**Introduction (2,000)**

1. **Introduction**
   1. **Submarine canyon**

Submarine canyons are steep-walled V-shaped valleys incised into continental margins (Shepard 1973; Shepard 1981), directly connecting continental shelves to deep ocean basins by transporting sediments and organic matters(OM) (Vetter and Dayton, 1999; Epping et al., 2002; Nittrouer and Wright, 1994). Shepard & Dill (1966) reviewed the distribution, characteristics, and origins of submarine canyons and mapped 96 major canyons around the world. Later, the more detailed bathymetric data was reported (De Leo et al., 2010), showing abundant and ubiquitous submarine canyons crossing continental margins globally.

Though the benthic community structure and productivity have been relatively less studied in canyons, some findings suggest that biomass hotspots and high benthic diversity in the canyon can be attributed to higher habitat heterogeneity (De Leo et al, 2014; McClain & Barry, 2010). For example, the higher trophic complexity of meiofauna assemblages varied in sediment environments along with heterogeneity between sampling localities (Ramalho et al., 2014). Moreover, economically important rockfishes are benefited from the natural refuge in Soquel Submarine Canyon in Monterey Bay, because the high-relief structures of boulders and rock outcrops in deep-water narrow canyons are less accessible to fishing activities (Yoklavich et al., 2000). Other remarkable ecological and physical characteristics of submarine canyons have also been reported, such as the focusing effect of intensified internal waves (Hall & Carter, 2011), the interaction of canyon between coastal ecosystem contributes significantly to high productivity through seasonal upwelling (Sobarzo et al., 2001), and the trapping effect on the dense aggregation of diel vertical migrators (Greene et al., 1988; Maycas et al., 1999).

Complex topographic features in submarine canyons are often characterized by water flow, sediment transport, and accumulation (de Stigter et al., 2007; Oliveira et al., 2007). Some oceanographic physical conditions or events inside canyons, such as bottom flows, accelerated currents, and dense water cascade caused by topographic and climate effects, increase the concentration of suspended particulate matter and transport of sediment (Keller et al., 1973; Puig et al., 2008; Gaudin et al., 2009). Such an increase OM from the coastal zone is not only the essential energy to the undernourished deep sea ecosystems(Rex et al., 2006; Wei et al., 2010), but also be responsible for enhancing biodiversity and productivity (Rowe 1971; Vetter & Dayton, 1998; Schlacher et al., 2007). Here, we studied the Gaoping submarine canyon (GPSC) and Gaoping Slope (GS) off southwestern Taiwan.

* 1. **Compare GPSC with GS**

Five geomorphic units comprise the source-to-sink dispersal system in the SW Taiwan, including the Gaoping River drainage basin, the Gaoping Shelf, the Gaoping Slope, the Gaoping submarine canyon and the Manila Trench in the northernmost South China Sea (SCS).

As a part of sediment dispersal system, the Gaoping Slope continues from the narrow (<10 km) continental shelf edge, extending southwest toward the northern SCS. The slope can be divided into an upper and a lower part with an isobaths of 1000 m to 1200 m in water depth (Yu et al., 2009). On the other hand, GPSC is with a distance of 260 km long, extending from the river mouth of Gaoping River (GPR), crossing through the shelf and slope, finally merging into the trench (Liu et al, 2016). The canyon comprises three geographically distinct segments. The upper section flows meandering southwestward on the slope area, ranging from 126 to 1750 m in water depth featured in great relief; The middle reach runs southeastward toward along with an elongate escarpment with a range of 1750 to 2800 m in water depth, making a sharp turn to the southwestern and connecting the lower section which ranges from 2800 to 3600 m in water depth, finally flowing downslope to the northern of the trench (Yu et al., 2009).

(POC 含量在canyon and slope 不同)

(distinct difference environmental factors→community structures)

As the head of GPSC is connected with the GPR, a small mountainous river characterized by high sediment load, it is reported to transport 14 to 49 MT sediments (Liu et al., 2009; Hsu et al., 2014) and turbidity currents every year (Liu et al., 2013, 2016; Gavey et al., 2017).

More than 27 g m-2 d-1 of sediments are accumulated on the upper GPSC seafloor, which is approximately 4 to 270 times less than the mass flux measured from the sediment traps (Hsu et al., 2014; Huh et al., 2009). Previous studies suggested that if organic carbon (OC) in both estimates are equal, most of the OC is likely exported down the canyon and buried in the deep South China Sea (Hsu et al., 2014; Kao et al., 2014; Liu et al., 2013; 2016). However, this view completely ignores the biological role of sediment benthos, which remineralize OC through feeding, burrowing, respiration, and predation and it may lead to mistaken estimates of the OC cycling on the seabed (Snelgrove et al., 2017).

despite a wealth of literature and interests in the GPSC’s unique geology, information is lacking on how benthic communities, especially the very small but numerically dominant meiofauna, respond to such extreme environmental conditions. This study thus attempts to conduct the first meiofauna diversity investigation in the GPSC and to contribute to the growing interests in understanding the ecological processes in the benthic communities in highly dynamic conditions.

former one acts as a major conduit for marine-terrestrial sediment and carbon transport while

The meandering, V-shaped, and entrenched thalweg with deep-cutting outer bends are characteristic features of the GPSC (Figure 1). These erosive features are believed to be maintained by turbidity currents triggered by (1) flood events (Liu et al., 2013, 2016), (2) turbulence mixing related to internal and surface waves (Wang et al., 2008; Lee et al., 2009; Chiou et al., 2011), (3) submarine groundwater discharges (Su et al., 2012), and (4) sediment collapses from over-steepening canyon walls following earthquakes (Hsu et al., 2008; Su et al., 2012; Gavey et al., 2017). The GPSC is filled with the effluent of Gaoping River, Kuroshio Current Water, and South China Sea Water, in which the mixing of these water masses is controlled by internal tides (Liu et al., 2002, 2006). The internal tides in the GPSC follow semidiurnal cycles (M2), in which the intensity increases toward the canyon head, or in other words, decreases with depth and with distance from the canyon head (Wang et al., 2008). The energy flux of internal tide in the GPSC is estimated to be 3–7 times greater than that in the Monterey Canyon (Lee et al., 2009); therefore, the isothermal displacement by the internal tides can be easily over a water depth of 200 meters in the GPSC (Liu et al., 2016). Another consequence of the strong internal waves is the year-round existence of a benthic nepheloid layer as thick as 100 m with the suspended sediment concentration reaching 30 mg/l (Liu et al., 2010). The turbulence mixing associated with internal tides and high suspended-sediment concentrations near the seabed are believed to result in significant sediment transport (Liu et al., 2016).

* 1. **Carbon flows in deep sea environment**

1. **Food web**
   1. **Importance**

　　The deep-sea benthic ecosystems depend on the slow sinking of detritus derived from primary production in the euphotic zone. Before settling on the seabed, suspension feeders first consume the detritus from the overlying bottom water (Gage and Tyler, 1996). Bacteria (Lochte and Turley, 1988) and deposit feeders (Blair et al., 1996) of all sizes, who respond rapidly to the change of food supplies with metabolic activities, such as growth and reproduction, consume the remaining detritus deposited on the seafloor (Tyler et al., 1982; C.R. Smith et al., 2008). Then, the detritivores are predated by larger animals such as megafauna and fish. The waste products of all consumers again become food for deposit-feeders and bacteria or are released back to the water column as dissolved inorganic carbon (DIC) or nutrients. In brief, the food web comprises the abiotic (detritus, DIC, etc.), biotic compartments, and the linkage of flows between one another. Identifying and quantifying energy flows in the food web is essential to understanding their functional interactions. However, the direct measurement and experimentation are notoriously tricky, even for relatively well-studied shallow-water benthic ecosystems (e.g., van Oevelen et al., 2006), not to mention the undersampled deep-sea ecosystems. A linear inverse model (LIM) has thus been developed and applied to marine food-web studies to deal with data limitations (Ve´zina and Platt, 1988).

* **Linear inverse modelling**

1. **Food web of submarine canyon** (**literature review)**
2. **Aim of this study**
   1. **First LIM model apply in GPSC**
   2. **Difference in carbon flow between GC1 and GS1**
   3. **Compare with other submarine canyons**

**Material and Method (2000)**

1. **Studying sites and sampling**

* **Map**
* **Cruises information**
* **Treatments of samples**
  + **Sediment-related**
  + **Biotic**
    - **Bacteria**
    - **Macrofauna**
    - **Meiofauna**

1. **Linear inverse model formulation**

* **Structure**
  + **Simple**

　　Linear inverse modeling starts with choosing relevant abiotic and biotic compartments and specifying the links between them (Fig. 14). We assumed that the influx POC is a complex assemblage of organic matters derived from the water column with a portion of energy flowing out the sedimentary system through the process of burial and/or export (orange flows). Then, the black flows assume that bacteria feed only on detrital OC; meiofauna feeds on bacteria and detrital OC; macrofauna feeds on meiofauna, bacteria, and detrital OC. Then, the meiofauna will be further divided into selective deposit feeders, non-selective deposit feeders, epigrowth feeders, and omnivores/predators (Liao et al., 2020). The macrofauna stocks will be divided into surface deposit-feeders, subsurface deposit-feeders, suspension-feeders, and predators/scavengers (Chen, 2018). Moreover, it is presumed that the predators of each size class prey on organisms of the same and smaller size classes. The grey flows indicate carbon loss as feces and consume by benthopelagic/pelagic predators (Fig. 14). In this LIM model, the compartments with orange color are part of the food web model, whereas the compartments with blue color are only considered carbon influx or efflux but are not directly modeled.

* **Mass balances**

　　A broadly accepted physical constraint is that mass is conserved for each chemical element, and this mass balance principle is the backbone of the food web model. First of all, the mass balance can be written as the general form:

(eq 1),

indicating that the temporal mass change of a compartment(X) is equal to the difference between the incoming( and outgoing( flows. Therefore, if is larger than , X will increase in time. Based on this principle, we can derive the mass balance equations of all the compartments with the assumption that all the compartments are invariant in time:

(eq 2)

Furthermore, this mass balance principle can also be applied to organisms’ physiological behaviors. For example, when organisms ingest food, only part of the food is assimilated, and the rest is expelled as feces. The assimilated food is used to maintain its basal metabolism, growth, and reproduction. For heterotrophic organisms, the energy needed for growth and maintenance is paid by respiration. Thus, we can write this process as:

(eq 3),

Where is the biomass of the organism, and is its growth rate. This mass-balance equation states that the biomass changes to the difference between feeding and loss terms. Note that the balance of all food web compartments is tightly linked. For instance, if species A feeds on species B, not only does an increased flux flow into A, but a loss of the same magnitude of flux flows out of B. As a result, the direction of the flows matters, and we can take the mass-balanced equation as sums and subtractions of these unknown quantities of flows. We classify this linear mass balance equation as the “equality equation”. It can be expressed with matrix notation in the general form:, in which x is a vector consisting of unknown flows, b is a vector consisting of changed rates of the component, and the flows are non-negative quantities, .

* + **Stock calculation**
    - **Sediment-related**
    - **Biomass**
* **Constraints**

　　　　On the other hand, the physiology and behavior of organisms impose a limitation on their feeding and growth rates with upper bound and lower bound. For example, when organisms search for food, not only the encounter rate but the external handling time determines the maximal foraging capacity (Holling, 1966). Also, physiological and digestive constraints regulate the process of assimilation of ingested food. Therefore, animals can only process a finite amount of food per unit per time. These maximum rates impose an upper bound on ingestion flows, providing important constraints on the magnitudes of the grazing flows in the model. Similarly, respiration flows are restricted by allometric rules (e.g., Mahaut et al., 1995). The minimal basal respiration rate required for sustain metabolism is imposed as lower bounds. Other physiological constraints restrict the relationships between flows. For example, growth efficiency is defined as the ratio of secondary production to assimilated food, which is suggested to be 60-80% (Calow,1977; Schroeder, 1981). These constraints can also be transformed into a matrix equation with inequality:, in which x is still unknown-flows vector, h is a vector comprise constraints. Most of these constraints can be extracted from literature. Here we will apply the four most used constraints in LIM studies (van Oevelen et al., 2006; Stratmann et al., 2018) to our model, including assimilation efficiency (AE), net growth efficiency (NGE), production (P), and respiration (R). AE is calculated as , where I is the ingested food and F is the feces (Crisp,1971). The minium-maximum range is set from 0.29 to 0.77 for meiofauna (Hendriks, 1999; van Oevelen et al., 2006) and from 0.62 to 0.87 for macrofauna (Stratmann et al., unpublished). NGE is calculated as , where P is the secondary production and R is respiration (Clausen and Riisgård, 1996). The minimum-maximum range is set from 0.6 to 0.9 for meiofauna (Hendriks, 1999), and from 0.6 to 0.72 for macrofauna (Navarro et al., 1994, Nielsen et al., 1995). The secondary production (P) is calculated as , and the for meiofauna is set between 0.05 and 0.2 (Hendriks, 1999), while for macrofauna is set between 0.01 and 0.05 (Tenore 1982). And the respiration is calculated as, where bsFR is the biomass-specific faunal respiration rate, which ranges from 0.021 and 0.032 (Moodley et al., 2008) for meiofauna, and 7.12×10-5 and 2.28 × 10−2 for macrofauna.

* + **Assimilation efficiency**
  + **Net growth efficiency**
  + **P/B ratio**
  + **Respiration rate**

The data types mentioned above are derived from the general principles applied to the most ecosystem; however, the in situ data is still necessary to deal with a food web model of a specific location. In our model, estimated biomass are the stocks of organism compartments, while the SCOC data and POC flux are served as directly measured flows. Because of the valuable information from site-specific measurements, this type of data is generally implemented as equality equations: , where f represents the vector that contains *in situ* data.

* **Likelihood method**
* **Model Solution:** To achieve the final model, we will combine three types of data, including mass balance equations, physiological constraints, and in situ data. The solution of this model is a set of flow values (**x**). Depending on the number of equations and the numbers of the unknowns, different methods of solution are used. Ideally, the equations lead to only one set of solutions that perfectly fits the data when the number of equations equals to the numbers of the unknowns. However, the most commonly encountered situation is that the number of equations is far less than the number of unknowns. As a result, there is no unique solution set, whereas an infinite number of valid solution sets exist, creating a multidimensional solution space. Earlier modeling studies usually selected one solution from this solution space. The principle of parsimony, the flow set with the minimal sum of squared value, had often been applied as the selection criterion (Vézina and Platt, 1988). However, the parsimonious food web model usually takes extreme values to meet the criterion (Difendorfer et al., 2001; Kones et al., 2006). Alternatively, a likelihood approach based on Markov Chain Monte Carlo (MCMC) algorithm has been developed, which calculates the mean values and standard deviations of the flows from the possible solution sets (Kones et al., 2006). We will use *LIM* package (Soetaert and Herman, 2009; van Oevelen et al., 2010) in R (R Development Core Team 2020) to set up and solve the conceptual food-web model (Fig. 14) using MCMC and likelihood approach.
* **Network flow indices of ecosystems:** After *LIM* solves the food web model, we will conduct network analysis to better understand the structural properties and energy transformations in the ecosystem. Several network indices will be calculated from the outputs of LIM to examine the food-web functioning with uncertainty estimation (Kones et al., 2009).
* The descriptions of symbols used in network indices calculations are shown in Table 2 and Table 3. Assuming that a system has compartments, and the flow value is defined as a sink-to-source flow (i.e. ). The total system throughput () is a measure of the growth and size of the system, obtained by summing all flow magnitudes, while the total system throughflow () is the sum of compartmental throughflows. These two indices infer the general properties of the food web system. That is, the more material or energy flowing through the system, the larger the value of and will be. The cycled portion of the total system through flow () is the sum of cycled flow in all through flows (Finn, 1976). The proportion of and is referred to as the Finn cycling index (), which summarizes the fraction of the material/energy that is generated by the recycling process (Allesina and Ulanowicz, 2004). Finally, the index average mutual information () based on communication theory measures the average amount of constraint placed on an arbitrary unit of flow from one compartment to another (Ulanowicz, 1997). Therefore, Ulanowicz (1980) proposed that AMI is indicative of the developmental status of a system. In other words, trophic specialization and climax community will result in a higher AMI value (Ulanowicz, 2004). More details on the calculation of the indices can be found by Ulanowicz (2004) and Kones et al. (2009). All the network indices will be directly calculated in R using R-package NetIndices (Kones et al., 2009).
* **Network indices**

**Result (1000)**

* **Environment data**
  + **CTD → bottom water temperature**
  + **Sediment → OC content**
  + **SCOC →TOU and BMU**
* **Benthic community structure**
  + **Abundance**
  + **Biomass**
  + **Seasonality**
* **Model results**
  + **Simple**
    - **Different**
    - **Web plot / segment chart**

**Discussion (1200)**

**Conclusion**

Table. 2. Nomenclature of symbols used in calculation of network indices.

|  |  |
| --- | --- |
| Term | Description |
|  | Number of internal compartments in the network, excluding 0 (zero), and |
|  | External source |
|  | Useable export from the food web |
|  | Unusable export from the food web |
|  | Flow from compartment to where represents the columns of the flow matrix and the rows |
|  | Flow matrix, excluding flows to and from the externals |
|  | Total inflows to compartment |
|  | Total outflows from compartment |
|  | Total inflows to compartment excluding inflow from external sources |
|  | Total outflows from compartment excluding outflow to external sources |
|  | A negative state derivative, considered as a gain to the system pool of mobile energy |
|  | A positive state derivative, considered as a loss from the system pool of mobile energy |
|  | Flow into compartment from outside the network |
|  | Flow out of the network for compartment to compartments and respectively |
|  | The number of species with which both interact divided by the number of species with which either or interact |
|  | Identity matrix |

Table. 3. Algorithms for the calculation of the network indices.

|  |  |  |
| --- | --- | --- |
| Index name | Code | Formula |
| Total system Throughput |  |  |
| Total system throughflow |  |  |
| Total system cylced throughflow |  |  |
| Finn's cycling index |  |  |
| Average mutual information |  |  |

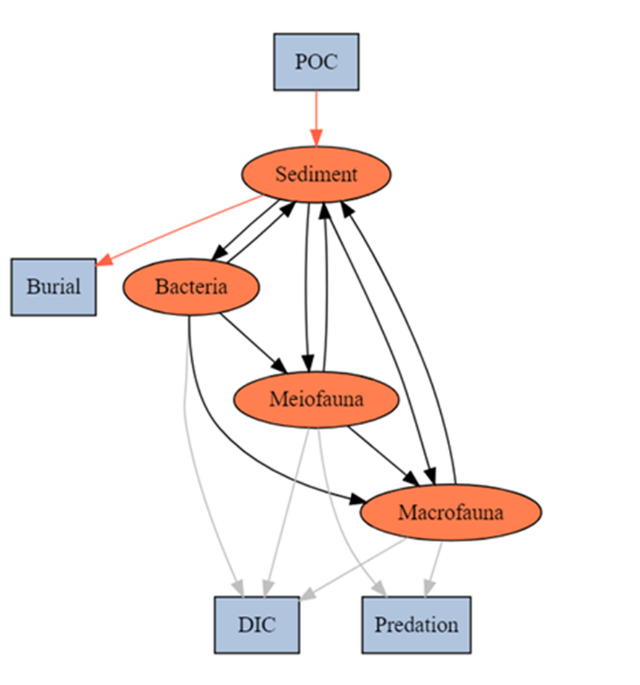
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Fig. 14. Conceptual benthic food web model off SW Taiwan