**Discussion**

In this study, the first quantitative analysis of carbon flows within food webs of GPSC and the adjacent slope was presented. The LIM model results provided a rare opportunity to study how the canyon affect food web structure in comparison with the slope habitat. Moreover, this offered an insight into the ecosystem functioning in the canyon from the aspect of energy flows and food web characteristics such as total system throughput, energy recycling and food web maturity.

**Carbon stock in different compartments**

First of all, the stock data included in our models were appropriately calculated and converted with empirical formulas or conversion factors.

For the abiotic detritus OC stock, the average TOC content in the upper 10 cm of the sediment was 0.39 % and 0.53% in GC1 and GS1, respectively. This value fits in the range of TOC content (c.a. 0.3-0.75 %) reported in previous studies in the southwestern area of Taiwan (Liu et al. 2006; Hsu et al., 2014). In addition, the quantity of converted detritus carbon stocks for the two habitats was of the same order of magnitude as that of the previously mentioned two submarine canyon studies (i.e. Rowe et al., 2008 and van Ovelen et al., 2011). That is, the detritus OC stock reported in Rowe et al. (2008) was 760,000 mg C/ m2in the Mississippi canyon head, and it was about 858,789 mg C/ m2 after summing up all OC input and conversing the unit in the Nazaré canyon head (van Ovelen et al., 2011). Yet, the quantity of detritus OC in the Gaoping submarine canyon head (350,270 ± 104003.4 mg C/ m2) is only half of the value in comparison with the two canyons.

The bacteria samples among the biotic OC stock, however, were only collected in one cruise and 10 times replicate counts were conducted. It has been suggested that the bacteria biomass and production controlling factors in sediments are varied and are often site-specific (van Duyl and Kop, 1994), such as temperature, physical disturbance, sediment substrate, and composition (Yamamoto and Lopez 1985; Alongi, 1988). For instance, seasonal variation in bacterial population and biomass was reported in the shallow slope site in the Baltic Sea (Meyer-Reil, 1983) and several sites ranging from 40 to 1570 m depth in the Cretan Sea (Danovaro et al., 2000). The bacterial abundance and biomass are mainly influenced by the vertical patterns of the distribution of labile organic compounds (Danovaro et al., 2000), while the stock is also changed in response to the food supply. Due to the lack of repeated sampling, it is hard to distinguish the existence of seasonal variation in bacteria stock in GPSC.

Given the impact of typhoons and the monsoon climate, rainfall is highly seasonal in the GPR basin (Liu et al., 2016). Distinct dry (winter) and wet (summer) seasons over the annual cycle of precipitation are attributed to the monsoon climate. In addition, typhoons mostly occur in the summer and early fall, which bring excessive rainfall. Under this circumstance, steep topography, highly erodible drainage basin, and intense human activities lead to extremely high suspended-sediment load and fluvial discharges into the ocean every year (Huh et al., 2009; Liu et al., 2013; Liu et al., 2016). On the other hand, frequent earthquakes events also give rise to the development of turbidity currents (Hsu et al., 2008; Talling et al., 2013; Carter et al., 2014), such as the significant submarine landslides and gravity flows in the lower GPSC and the nearby Fangliao Submarine Canyon triggered by 2006 Pingtung earthquake (Hsu et al., 2008; Su et al., 2012). Therefore, whether the seasonal difference existing in each stock collected between different seasons or not is specially handled with care. Only the OC stock of meiofauna showed a significant difference between seasons, while the limitation of the small sample size of meiofauna was recognized. The unremarkable OC stock difference between seasons might be related to our sampling cruises, which were mostly in the relatively dry spring (March to April) and fall (October to November). Without a notable seasonal difference, each OC stock for all the size groups from respective sites was merged from available data (Table 5), and only the mean value was used in the LIM model.

On the other hand, it had to be recognized that larger size group of benthic animals, such as megafauna and fish were not included in the food web model. Despite that the abundance and biomass of larger organisms are significantly lower and decrease rapidly in the deep sea (Rex et al., 2006), megafauna and fish are found with a great density in some study areas (e.g. Sibuet, 1977; Hecker, 1994; Fodrie et al., 2009). It has been reported that the high density of benthic invertebrates can control the redistribution and quality of OM in the marine sediments (Smallwood & Wolff, 1999). Overall, the role played by megafauna and fish in OM cycling in the communities of current study areas remains unclear.

**Implemented constraints and model limitations**

Except for the OC stocks, the modelled food webs were combined with several physiological and geochemical constraints from the literature (Table 2). These data were implemented as inequalities through setting the minimum and maximum value as lower and upper bounds, respectively. These constraints create the possible solution space for the algorithm to iterate and find a solution set of all flows. However, the input of these constraints creates two level of uncertainty.

Firstly, the physiological constraints in our models were all come from the reference, including *in situ* and laboratory experiments, which were considered low quality (van Oevelen et al., 2010) due to the derivation from other food webs and even different study areas. Due to practical and technical difficulties in invertebrate physiological experiments, there is no constraints of benthic species have been quantified in our study sites. Despite of the lack of site-specific physiological constraints, we used the reference constraints as other LIM studies did. For example, Stratmann et al. (2018) studied the abyssal plain food web of the Peru Basin, and some physiological constraints of benthos which they imposed on the food webs were derived from the studies which focused on shallow-water or intertidal species (e.g. Drazen et al., 2007; Koopmans et al., 2010). In some other food web studies, the physiological constraint of the dominated species would be chosen as the representative for that size group or be separated from the size group as an independent compartment (e.g. De Smet et al., 2016). Though these low-quality constraints bring some uncertainty in our model results, the solution of flows were still more convinced than that without any constraint, such as the external flow of the predated meiofauna and macrofauna (MEI→EXP\_B and MAC→EXP\_B in Fig. 2), which were left to be solve by the model with the only assumption of mass balance for the stock.

On the other hand, the geochemical constraints imposed on our models are site-specific, which are considered high quality (van Oevelen et al., 2010). Although the sedimentation rates and sediment burial efficiency were not directly estimated in GC1 and GS1, these value extracted from GPSC studies (i.e. Huh et al. 2009 and Hsu et al. 2014) were relatively reliable than general accepted values.

Although the direct measured DOU was not used as model input, DOU flow was set to 30% of the *in situ* TOU as the maximum of the DOU constraint. Surprisingly, the results of the DOU flow increased the level of confidence in the model. In GC1, the measured DOU was 19.81 mg C/ m2/ d, which was slightly higher than that resulted from LIM (15.13 mg C/ m2/ d); In GS1, the measured one was 11.66 mg C/ m2/ d, which corresponded well to the direct measurement (11.53 mg C/ m2/ d). In addition, the magnitude of modeled TOU flows was the same as *in situ* data, enhancing the credibility of LIM results.

However, here comes the difficulty to quantify the accurate amount of BMU. Though it seems like only the respiration of meiofauna and macrofauna was considered in our food web structure (Fig. 2), the actual meaning of BMU was incompatible with this simplified process. This parameter not only includes the faunal respiration but the oxygen uptake related to biological activities (Glud et al., 2003). Numerous studies suggest macrobenthos play an important role in diagenetic reactions, sediment-water exchange, and the composition of sediments (e.g. Aller, 1982, 1994) through their activities, such as feeding, burrowing, tube construction, bioirrigation (Jørgensen et al., 2005), and even bioresuspension (Graf & Rosenberg, 1997). For example, Forster & Graf (1995) reported that two macrofauna species, Callianassa subterranea (Decapoda) and Lanice conchilega (Polychaeta) enhance TOU by 85% through their pumping behavior in the shallow North Sea. The animal-induced changes in oxygen distribution are notoriously difficult to quantify and even separate from respiration. Therefore, the simplest and most robust procedure to evaluate the fauna activities in mixed communities is to subtract DOU from TOU (Glud, 2008). Unfortunately, our biomass-based modeled BMU can only consider the respiration of fauna, and thus it turned out to be far less than the calculated results.

On the other hand, the total biomass of meiobenthos and macrobenthos was significantly higher on the slope, which could be explained by our modeled BMU with a higher value in GS1. The calculated *in situ* BMU, however, was not distinctly different in both sites (GC1: 62.34 mg C/ m2/ d; GS1:62.01 mg C/ m2/ d). It reflects the fact that the biomass is poorly related to the bioturbation and thus calculated BMU, which has been pointed out in previous *in situ* experimental studies. In Glud et al. (2003), they found it difficult to relate faunal biomass to bentho-mediated oxygen uptake of a community undergoing seasonal changes. Therefore, the biomass of macrobenthos is not a good proxy to estimate fauna-related oxygen uptake in natural benthic communities.

Liao et al. (2017) have examined the vertical distributions of macrofauna in the sediments, and their results have indicated that the abundance-weighted mean vertical positions of macrobenthos were significantly deeper in the sediment of upper GPSC than that of the slope. In addition, several polychaetes families capable of burrowing deep into the sediment, including paraonids, cossurids, capitellids, and sternaspids, were found thriving in the canyon habitats (Liao et al., 2017). In contrast, the discretely motile, surface deposit, and suspension feeders (e.g. cirratulids, ampharetids, and spionids) were found in the sediment of the slope but diminished in that of the canyon. Therefore, the high BMU value in GC1 may be caused by the active bioturbation.

In fact, SCOC is a generally accepted measure of total benthic carbon degradation in marine sediments, and it is considered to be the most reliable proxy because it integrated degradation through several biogeochemical processes (e.g. aerobic activity, nitrification, and re-oxidation of reduced inorganic compounds) (Stratmann et al.,2019). Therefore, a benthic activity which response to a variation in POC input should be reflected by a variation in SCOC. Early in Smith (1987), however, it had been pointed out that the vertical POC flux determined by sediment traps does not match the carbon demand of the benthic community. Smith and Kaufmann (1999) reported a long-term discrepancy between food supply and demand in the Eastern North Pacific, the POC fluxes contributed only 52% to 59% of the SCOC. On the abyssal plain in the deep Arabian Sea, the imbalance between carbon supply and demand varied regionally (Witte & Pfannkuche, 1999), the trap fluxes matched 50% of the benthic carbon demand in their southernmost station but only 20% in the westernmost station. These mismatches were mainly explained as the uncertainties in respect to relatively short-term SCOC incubations via long-term sediment trap deployment (Witte & Pfannkuche, 1999). In addition, several studies suggested the quantity and the quality of settling OM should play a crucial role in the benthic response (Soetart et al., 1996; Rabouille et al., 1998).

Besides, the benthic oxygen consumption rates can be affected by a combination of factors, including primary production, quality of OM, and bottom-water oxygen concentrations (Jahnke, 1996; Wenzhöfer and Glud, 2002). It has been reported that the dissolved oxygen concentration in bottom water increased toward the canyon head in GPSC (Liao et al., 2017). Also, Wang et al. (2008) have reported that the flow velocity near the head of GPSC regularly exceeded 1 m/ s with the *in situ* observations from moored and shipboard acoustic Doppler current profilers (ADCP). This high flow velocity leads to strong bottom-water currents and strong resuspension of surficial sediments (Moodley et al., 1998), which may result in the high oxygen consumption rates measured at GC1. In short, the peculiarly high value of calculated *in situ* BMU in GC1 might be consumed by the underestimated bioturbation, physical disturbances, and chemical oxidation.

Another issue is that the difference between flow values calculated by different algorithms (Fig. 12). As previously mentioned, the food web of GPSC and the adjacent slope were modeled based on a large data set comprising site-specific biogeochemical data, physiological constraints, and empirical relations from the literature. Despite that a variety of constraints was imposed in our model, it was still insufficient to quantify a unique solution set. These constraints, however, imply that a ‘‘solution space’’ exists (van Oevelen et al., 2010). Within the solution space, an infinite number of solutions set which are consistent with the data are present (Soetaert and van Oevelen, 2009). While the conventional single-solution modeling approach typically provided a mathematically “the best” solution set, the solution of flows was mostly close to the boundaries of the solution space as shown in (Fig. 12). On the other hand, the likelihood method based on the MCMC algorithm provided multiple solution sets, which could form a distribution of a probability density function (PDF) in the solution space. With this multi-solution approach, the solution sets are sampled from the solution space (Van den Meersche et al., 2009), and the mean of this sampled set could represent the central flow values which are less sensitive to the boundaries of the solution space (Van Oevelen et al., 2010). For each flow in our model, the mean and standard deviations of the 10,000 solutions were calculated. Though the standard deviation represents how the uncertainty in the data set propagates to an uncertainty on the flow value (Van Oevelen et al., 2010), it still should be noted that the standard deviation was artificially set to a ±2% error margin to iterate until the convergence of solution sets.

**Carbon demand from the benthic community**

The initial attempt to insert the POC rain flux from the reference failed. This conflict problem is often seen in LIM studies (e.g. van Ovelen et al., 2011; De Smet et al., 2016). For example, De Smet et al. (2016) studied the *L. conchilega* reef with LIM models. Most of their models could not be solved when they direct set the *in situ* primary production rates as the input, because this rate did not take into account the OM brought from the external water flow. Therefore, they added a flow as additional OM input, and then left the value of which to be determined by the model itself. Similarly, in our food web structure, only the particulate form of OC was considered as the input of POC rain flux, which may ignore the direct dissolved organic matter (DOM) assumption by the bacteria. As a result, the reference value (53.85 mg C/ m2/ d) was not sufficient for supporting the whole system. DOM is expected to be taken up more easily than POM for bacteria because they need to produce enzymes to hydrolyze polymeric sinking particles before the material pass through cell membranes and the metabolization (Verdugo et al., 2004). Moreover, Pape et al. (2013) conducted experiments to evaluate the fate of DOM carbon in different benthic environments (North Atlantic and Western Mediterranean slope sites), which resulted in bacteria dominating DOM carbon uptake.

To solve the deficiency of OC input and the contradiction of the model, our research question should be revised to quantify the amount of the least carbon demand in the system under our simplified food web structure. From the LIM results (Fig. 13 and Fig. 14), the OC demand for the two sites (GC1: 131.08 mg C/ m2/ d; GS1: 78.95 mg C/ m2/ d) was larger than the reference value, especially in the canyon head, which was larger by a factor of three. This indicates a substantial proportion of carbon that may enter the microbial loop as dissolved form. Besides, the converted POC flux reported in Liu et al. (2006) was 6 to 10 times higher than both the reference estimation (Huh et al., 2009) and our modelled value. This discrepancy has also been found in the Nazaré Canyon (de Stigter et al. 2007), which may be resulted from the sediment resuspension triggered by the strong bottom currents.

**Network characteristics**

Indices base on network are often calculated to describe the function of food web (Kone et al., 2009). Here, five indices were used to estimate the food webs in GC1 and GS1.

and quantify the energy which belongs to the system as the sum of flows, as a result, the magnitude of these two indices directly link to the growth of the ecosystem. The higher carbon processing in the canyon head is reflected by higher value of and , which represent the total amount of energy flow through the system (Ulanowicz, 1986; 2004). However, the growth cannot provide detail about how the material is distributed within the system, in other words, two systems with totally different structure may be featured with the same (Bodini, 2012). Therefore, two other index analyses were carried out to estimate the maturity of the two ecosystems. According to Odum (1969), a mature ecosystem should involve a higher information content, high biomass and a high capacity to seize and hold the nutrients for cycling within the system. The Finn cycling index(), developed by Finn (1976), measure the fraction of total carbon cycling generated by recycling processes. Our data show that the is marginally greater in GS1 than in GC1, indicating that the slope system with a higher degree of energy recycling is a mature ecosystem which develops completed routes for nutrient conservation (Odum, 1969) in contrast to the canyon system. Moreover, the relatively higher biodiversity (Fig. 7 and Fig. 9) and carbon stock (Table 5) in GS1 also shows that the ecosystem on the slope is more mature than the frequently disturbed canyon, which mainly dominated by the bacteria-related process. The low carbon stock of larger size faunal group in GC1 indicates that the head of Gaping Submarine Canyon is a fragile ecosystem under the severe physical perturbation as reported in Liao et al. (2017) and Liao et al. (2020). The in different sections of Nazare canyon and previously reported benthic ecosystems are found in the range of 5% to 20% (van Oevelen et al., 2011; Kones et al., 2009; Anh et al., 2015),while our are still within this range (GC1: 7 %; GS1: 13%).

The rest index, , is suggested to be an indicative index for the developmental status of an ecological network (Ulanowicz,1980). The magnitude of value is determined by the number of constraints, that is, the more the constraint are in effect, the less the uncertainty is in the system, therefore, the higher value the will be.

In the aspect of model structure, if the distribution of the energy passes through only few, efficient route, the cost of maintenance for the whole system would decrease (Bodini, 2012). On the other hand, a highly redundant network which is less organized would have a lower value. It follows that value is expected to be lower at early immature stage of the ecosystem(Mukherjee et al., 2019). From our data, though the of GS1 was insignificantly higher than that of GC1, it would be higher at low disturbance condition.

The turnover rate (or residence time) of OM can be considered as a function of stock size and energy transfer in/out of the stock. In deep-sea studies, scientists quantify the sediment stock and the POC fluxes and thus derive the turnover rate (e.g. Rowe et al., 2008). However, the quantification of OM turnover is far more complicated because of the various sediment composition and organism taxa assemblages with the change of locations. From another point of view, the turnover rate also describes the mechanism for consuming OM through aerobic or anaerobic utilization by the whole benthic community (Rowe et al., 1990). Therefore, carbon stocks divided by the oxygen demand (i.e. TOU, DOU, and BMU) in terms of carbon equivalents can be adopted as an alternative method of OC turnover rate derivation.

The turnover time of total OC estimated by the model results (table.) was the order of decade in the canyon head, while it appeared to be over a century on the slope. The turnover time in GC1 (63year) is similar to the turnover rate reported at the head of Mississippi Canyon (57 years; Rowe et al., 2008). Similarly, this rate of GS1 (101 years) is also similar to the turnover on the slope station near the Demerara Abyssal Plain (132 years; Rowe et al., 1990). The longer residence time in GS1 corresponds to the interpretation of , revealing the carbon is recycled in the slope habitat.

On the other hand, though the turnover time derived from the direct measurement was shorter than that derived from modeled estimations, it is not unlikely to be true. For example, Rowe et al. (1991) reported the residence time on a mean of 11 years on the continental shelf which is 150 meters deep. Hence, this contradiction might be attributed to the underestimated bioturbation or physical disturbance in the real environment.

**Burial efficiency and carbon sequestration in the GPSC**

In our model, the burial efficiency was calculated as the ratio of burial flow (Sediment→Burial in Fig. 2) to POC flux (POC→Sediment in Fig. 2). While this fraction of the two study sites was peculiarly high, which might be resulted from multiple factors. The burial flow was constrained by the sedimentation rate measured in Huh et al. (2009) and Hsu et al. (2014). Then, the quantity of this flow is again used as the constraint of the POC flux as the burial efficiency estimated by Hsu et al. (2014). Herein lies the high uncertainty of the burial efficiency. Though the study site in Hsu et al. (2014) is on the Gaoping continental shelf which is close to the GPSC and adjacent slope, this literature source is still accepted as the less strict data (van Ovelen et al., 2010). That is, the reported burial efficiency (24%; Hsu et al.,2014) was set as the lower bound of the constraint, and the upper bound of which was set as 100%. Finally, the quantity of all flow in the whole food web was calculated with the MCMC algorithm considering all biogeochemical constraints in the system. Hence, the unusually high burial efficiency is not groundless, and it is a logical outcome under the current model structure and input setting.

Submarine canyon head has been considered significant for carbon sink and the process of carbon sequestration. It has been suggested that the burial efficiency in the Nazaré Canyon head be about 30%-80% (Masson et al. 2010) according to different estimation techniques. Furthermore, Krause-Jensen & Duarte (2016) suggests macroalgal detritus can be sequestrated through the burial and transport in the submarine canyon. It has also been reported that the submarine canyon in the northwestern Mediterranean features efficient carbon sequestration through the dense water cascading along with phytoplankton blooms (Canals et al.,2022). As a part of the carbon “source to sink” system, the GPSC not only transports a large amount of matter from the continental shelf to the deep ocean basin but also performs the important function of carbon sequestration.

In Taiwan, another often discussed blue carbon ecosystem is the relatively well-studied mangrove area distributed along the western coast. Given the mangrove wetlands locates between rivers downstream and the coastline, mangroves also play a crucial role in carbon sequestration. Owing to their high productivity (Bouillon et al., 2008), the mangroves can store up to 88% of their OC in the deeper sediment (Donato et al., 2011). However, multiple reasons could affect the carbon burial rates in different mangrove ecosystems, such as temperature, seasonal differences (Alongi et al., 2004; Van Santen et al., 2007), and hydrological disturbance (Marchio et al., 2016). Li et al. (2018) have reported that the carbon burial rates in Taiwan are much lower than the global average rate, which might be resulted from the faster decomposition process. On the other hand, deforestation and rapid sea-level elevation are major threats to mangroves (Polidoro et al., 2010), causing a 35-86% decline over the past quarter-century (Duke et al., 2007). When mangrove areas become fragmented, their long-term survival is at great risk, and their ecosystem services may functionally disappear. Consequently, it is important to focus on the study of other effective carbon sinks which may help achieve carbon neutrality. The current study revealed the high carbon burial rates in the benthic community in the GPSC, which not only extends our knowledge of ecosystem functioning in this area but also improves the understanding of natural carbon storage in a part of the “S2S” system.

Moreover, investigating the particle fluxes helps us better understand the transfer and fate of materials loads to the deep-sea ecosystem, which may help develop better research strategies for predicting the potential impacts of climate change.

**Conclusion**

This is the first carbon cycling of the food web model study applied in the GPSC and on the adjacent slope. Moreover, it is the first study applied with the LIM technique in Taiwan. There was no significant difference in each OC stock between different sampling seasons. However, the standing stocks of each compartment in the two habitats were significantly different. In the canyon head, the relatively lower biodiversity and faunal carbon stocks show that this fragile ecosystem is under severe physical perturbation. The model results revealed that the canyon head of the GPSC was mainly dominated by the bacteria-related process. By contrast, the higher contribution of fauna in carbon processing on the adjacent slope presents a relatively mature ecosystem. In addition, our models revealed a higher carbon burial rate in GC1, indicating the GPSC not only transports sediment to the deep SCS but functions as an important role in carbon sequestration. Though our simplified models may ignore the influence of larger size faunas, they effectively quantified the matter and energy transfer across the deep-sea systems which are notoriously difficult to study.

Owing to the ongoing climate change, the geohazards in the submarine canyons might be more frequently triggered as a consequence of new weather systems with a higher intensity of flooding in SMRs. The study of matter and energy transfer in the ocean will help us understand how deep ecosystems are fueled, and determine their capacity to capture and store carbon. By better understanding carbon cycling in submarine canyons like GPSC, we may be able to predict the impact of climate change or human influence on deep-sea ecosystems.