., Gascuel, D., Kulbicki, M. Trophic model of lagoonal communities in a large open atoll (Uvea, Loyalty islands, New Caledonia). Aquatic Living Resources, 2004, 17(2), 151-162.

[21] Arias-González, J.E. Comparative study on the trophic functioning of two coral reef ecosystems. Proceedings of the 8th International Coral Reef Symposium 1997, 2, 921-926.

[22] Opitz, S. Trophic interactions in Caribbean coral reefs. ICLARM Tech. Rep. 1996, 43, 341 p.

[23] Aliño, P.M., McManus, L.T., McManus, J.W., Nañola, C.L., Jr., Fortes, M.D., Trono, G.C., Jacinto, G.S., Initial parameter estimations of a coral reef flat ecosystem in Bolinao, Pangasinan, Northwestern Philippines. In: Christensen, V., Pauly, D. (Eds.), Trophic models of aquatic ecosystems. ICLARM Conference Proceedings, 1993, 26, 252-258.

[24] Bundy, A., Pauly, D. Selective harvesting by small-scale fisheries: Ecosystem analysis of San Miguel Bay, Philippines. Fisheries Research, 2001, 53 (3), 263-281.

[25] Duan, L.J., Li, S.Y., Liu, Y., Jiang, T., Failler, P. A trophic model of the Pearl

River Delta coastal ecosystem. Ocean & Coastal Management, 2009, 52(7), 359-367.

[26] Tsagarakis, K., Coll, M., Giannoulaki, M., Somarakis, S., Papaconstantinou, C., Machias, A. Food-web traits of the North Aegean Sea ecosystem (Eastern Mediterranean) and comparison with other Mediterranean ecosystems. Estuarine, Coastal and Shelf Science, 2010, 88(2), 233-248.

[27] Harvey, C.J., Bartz, K.K., Davies, J., Francis, T.B., Good, T.P., Guerry, A.D., ..., Ruckelshaus, M.H. A mass-balance model for evaluating food web structure and community-scale indicators in the central basin of Puget Sound. U.S. Dept. Commer., NOAA Tech. Memo. 2010. NMFS-NWFSC-106, 1-180.

[28] Regalado, J., Campos, W., Santillan, S. Population biology of Tripneustes gratilla (Linnaeus) (Echinodermata) in seagrass beds of Southern Guimaras, Philippines. Science Diliman, 2011, 22(2), 41-49.

[29] Campos, W.L. An ecosystem model of San Pedro Bay, Leyte, Philippines: initial parameter estimates, 353-364. In (eds.) Assessment, management and future directions for coastal fisheries in Asian countries. WorldFish Center Conference Proceedings, 2003, 67, 1,120 p.

[30] Fortes, M.D. Seagrass resources in East Asia: Research status, environmental issues and management perspectives. In: ASEAMS/UNEP Proc. First ASEAMS Symposium on Southeast Asian Marine and Environmental Protection. UNEP Regional Seas Reports and Studies No. 116. UNEP, 1990, 135-144.

[31] Springsteen, F.J., Leobrera, F.M. Shells of the Philippines. Manila, Philippines: Carfel Seashell Museum. 1986, 1-377.

[32] Sarcia, S.M., Ang, M.P., Clores, M.A., Oropesa, L.B. (In Press). Grazing Activity of Tripneustes gratilla (Linnaeus, 1758) (Collector Urchin) on the leaf stratum of seagrasses in Sabitang-Laya Island, Caramoan Peninsula, Philippines. Bicol Science Journal. Partido State University Press.

[33] Pechenik, J.A. Biology of the invertebrates. Boston: McGraw Hill Higher Education, 2011, 1-636.

[34] Nybakken, J., Bertness, M.D. Marine biology: An ecological approach, 6th edition. Benjamin Cummings. 2004, 1-579.

[35] Ullah, M.H., Rashed-Un-Nabi, M., Al-Mamun, M.A. Trophic model of the coastal ecosystem of the Bay of Bengal using mass balance Ecopath model, Ecological Modelling, 2012, 225, 82-94.

[36] Christensen, D.V., Walters, C. Ecopath, ecosim and ecospace as tools for evaluating ecosystem impact to fisheries. ICES Journal of Marine Science, 2000, 57(3), 697-706.

[37] Ulanowicz, R.E., Puccia, C.J. Mixed trophic impacts to ecosystems. Coenoses, 1990, 5(1), 7-16.

[38] Ulanowicz, R.E. Growth and development: Ecosystems phenomenology. Springer-Verlag, New York, 1986, 1-178.

[39] Christian, R.R., Baird, D., Lucxkovich, J.J., Johnson, J.J. Role of network analysis in comparative ecosystem ecology of estuaries. Aquatic Food Webs. In: Belgramo, A, Scharler, U.M., Dunne, J, Ulanowicz, R.E. (Eds.). Aquatic foodwebs: An ecosystem approach., Chapter: 3, Publisher: Oxford University Press, 2005, 25-40.

[40] Odum, E.P. The strategy of ecosystem development. Science, 1969, 164(3877), 262-270.

[41] Kay, J.J., Graham, L.A, Ulanowicz, R.E. A detailed guide to network analysis. In: Wulff, F., Field, J.G., Mann, K.H. (eds), Network analysis in marine ecology: methods and applications. Springer-Verlag, Heidelberg, 1989, 15-61.

[42] Liu, P., Shao, K.T., Jan, R.Q., Fan, T.Y., Wong, S.L., Hwang, J.S., ..., Lin, H.J. A trophic model of fringing coral reefs in Nanwan Bay, southern Taiwan suggests overfishing. Marine Environmental Research, 2009, 68(3), 106-117.

[43] Ortiz, M., Wolff, M. Trophic models of four benthic communities in Tongoy Bay (Chile): Comparative analysis and preliminary assessment of management strategies. Journal of Experimental Marine Biology and Ecology, 2002, 268(2), 205-235.

[44] Cruz-Escalona, V.H., Arreguın-Sanchez, F., Zetina-Rejon, M. Analysis of the ecosystem structure of Laguna Alvarado, western Gulf of Mexico, by means of a mass balance model. Estuarine, Coastal and Shelf Science, 2007, 72(1-2), 155-167.

[45] Wolff, M. A trophic model for Tongoy Bay-a system exposed to suspended scallop culture (Northern Chile). Journal of Experimental Marine Biology and Ecology, 1994, 182(2), 149-168.

[46] Christensen, V., Walters C.J., Ecopath with Ecosim: Methods, capabilities and limitations. Ecological Modelling, 2004, 172(2-4), 109-139.

[47] Monaco, M., Ulanowicz, R. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Marine Ecology Progress Series, 1997, 161, 239-254.

[48] Heymans, J., Baird, D., A carbon flow model and network analysis of the northern Benguela upwelling system, Namibia. Ecological Modelling, 2000, 126(1), 9-32.

[49] Christensen, V., Pauly, D. Trophic Models of Aquatic Ecosystem. International Center for Living Aquatic Resources Management. Conference Proceedings 26, Manila, Philippines, 1993, 390 pp.

[50] Smit, A.J., Brearley, A., Hyndes, G.A., Lavery, P.S., Walker, D.I. Carbon and nitrogen isotope analysis of an Amphibolis griffithii seagrass bed. Estuarine, Coastal and Shelf Science, 2005, 65(3), 545-556.

[51] Boström, C., Mattila, J. The relative importance of food and shelter for seagrass associated invertebrates: A latitudinal comparison of habitat choice by isopod grazers. Oecologia, 1999, 120(1), 162-170.

[52] Kharlamenko, V.I., Kiyashko, S.I., Imbs, A.B., Vyshkvartzev, D.I. Identification of food sources of invertebrates from the seagrass Zostera marina community using carbon and sulphur stable isotope ratio and fatty acid analyses. Marine Ecology Progress Series, 2001, 220, 103-117.

[53] Lugendo, B.R., Nagelkerken, I., van der Velde, G. The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: gut content and stable isotope analyses. Journal of Fish Biology, 2006, 69(6), 1639-1661.

[54] Unsworth, R.K.F., Taylor, J.D., Powell, A., Bell, J.J., Smith, D.J. The contribution of parrotfish (scarid) herbivory to ecosystem dynamics in the Indo-Pacific. Estuarine, Coastal and Shelf Science, 2007, 74(1), 53-62.