Highly Productive Tropical Seagrass Beds Support Diverse Consumers and a Large Organic Carbon Pool in the Sediments

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Abstract: Tropical seagrass beds are productive coastal ecosystems that are important blue carbon sinks and crucial habitats and feeding grounds for consumers at high trophic levels. To understand how energy sustains the ecosystem from seagrass production, we constructed an Ecopath trophic model to reveal the possible pathways of energy flow in the tropical seagrass beds around Dongsha Island, South China Sea. The model indicates that Dongsha seagrass beds were developing but well-structured ecosystems. The productive seagrasses were rarely directly consumed by herbivores and, ultimately, flowed into detrital pools. Detritus was the main food source used to support diverse consumers in the food web. Nevertheless, the low cycling rate (2.74%) suggests that most detritus was not reused or exported and was stored as a large organic carbon pool in the sediments. The detritus-feeding invertebrates are keystone groups in the Dongsha seagrass beds, as they recycle energy from detritus and transfer to top predators such as sharks. The predation of top predators affected the biomasses of other compartments, leading to strong top-down control via a trophic cascade effect.

Keywords: biodiversity; blue carbon; Ecopath; network analysis; seagrass beds; South China Sea

1. Introduction

Tropical seagrass beds may serve many ecological functions. High primary production can fix a large amount of CO₂ into their biomass [1,2]. They can provide a major source of organic matter in coastal areas after littering [3,4]. They are also recognized as crucial habitats or nursery grounds for marine animals [5,6]. Tropical seagrass beds can also support abundant and diverse resources for coastal fisheries [5,7]. However, the structure and functioning of tropical seagrass beds remain unclear.

Seagrass beds generally harbor abundant and diverse fauna, from benthic invertebrates to large animals such as sea turtles, dugongs, and sharks. Nevertheless, few seagrass tissues are directly consumed by herbivores [8,9]. Most seagrass production becomes detritus [10,11]. Detrital decomposition is often affected by environmental factors, canopy structure, and decomposers [12]. As a result, the consumption and recycling rates of seagrass production are highly variable in different seagrass beds.

Large areas of seagrass beds are the main seascape at the Dongsha Island, South China Sea. Because of isolation and military restriction, low human impact and less fishery pressure, Dongsha Island still has rather pristine seagrass beds and coral reefs. Coral reefs and seagrass beds are often mixed in the shallow waters around Dongsha Island, forming highly complex habitats [13]. Previous studies indicated high primary production as well as high biodiversity in the seagrass beds of Dongsha Island [13–16]. However, the energy flows of seagrass production within this tropical atoll remain unclear. How does massive...
seagrass production lead to high faunal diversity within the food web around Dongsha Island? Because of the complex pathways of energy flow within the seagrass beds, it is necessary to view the whole seagrass beds with a holistic scale when conferring ecosystem structure and functioning.

Modeling is a useful tool for understanding the structure and function, representing the knowledge gap, and testing hypotheses within the ecosystem [17]. Modeling can also characterize ecosystem structure and function by comparison with other ecosystem models [18,19]. Understanding this information is helpful for resource management, conservation, and restoration. The pristine condition of Dongsha Island is suitable for a reference or baseline goal of tropical seagrass beds. In this study, we aim to understand the trophic structure and function of Dongsha seagrass beds by constructing an Ecopath trophic model. The purposes are: (1) to understand the trophic structure and energy flows in Dongsha seagrass beds, (2) to determine the keystone groups, and (3) to determine the trophic role of each functional group within the seagrass ecosystems.

2. Material and Methods
2.1. Study Site

Dongsha Island, also called Pratas Island (20°43’ N; 116°42’ E), is situated on the western side of a coral atoll in the South China Sea (Figure 1). The area of this coral island is approximately 1.74 km². There is little freshwater flow into the sea from the island. A semienclosed lagoon (0.64 km²) occupies the central part of the island. An open inlet located on the western side of the island is the only channel that permits seawater exchange between the lagoon and the open ocean, and the rate of water exchange is dependent upon the tidal cycle (tidal ranges: 0.85 ± 0.21 m). The modeling area covers 11.85 km², mainly seagrass beds around Dongsha Island (including the lagoon). The water depth is mostly shallower than 8 m. Seagrass beds extend from the intertidal to the subtidal zones around the entire island. There are seven seagrass species at Dongsha Island [20], including *Thalassia hemprichii*, *Halophila ovalis*, *Cymodocea rotundata*, *C. serrulata*, *Halodule uninervis*, *Syringodium isoetifolium*, and *Thalassodendron ciliatum*. The coverage of seagrass beds was mostly >75% around the island. There were approximately 20 coral species around Dongsha, mostly reef-building corals. Some massive *Porites* corals are associated with merulinid and *Acropora* corals mixed in the seascape. Although Dongsha Island is dominated by a tropical climate and water temperatures around the island average 27.6 °C, the intense northeast monsoons from October to early March can markedly reduce the water temperature to 19 °C.

2.2. Ecopath Modeling

The Ecopath trophic model of seagrass beds around Dongsha Island was constructed by the Ecopath with Ecosim 6.3 (EwE) software system [21,22] to quantify organic matter flows within the food web. The basic concept of the Ecopath model is mass balancing within the system. The parameterization of the Ecopath model is based on the two main equations. First, for each compartment (i), a mass-balanced budget can be expressed as (1):

\[
P_i - B_i \times M2_i - P_i (1 - EE_i) - EX_i - AC_i = 0
\]

where \(P_i\) is the production of \(i\), \(B_i\) is the biomass of \(i\), \(M2_i\) is the predation mortality of \(i\), \(EE_i\) is the ecotrophic efficiency (EE) of \(i\) (i.e., the part of the production that passes up the trophic level, used for biomass accumulation or export), \(1 - EE_i\) is “other mortality”, \(EX_i\) is the portion of \(i\) exported to other systems through sedimentation or fishery activities, and \(AC_i\) is the accumulation of \(i\) during the study period. \(EE\) value ranges from 0 to 1. The higher value indicates that this trophic group was highly consumed by other consumers within the system.

Second, the consumption of a predator compartment (j) can be expressed as Equation (2):
Consumption = production + respiration + unassimilated food

\[ \sum_j B_j \times (Q_j/B_j) = P_j + R_j + UN_j \]  

(2)

where \( j \) is a consumer species, \( (Q_j/B_j) \) is the consumption:biomass ratio of consumer \( j \), \( P_j \) is the production of \( j \), \( R_j \) is the respiration of \( j \), and \( UN_j \) is the unused consumption of \( j \).

Finally, the main equation of the Ecopath model can be integrated as (3) [22]:

\[ B_i \times (P_i/B_i) \times EE_i - \sum_j B_j \times (Q_j/B_j) \times DC_{ji} - EX_i - AC_i = 0 \]  

(3)

where \( P_i/B_i \) is the production:biomass ratio of \( i \), \( Q_j/B_j \) is the consumption:biomass ratio of predator \( j \), and \( DC_{ji} \) is the fraction of prey \( i \) in the average diet of predator \( j \). The diet composition was assumed to remain stable, with nonsignificant biomass accumulation during the study period.

In the Ecopath model, some of the parameters do not have to be entered since the Ecopath model links the production of each compartment with the consumption of all the other compartments and uses the linkages to estimate missing parameters. DC and EX must always be entered, while the entry of one of any of the other four parameters (B, P/B, Q/B, and EE) is optional [21,22].

2.3. Model Compartment Sampling

Data for the Ecopath model were obtained from various research studies around Dongsha Island from 2009 to 2012 [14,15]. Five study sites were established for long-term monitoring stations during the study period. Three of the five sites were located along the gradient of seawater exchange from the inner to the inlet of the lagoon. The other two sites were located on the northern and southern coast of Dongsha Island. Most organisms collected from seagrass beds were quantified and classified into 24 functional compartments by their trophic or habitat characteristics in the Ecopath model (Tables 1 and 2).
Table 1. The input parameters and calculated output of compartments in the Dongsha seagrass bed model. The values in parentheses were estimated by Ecopath. Shaded compartments are the top five influential compartments in the model by keystone index and relative total impact. B, biomass (g, wet weight (WW) m⁻²); P/B, production/biomass ratio (yr⁻¹); Q/B, consumption/biomass ratio (yr⁻¹); and EE, ecotrophic efficiency.

| Group                     | Basic Input | Calculated Output |
|---------------------------|-------------|-------------------|
|                           | B           | P/B               | Q/B | EE | Trophic Level | Net Efficiency | Omnivory Index | Flow to Detritus | Keystone Index | Relative Total Impact |
| 1 Pelagic sharks          | 0.23        | 0.32              | 3.90 | (0.00) | 3.82 | 0.10           | 0.35           | 0.25           | 0.02           | 0.78               |
| 2 Lemon sharks            | 3.25        | 0.31              | 2.60 | (0.01) | 3.74 | 0.15           | 0.37           | 2.69           | 0.06           | 0.86               |
| 3 Rays                    | 3.86        | 0.63              | 3.30 | (0.00) | 3.17 | 0.24           | 0.07           | 4.97           | −0.20          | 0.47               |
| 4 Piscivorous fish        | 12.46       | 0.64              | 5.49 | (0.28) | 3.49 | 0.14           | 0.25           | 19.38          | 0.13           | 1.00               |
| 5 Large carnivorous fish  | 52.44       | 1.55              | 8.08 | (0.26) | 3.04 | 0.24           | 0.02           | 144.99         | −0.09          | 0.61               |
| 6 Small carnivorous fish  | 13.69       | 1.61              | 12.59 | (0.83) | 3.01 | 0.16           | 0.02           | 38.14          | −0.51          | 0.23               |
| 7 Omnivorous fish         | 2.60        | 2.27              | 19.79 | (0.58) | 2.79 | 0.14           | 0.21           | 12.74          | −0.66          | 0.17               |
| 8 Detritivorous fish      | 2.79        | 1.60              | 17.42 | (0.71) | 2.00 | 0.11           | 0.00           | 11.00          | −1.46          | 0.03               |
| 9 Herbivorous fish        | 15.06       | 1.79              | 29.94 | (0.38) | 2.00 | 0.07           | 0.00           | 107.02         | −0.16          | 0.52               |
| 10 Algae                 | 6.13        | 4.39              | 24.75 | (0.34) | 2.00 | 0.22           | 0.00           | 48.02          | −0.47          | 0.25               |
| 11 Hawksbills            | 0.00        | 0.10              | 3.50 | (0.22) | 2.97 | 0.04           | 0.09           | 0.00           | −3.65          | 0.00               |
| 12 Green turtles          | 0.01        | 0.11              | 6.76 | (0.08) | 0.20 | 0.02           | 0.00           | 0.01           | −3.84          | 0.00               |
| 13 Cephalopods            | 0.12        | 3.10              | 15.50 | (0.48) | 3.07 | 0.25           | 0.09           | 0.56           | −2.70          | 0.00               |
| 14 Urochids              | 2.92        | 1.54              | 7.70 | (0.41) | 2.00 | 0.25           | 0.00           | 7.13           | −1.01          | 0.07               |
| 15 Carnivorous invertebrates | 5.55      | 8.27              | 41.36 | (0.16) | 2.82 | 0.25           | 0.17           | 84.27          | −0.65          | 0.17               |
| 16 Omnivorous invertebrates | 145.35    | 13.48             | 67.41 | (0.47) | 2.02 | 0.25           | 0.02           | 3195.91        | 0.07           | 0.93               |
| 17 Filter invertebrates   | 43.92       | 8.21              | 41.05 | (0.82) | 2.01 | 0.25           | 0.01           | 426.08         | 0.02           | 0.80               |
| 18 Herbivorous invertebrates | 4.28     | 6.80              | 34.00 | (0.26) | 2.00 | 0.25           | 0.00           | 50.67          | −0.55          | 0.21               |
| 19 Cnidarians             | 6.12        | 2.09              | 10.45 | (0.40) | 2.15 | 0.25           | 0.24           | 19.20          | −1.20          | 0.05               |
| 20 Zooplankton            | 0.60        | 32.00              | 192.00 | (0.81) | 2.01 | 0.21           | 0.12           | 26.77          | −1.34          | 0.03               |
| 21 Macrura               | 124.54      | 19.70              | 15.90 | (0.16) | 1.00 | 0.00           | 0.00           | 2070.21        | −0.15          | 0.56               |
| 22 Microalgae            | 1.42        | 26.55              | 0.71  | (0.01) | 1.00 | 0.00           | 10.99          | −1.82          | 0.01           | 0.01               |
| 23 Seagrasses            | 1836.90     | 37.18              | 0.01  | (0.01) | 1.00 | 0.00           | 67748.51       | −0.79          | 0.62           |                   |
| 24 Detritus               | 30.31       | (0.15)             | 1.00  | (0.00) | 1.00 | 0.00           | 0.07           | 0.00           |                   |                   |

2.3.1. Fish (Compartments 1–10)

Fish were surveyed bimonthly during the daytime by underwater visual censuses at each station. Our surveys were carried out among different habitats and tidal periods within each station to understand the dynamics of fish assemblages. Fish species, individual numbers, and body lengths (TL) were recorded. All fish species were identified and classified into 10 fish compartments according to previous studies [13,15,16] or information from Fishbase [23]. The fish species are pelagic shark (Galeocerdo cuvier and Cararcharhinus limbatus), lemon shark (Negaprion acutidens), ray (Aetobatus ocellatus, Panteobatis fai, and Taeniurops meyeni), apex-piscivore fish (25 species, including carangids, epinephelinaes, and sphyraenids), large carnivore fish (52 species, including lethrinids, lutjanids, and haemulids), small carnivorous fish (89 species), omnivorous fish (53 species), detritivorous fish (5 species, mostly mugilids and Chanos chanos), seagrass herbivorous fish (3 species: mostly Leptoscarus vaigiensis and Hemirampus fus) and algae herbivorous fish (17 species, including acanthurids, scolids, and siganids). Fish biomass in terms of wet weight (WW) was calculated by weight-length empirical equations. P/B and Q/B values of fish were estimated using the empirical equations of [24] and [25,26], respectively. The diet of each fish compartment was derived from the weighted average of the diet composition of different species within each compartment. Most diet composition was based on stomach content analysis in Dongsha seagrass beds [14–16]. Some fish species without local diet information were referred from Fishbase [23]. Many subadult lemon sharks and stingrays had traumatic bite scars of other sharks on their bodies, so we set parts of sharks and rays as the food sources of lemon sharks and pelagic sharks.

2.3.2. Sea Turtle (Compartments 11–12)

Green turtles (Chelonia mydas) and hawksbill turtles (Eretmochelys imbricata) are the only two sea turtle species at Dongsha. Their densities were relatively low according to reef surveys around the island. Biomass data were recorded from the wildlife medical
station of Dongsha Marine National Park Headquarters. Other parameters, such as P/B, Q/B and diet, were referred from previous studies [27–31]. Seagrass is the main food item for the green turtle. However, we observed green turtles feeding on *Cassiopea Andromeda* in the seagrass beds, so we set Cnidarians as a small part of their diet composition.

### 2.3.3. Macroinvertebrates (Compartments 13–18)

Macroinvertebrates (e.g., decapods, mollusks, and echinideas) were recorded by the same underwater visual censuses as fish bimonthly. For collecting infauna and smaller invertebrates (e.g., polychaetes, amphipods, and Tanaidaceas), we used a stainless-steel corer (diameter = 7.5 cm) at a depth of 10 cm of the sediments randomly for 15 replicates within each site. All samples were sorted, narcotized using magnesium chloride or menthol, and fixed in 5% formalin for identification, weighing and recording. We classified all macroinvertebrates into eight functional compartments according to their trophic functions: large crustaceans, small crustaceans, cephalopods, urchins, carnivorous invertebrates, omnivorous invertebrates, filter invertebrates, and herbivorous invertebrates.

The production of invertebrates was calculated from biomass and abundance data by equations [32,33] except the production of cephalopods (mostly *Sepioteuthis lessoniana*) which referred to [34]. The total P/B of each invertebrate compartment was calculated by the weighted average of the relative abundance of species within each compartment. The Q/B value of invertebrate compartments was estimated on the basis of gross alimentary conversion efficiency (P/Q) as 0.2 [35].

The diets of decapods, cephalopods, and urchins were analyzed during the study period. The cephalopods fed on many pelagic invertebrates that were not found around our study sites. Hence, we set some of their food sources from imports from outside ecosystems. The diets of other invertebrates referred to other inshore reef Ecopath models [19,36].

### 2.3.4. Cnidarians (Compartment 19)

The most common cnidarians were upside down jellyfish (*Cassiopea andromeda*) and swimming sea anemones (*Boloceroides mcmurrichi*) in the seagrass beds. Their biomass and P/B values were estimated to be similar to those values of invertebrate compartments as described above. In terms of corals, the biomass of the main species (*Acropora* spp. and *Porites* spp.) was recorded as the tissue extraction method following [19]. The total P/B value of cnidarians was calculated by the weighted average of the corals as 1.09, referring to the jellyfish and sea anemones of the Caribbean coral reef model [36]. The Q/B value of cnidarians was estimated following the method of invertebrate compartments.

Most cnidarians in shallow waters are both primary producers and consumers. We assumed that 60% of the energy of cnidarians was from zooxanthellae or imported from outside, and the other 33% and 6% were from detritus and feeding invertebrates, respectively [19].

### 2.3.5. Zooplankton (Compartment 20)

Zooplankton samples were collected by towing double Bongo nets (45 cm in diameter with mesh size 330 µm) below the seawater surface bimonthly. Samples were identified, and the density was counted. The dry biomass of zooplankton was estimated by the length-weight relationship of dominant species using the empirical equation of [37]. The P/B and Q/B values of zooplankton were derived from the values in the South China Sea model [38]. The diet of zooplankton was mostly imported from outside since the concentrations of dissolved organic matter (DOM), particulate organic matter (POM), and phytoplankton were relatively low in our Ecopath model.

### 2.3.6. Primary Producers (Compartments 21–23)

Seagrass and macroalgae were sampled from the surveys of three permanent 50 m transects at each station bimonthly. All transects were parallel and separated from each other by at least 5 m. Five replicate 10 cm × 10 cm quadrats were randomly deployed
along each transect to collect seagrass or macroalgal biomass. Seagrass leaf production was quantified bimonthly by the leaf marking method [39]. The production of macroalgae was recorded by the changes in dissolved O\(_2\) concentrations in the BOD incubations of dominant species. The detrital export of seagrass and macroalgae was set as 10% according to previous studies [12].

The biomass of microalgae and phytoplankton was estimated by measuring chlorophyll a concentration [40]. Water samples in triplicate from each station were filtered through Whatman GF/F filters in the field. The filters were then extracted in 90% acetone for 24 h at 4 \(^{\circ}\)C in the dark. Phytoplankton production referred to [41] by the in situ \(^{14}\)C assimilation method. The benthic microalgae were collected randomly from the sediments and seagrass leaves at each station. The production of benthic microalgae was measured seasonally by the closed-chamber CO\(_2\) flux method [42,43].

2.3.7. Detritus (Compartment 24)

Detritus comprises the organic matter in the water column and sediments. Dissolved and particulate organic matter was analyzed by the methods of [44,45] bimonthly. Phytoplankton biomass was subtracted from the detrital mass by calculating the sum of chlorophyll a and pheophytin in the water column assuming a carbon:pigment ratio of 35:1 [46]. Detritus in the sediments was collected by using a 7.5-cm diameter core tube in three replicates at a depth of 10 cm at each station. Samples were dried in an oven at 60 \(^{\circ}\)C for 24 h and then ground to a powder for organic matter analysis. The export of detritus was set as 10%, according to previous studies [12].

2.4. Model Balancing and Verification

The first step was to check whether all the EE values of compartments were >1.0. The model assumes that any compartment cannot be consumed in excess of its production. To correct compartments with EE >1.0, we adjusted some input data for balancing. In our model, the biomass and P/B values were derived mostly from locally reliable data. However, the Q/B and diet of most invertebrates referred to other literature and were considered less reliable in our model. Hence, we gradually adjusted the Q/B or diet composition individually for balancing. Most of the changes were small and remained within 20% of the input values. The second step was to check if the GE (the gross food conversion efficiency, e.g., the production and consumption ratio) was in the range of 0.1–0.3, as the production of most compartments is approximately 10–30% of the consumption. In addition, the P/Q ratio cannot be higher than the net efficiency (the ratio between production and assimilated food).

The sensitivity routine [47] (in EwE 5.8) was used to check the effect each input parameter had on all of the “estimated” parameters for each compartment in the model by varying all basic input parameters in steps from −50% to +50% changes. Sensitivity analysis was performed on all input parameters of our final model. An increase of 30% in the biomass or P/B value of a group would result in a decrease of approximately 24% in its own estimated EE value and an increase of approximately 13% in the EE values of its prey groups. A 30% increase in Q/B would result in only an approximate 4% increase in the estimated EE values of its prey groups, suggesting that the biomass and P/B values were more sensitive in determining the EE values in our model and that our model was reliable, as the biomass and P/B values were derived mostly from locally reliable data.

2.5. Ecosystem Parameter Analysis

The balanced model shows the trophic level (TL), ecotrophic efficiency (EE), and omnivory index of each trophic group. All primary producers and detritus belonged to trophic level 1. The predatory groups had higher trophic levels than the herbivore or detritus feeding groups. The omnivory index shows the variety of food intake (a value between 0 and 1). A higher value represents a wide diet breadth of food sources.
Table 2. Diet composition matrix in percentage of prey groups (in rows) for each consumer group (in columns) for the Dongsha seagrass bed model.

|       | 1 Pelagic sharks | 2 Lemon sharks | 3 Rays | 4 Piscivorous fish | 5 Large carnivorous fish | 6 Small carnivorous fish | 7 Omnivorous fish | 8 Detritivorous fish | 9 Seagrass herbivorous fish | 10 Algae herbivorous fish | 11 Hawksbill turtles | 12 Green turtles | 13 Cephalopods | 14 Urchins | 15 Carnivorous invertebrates | 16 Omnivorous invertebrates | 17 Filter invertebrates | 18 Herbivorous invertebrates | 19 Crinarians | 20 Zooplankton | 21 Macroalgae | 22 Micr algae | 23 Seagrasses | 24 Detritus | Input from outside |
|-------|------------------|----------------|--------|-------------------|--------------------------|-------------------------|-------------------|---------------------|--------------------------|-----------------------------|---------------------|----------------|---------------|---------|----------------------|---------------------|---------------------|----------------------|---------------|--------------|--------------|----------|----------|-----------|-----------------|
| 1     |                  |                |        | <0.001            |                          |                         |                   |                     |                          |                             |                     |                | <0.001        |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.100            |
| 2     |                  |                |        | 0.010             |                          |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.100            |
| 3     |                  |                |        | <0.001            |                          |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | <0.001            |
| 4     |                  |                |        | 0.254             | 0.221                     | 0.001                   | 0.001             | 0.001               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | <0.001            |
| 5     |                  |                |        | 0.355             | 0.387                     | 0.001                   | 0.249             | 0.001               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | <0.001            |
| 6     |                  |                |        | <0.001            | 0.010                     | 0.186                   | 0.013             | 0.002               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.001            |
| 7     |                  |                |        | 0.050             | 0.005                     | <0.001                  | 0.039             | 0.001               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.002            |
| 8     |                  |                |        | <0.001            | 0.025                     | 0.001                   | 0.036             | 0.001               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | <0.001            |
| 9     |                  |                |        | 0.110             | 0.240                     | 0.001                   | 0.103             | 0.002               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.002            |
| 10    |                  |                |        | 0.210             | 0.121                     | 0.001                   | 0.103             | 0.002               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.002            |
| 11    |                  |                |        | <0.001            |                          |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | <0.001            |
| 12    |                  |                |        | <0.001            |                          |                         |                   |                     |                          |                             |                     |                | <0.001        |          |                      |                     |                     |                      |               |              |              |          |          |          | <0.001            |
| 13    |                  |                |        | <0.001            |                          |                         |                   |                     | <0.001                 | 0.001                       |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.001            |
| 14    |                  |                |        | 0.100             | 0.001                     |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.001            |
| 15    |                  |                |        | 0.106             | 0.002                     | 0.010                   | 0.005             | 0.015               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.001            |
| 16    |                  |                |        | 0.415             | 0.281                     | 0.968                   | 0.964             | 0.557               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.001            |
| 17    |                  |                |        | 0.309             | 0.100                     | 0.009                   | 0.155             | 0.250               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.245            |
| 18    |                  |                |        | 0.055             | <0.001                    | 0.001                   | 0.003             | 0.001               |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.245            |
| 19    |                  |                |        | <0.001            |                          |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.001            |
| 20    |                  |                |        | <0.001            |                          |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | <0.001            |
| 21    |                  |                |        | 0.224             | 0.031                     | 0.022                   | 0.856             | 0.050               | 0.048                   |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.250            |
| 22    |                  |                |        | 0.001             | 0.003                     |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.250            |
| 23    |                  |                |        | 0.974             | 0.005                     |                         |                   |                     |                          |                             |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.974            |
| 24    |                  |                |        | 0.001             | 0.018                     | 0.020                   | 0.964             | 0.004               | 0.138                   |                          |                     |                |              |          |                      |                     |                     |                      |               |              |              |          |          |          | 0.100            |

Input from outside: | 0.100 | 0.100 | 0.010 | 0.600 | 0.880 |
The details of trophic transfer in the Dongsha seagrass bed model were revealed by ecological network analysis \[48,49\]. Network analysis shows trophic structure and path-way routes \[49,50\]. Network analysis is also a tool for comparative analyses with other ecosystems \[51\] that can be used to characterize the trophic structure and function of our seagrass bed model (Table 3). The total system throughput (TST) represents the size of an ecosystem in terms of flows \[48\]. TST is the sum of consumption, exports, respiratory flows, and flows into detritus and is indexed in terms of how much matter the system processes. The total biomass/TST ratio (B/TST) represents the amount of biomass necessary to maintain one unit of flow. B/TST is expected to increase along with ecosystem maturity \[52\]. The net primary production/respiration (P/R) ratio and the net primary production/total biomass (P/B) ratio were used to describe how mature the Dongsha model was. The cycling of matter is considered a critical process in the functioning of natural ecosystems, as it can facilitate homeostatic control over the magnitude of flows \[52\]. The Finn cycling index (FCI) \[53\] was used to reveal the relative importance of cycling to the TST in the Dongsha model. The detritivory/herbivory (D/H) ratio is a measure of the relative importance of detritivory flows in the system. The ascendency was used to reveal the development of the system from the TST \[48,54\]. Lindeman trophic analysis \[53\] summarized complicated food webs in terms of a single linear food chain. The trophic transfer efficiency (TE) from one aggregated trophic level to the next can be calculated as the fraction of the input of organic matter to a given level that was transferred to the next higher level.

### Table 3. Ecosystem parameters of network analysis used to characterize the trophic structure and function of the Dongsha seagrass bed model.

| Parameter                        | Abbreviation | Description                                                                 | Unit      |
|----------------------------------|--------------|-----------------------------------------------------------------------------|-----------|
| Ascendency                       | A            | A measure of the magnitude of organic matter flowing through a food web     | %         |
| Detritivory/herbivory ratio      | D/H          | A measure of the importance of detritivory flows relative to herbivory flows in a system |           |
| Finn cycling index               | FCI          | A measure of the relative importance of cycling to the total system throughput (TST) in a system | %         |
| Net primary production/total biomass ratio | P/B        | The relationship between net primary production and total biomass in a system |           |
| Net primary production/respiration ratio | P/R      | The relationship between net primary production and respiration in a system |           |
| Omnivory index                   |              | A measure of the distribution of feeding interactions among trophic levels in a system |           |
| Total biomass/TST ratio          | B/TST        | The amount of biomass necessary to maintain one unit of flow in a system    | g WW m \(^{-2}\) yr \(^{-1}\) |
| Total system throughput          | TST          | Sum of all flows in a system; a measure of system activity                  |           |
| Trophic transfer efficiency      | TE           | A measure of the fraction of the input of organic matter to a given level that was transferred to the next higher level | %         |

The keystone index and relative total impact were also used to reveal the trophic influence of each compartment within the food web \[55\]. A compartment with an impact on more other compartments would have a higher relative total impact value. The mixed trophic impact (MTI) \[56\] was used to assess the effects that changes in the biomass of a compartment would have on the biomass of other compartments by trophic relationship. As a result, the MTI can be regarded as a form of sensitivity analysis for the input parameters of the model.

### 3. Result

#### 3.1. Trophic Flows and Networks

The trophic flow diagram shows that there were four trophic levels (TLs, hereafter), and energy flowed from TL 1 primary producers (seagrass, macroalgae, and microalgae) and detritus to TL 3.82 top predators (pelagic sharks) (Figure 2). The total living biomass of
our model was 2295.27 g WW m$^{-2}$ yr$^{-1}$. Seagrasses comprised 79.36% of the total biomass since they were the main seascape in our model. The production of seagrass contributed 21.37% to the total production. The ecotrophic efficiency (EE) values of microalgae and macroalgae were 0.16 and 0.70, respectively, while the EE value of seagrasses was lower than 0.01. This result suggests that most seagrass production was not used by herbivores and, ultimately, flowed into the detrital pathway at Dongsha (Table 1).

![Figure 2](image)

**Figure 2.** Trophic flow diagram of the Dongsha seagrass bed model. The area of each compartment represents the proportion of the total biomass of the model contained by the compartment. The line between each compartment represents the trophic relationship between them. Line width represents the relative flux between compartments. The numerical legend for compartments is: 1. pelagic sharks; 2. lemon sharks; 3. ray; 4. piscivorous fish; 5. large carnivorous fish; 6. small carnivorous fish; 7. omnivorous fish; 8. detritivorous fish; 9. seagrass herbivorous fish; 10. algae herbivorous fish; 11. hawksbill turtles; 12. green turtles; 13. cephalopods; 14. urchins; 15. carnivorous invertebrates; 16. omnivorous invertebrates; 17. filter invertebrates; 18. herbivorous invertebrates; 19. cnidarians; 20. zooplankton; 21. macroalgae; 22. microalgae; 23. seagrasses; and 24. detritus.

Most invertebrate groups were distributed in TLs 2 and 3. Their omnivory indices were mostly <0.2, indicating their narrow diet breadth. Omnivorous invertebrates (TL: 2.02), filter invertebrates (TL: 2.01), cephalopods (TL: 2.97), and zooplankton (TL: 2.01) had rather high EE values (0.47, 0.82, 0.48, and 0.81, respectively) among all invertebrate groups. In terms of fish groups, pelagic sharks (TL: 3.82), lemon sharks (TL: 3.74), and piscivorous fish (TL: 3.49) were the top predators in our model. Their omnivory indices ranged from 0.25–0.37 since they consumed a variety of trophic groups in our model.

Total system throughput (TST) of Dongsha seagrass system was 158543 g WW m$^{-2}$ yr$^{-1}$. The low B/TST (0.02) and high P/B (30.99) ratios revealed the development status of the Dongsha seagrass ecosystems. The ascendency of 57%, however, represented that the food web of Dongsha seagrass beds was well-structured. The Finn cycling index (FCI) value shows that all cycled flows accounted for only 2.74% of the TST. The Dongsha seagrass bed model was an autotrophic system since the net primary production/respiration ratio (P/R) was 8.59.

The Lindeman trophic analysis reveals the TST in a food chain with seven integrated trophic levels (Figure 3). More organic matter flows were derived from detritus than primary production in our model. The detrivory/herbivory (D/H) ratio (1.23) also indicates that more energy was derived from detritus. The geometric mean trophic transfer efficiencies (TE) of the food chain were 5.76%. The highest TE was at trophic level II (8.42%). The TE then decreased gradually at higher trophic levels.

### 3.2. Keystone Species and Mixed Trophic Impacts

Keystone indices show that omnivorous invertebrates, filter invertebrates, piscivorous fish, lemon sharks, and pelagic sharks were the top five keystone groups in our model.
(Table 1). They had positive keystone indices and high relative total impact values (>0.75). Both the omnivorous and filter invertebrate groups fed mainly on detritus. They were also the main food sources of many other trophic groups. Their high ecotrophic efficiency (EE) values represent the high consumption proportions by other compartments in our model. The top predator groups, including pelagic sharks, lemon sharks, and piscivorous fish, affected a variety of trophic groups by their predation. Piscivorous fish had the top keystone index (0.13) and relative total impact values (1.00) among all trophic groups, indicating that their predation would affect all trophic groups in our model.

**Figure 3.** Lindeman spines of organic matter (g wet weight m⁻² yr⁻¹) and trophic efficiencies (TE, %) in different trophic levels from Level I including primary producer (P) and detritus (D) to consumers at Level II–VI in the Dongsha seagrass bed model. P: primary producers; D: detritus; TL: trophic level; TST: Total system throughput; and TE: transfer efficiency.

**Figure 4.** Mixed trophic impacts of the Dongsha seagrass bed model. The figure reveals the direct and indirect trophic impacts that an increase in the biomass of the compartments listed on the right would have, both with positive (white histograms) and negative (black histograms) influences listed. The proportion of the impact is represented by the size of the histogram.

MTI analysis (Figure 4) shows that an increase in the biomass of omnivorous and filter invertebrates would have large effects on many predator and prey compartments. Since they recycled detrital food sources and were then consumed by many fish compartments, they became the most influential invertebrates in seagrass beds. A significant trophic
cascade can be found in pelagic sharks, lemon sharks, and piscivorous fish. Increasing the biomass of piscivorous fish would have negative effects on other fish groups, leading to large positive effects on a variety of lower TL invertebrates. Lemon sharks had a great negative effect on piscivorous fish but had positive effects on other fish groups and filter invertebrates. Pelagic sharks had negative effects on most fish groups and two sea turtles but had a positive effect on piscivorous fish.

Increasing seagrass biomass would have positive effects on seagrass-herbivorous fish, green turtles, urchins, and herbivorous invertebrates. An increase in biomass in macroalgae and detritus would have great positive effects on the biomass of most fish and invertebrate compartments, which indicates that macroalgae and detritus were the main food sources for most primary consumers. An increase in detrital mass would also have negative effects on zooplankton and microalgae because detritus often accompanies these two compartments in the diets of many consumers. However, the large flows into detrital mass show that detritus was little affected by changes in the biomass of other compartments.

4. Discussion

In our model, the low ecotrophic efficiency (EE) value of seagrasses indicated that most of their production flowed into detritus. Unlike algae, seagrasses are considered a poor-quality food source because their cellulose-rich leaves are difficult to digest for most herbivores [8,9]. Only parrotfish, sea urchins, and some mesograzers (e.g., isopods and nerites snail) can directly consume seagrasses at Dongsha [57]. Seagrasses are often represented as “macrophytes” or “benthic autotrophs” by combining with macroalgae in many other trophic models. However, the nutrient content, cellulose shoot, and palatability of seagrasses are distinctly different from those of most macroalgae. Similar to our findings of the seagrass beds around Dongsha Island, stable isotope analysis also showed that macroalgae were generally the main food sources of herbivores in other tropical seagrass ecosystems [58–60]. For better resolution of production, consumption, and energy flows, we suggest distinguishing seagrasses and macroalgae as different compartments of primary producers when constructing trophic models of seagrass beds.

High seagrass production and a large amount of unconsumed detritus lead to high total system throughput (TST) and detrital pathways in the Dongsha seagrass bed model. The high P/B and P/R values reveal a rather low level of consumers relative to primary production, also suggesting that Dongsha seagrass beds may harbor more available trophic space for additional consumers in seagrass ecosystems. The detritivory/herbivory (D/H) ratio also reveals that more energy utilized was derived from detritus rather than primary production. Detritus recycling is a common energy route in coastal systems [18,61–63]. However, the FCI value in our model indicates that only 2.74% of the energy is recycled in our system. Although many detritus-feeding animals reused detritus, the seagrasses still produced overwhelming amounts of detritus in our model. In addition, a previous study indicated that seagrass detritus exported only approximately 10% of its mass at Dongsha [12]. As a result, a large part of unconsumed seagrass detritus would be buried in the organic carbon pool of the sediments. On the coastline around Dongsha Island, a large number of detrital layers have accumulated on the sediments of the intertidal zone, similar to seagrass detritus layers in the Mediterranean Sea [64,65]. The detritus layers in the inner lagoon and west inlet of Dongsha Island can reach over 1 m in depth due to the high water residence time in these regions. The detritus may become part of the carbon sink in the sediments. The vast seagrass beds around Dongsha Island are estimated to accumulate 11,367 tons of carbon per year [12,14]. The high detrital production and low recycling make tropical seagrass beds ideal blue carbon sinks in the atoll.

Detritus feeding consumers, including omnivorous invertebrates and filter invertebrates, play critical roles in the Dongsha seagrass beds. These consumers, including deposit-feeding crustaceans, polychaetes, and mollusks, feed mostly on benthic detritus. These invertebrate biomasses become secondary production, as they were also crucial food
sources for the predators in our model. Previous studies have indicated that many benthic invertebrates play indispensable roles as they reuse detritus within food webs [66–68]. Moreover, we found a higher transfer efficiency (TE) in TL II (8.42%) than in TL I (4.11%) because most consumers in our models are carnivorous fish. They feed mostly on these secondary consumers, which links the detrital energy source to higher trophic levels. Similar higher TEs at secondary consumer levels can be observed in other tropical coastal ecosystems that also use more detrital food sources [69,70]. In the Dongsha seagrass beds, these invertebrates became an important key link, transferring energy from recycled detritus to consumers at higher trophic levels. Consequently, our results suggest that detritus-feeding invertebrates controlled the main trophic flows in tropical seagrass beds.

In addition to detritus-feeding invertebrates, piscivorous fish, lemon sharks, and pelagic sharks were also the keystone groups in the Dongsha seagrass ecosystems. Large predatory fish affected other compartments by predation, leading to strong top-down control via trophic cascade effects. Top-down control by top predators can reduce competition, differentiate resources, and enhance biodiversity within the system [71,72]. Carangids and sphyraenids were the dominant piscivorous fish in the Dongsha seagrass beds. They frequently rove above seagrass meadows and hunt for small fish. They themselves were also important food sources for sharks. These predations suggest that piscivorous fish can also transfer energy to the groups of top predators in the Dongsha seagrass beds.

### Table 4. Common elasmobranchs and their ecological information at Dongsha.

| Species                                      | Family            | Density (per ha) | Body-Length Range (cm) | Diet                                      | Major Habitat          | Functional Group |
|----------------------------------------------|-------------------|------------------|------------------------|-------------------------------------------|------------------------|------------------|
| Tiger shark *(Galeocerdo cuvier)*           | Carcharhinidae    | <0.01            | 220–370                | Fish, shark, ray, sea turtle *             | Seagrass bed, Reef     | pelagic shark    |
| Black tip shark *(Carcharhinus limbatus)*   | Carcharhinidae    | 1.29             | 90–200                 | Fish (mostly carangid, lethrinid lutjanid) | Reef                   | pelagic shark    |
| Sharptooth lemon shark *(Negaprion acutidens)* | Carcharhinidae | 23.01            | 60–200                 | Fish (mostly mugilid, carangid, lethrinid lutjanid, scard) | Seagrass bed, Inner lagoon, Reef | lemon shark     |
| Pink whip ray *(Pateobatis fai)*            | Dasyatidae        | 12.11            | 60–150                 | Squid *(Sepioteuthis lessoniana)*          | Seagrass bed, Inner lagoon | ray             |
| Round ribbon-tail ray *(Taeniura meyeni)*   | Dasyatidae        | 1.60             | 100–200                | Crab, Shrimp, Clam, Snail, Urchin          | Seagrass bed, Reef     | ray             |
| Ocellated eagle ray *(Aetobatus ocellatus)* | Aetobatidae       | 8.09             | 50–160                 | Crab, Clam, Snail                         | Seagrass bed, Reef     | ray             |

* Data from Fishbase.

Seagrass beds also support food sources for many elasmobranchs (e.g., sharks and rays) at Dongsha (Table 4). Indeed, previous studies pointed out that shallow seagrass beds are crucial habitats for many sharks and rays in coastal waters. Pink whip rays *(Pateobatis fai)* and ocellated eagle rays *(Aetobatus ocellatus)* are common ray species in the Dongsha seagrass beds. They enter shallow seagrass beds and consume burrowed crustaceans and mollusks during flood tide [73]. Lemon sharks were the most common elasmobranchs at Dongsha. They use seagrass beds as their nursery habitats and feeding grounds [16]. Most individuals present in the Dongsha seagrass beds are in young years or 1–2 years of age sharks (body-length range: 60–200 cm in total length). The same genus species, *Negaprion brevirostris*, from the Atlantic Ocean shows an ecological niche similar to our results. They also use shallow seagrass beds as their juvenile habitats and foraging grounds [74,75]. Large pelagic sharks had rather lower densities than rays and lemon sharks. Black tip shark *(Carcharhinus limbatus)*, which is found mostly in reef areas, sometimes enters subtidal seagrass beds, especially on the northern and southern coasts of Dongsha. They frequently enter seagrass beds for night-time foraging grounds in the Atlantic Ocean [75,76]. Few tiger sharks *(Galeocerdo cuvier)* were recorded in the Dongsha seagrass beds. Their young also use shallow seagrass beds for both nursery and foraging grounds [77,78]. The occurrence of these young apex predators suggests that the productive seagrass beds around Dongsha can not only be feeding grounds for consumers at high trophic levels but may also become potential nursery grounds for top predators.
Seagrass beds have been known to provide valuable ecosystem services to humankind [79]. Tropical seagrass beds are highly productive [1] and can efficiently sequester large quantities of CO$_2$ [12,80]. Unfortunately, seagrass beds are in decline worldwide due predominantly to anthropogenic activity, such as coastal development and seawater pollution [81]. While seagrasses were often a small part of vegetation in other coastal trophic models [19], seagrass beds are the main seascape around Dongsha Island. Our Ecopath model shows the structure and function of pristine tropical seagrass beds around Dongsha Island. This Dongsha seagrass bed model can be used as a reference or baseline goal of tropical seagrass beds when comparing with other impacted seagrass ecosystems.

5. Conclusions

In summary, the seagrass beds around Dongsha were developing but well-structured ecosystems. Most seagrass production flowed into detrital pathways, and part of the detritus became the main food source as secondary production (detritus feeding invertebrates) in the seagrass ecosystem. Dongsha seagrass beds support diverse consumers, including predatory elasmobranchs. Nevertheless, the high production and low cycling rate of seagrass detritus would ultimately become a large organic carbon pool in the sediments.

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