**Introduction (< 3,500)**

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 deepsea 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 in terms of physical conditions and community structure**

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 the 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 isobath 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 north of the trench (Yu et al., 2009).

The physical settings at the GPSC and GS are markedly different along with the distinct topographic features. Hsu et al. (2013) suggested that the “filling-and-spilling” plays a key sedimentary process on the overall GS, whereas the transporting processes of tectonic activities, mass wasting events, and canyon and channel feedings diversified the mechanisms from the inner to outer slopes. Moreover, in contrast to the lower GS, higher accommodation rates and relatively slower deposition rates on the upper GS were reported (Hsu et al., 2013). On the other hand, much more complex depositional and transport systems lie in the submarine canyons. Despite the downward particle fluxes, the erosional process (Mulder et al., 2001) caused by gravity currents such as turbidity currents and hyperpycnal flows dominated the submarine canyons. The GPSC is also subjected to the strong internal tides which originate from the Luzon Strait and southeastern Taiwan Strait (Chiou et al., 2011; Jan et al., 2008). Accompanying the semidiurnal tides (M2), the head-ward propagation of the internal tidal waves converges as beam parallel waves at the bottom canyon (Wang et al., 2008). Also, the existence of isopycnal surfaces in the head region of GPSC can be conducive to the generation and propagation of internal tides (Lee et al., 2009; Liu et al., 2002; Wang et al., 2008). Above the canyon seafloor, the thick benthic nepheloid layer (BNL) maintained by currents-caused resuspension could be greater than 100 m, and the suspended sediment concentration (SSC) in the BNL could exceed 30 mg/l (Liu et al., 2002).

In addition, food availability has been considered as the most important driving force for the abundance, diversity, and composition of the deep-sea benthic ecosystem (McClain et al., 2012; Rex et al., 2006). Some proxies have been widely used to determine sedimentation sources. For example, the total organic carbon (TOC) content in marine sediments is a common proxy for OM deposition from the water column to the seafloor. Meanwhile, because the consumed rate of nitrogen is higher than carbon (Danovaro, 2010; Meyers, 1994), the TOC to nitrogen (C/N) ratio can provide the estimations on the aging and sources of OM. Generally, the benthic population densities decline with depth because of the declinature of sinking POM flux (McClain and Rex, 2015; Wei et al., 2010), while higher population densities are expected in the submarine canyon head due to the concentration of OM. Liao et al. (2017) compared the GPSC and GS in terms of the TOC contents and C/N ratios, however, the results of which surprisingly against their expectation. The TOC was negatively related to the tidal currents speed, resulting in a lower faunal abundance and diversity in the surface sediments in the canyon head. While the TOC increased toward the GS with a result of overall higher benthos population density, indicating that there were significant influences of food supplies on benthic community structure.

The benthic macrofaunal and meiofaunal community structure in the GPSC and GS were thoroughly studied in Liao et al. (2017) and Liao et al. (2020). Unlike previously mentioned high productivity submarine canyons, the upper GPSC was severely impacted by physical disturbance triggered by internal tides and the gravity flows. These physical extremes overwhelmed the function of enhancing food availability in the active submarine canyons. Moreover, the biological response to frequent disturbance such as reduction and loss in species richness or total abundance, alteration of taxonomic composition, and the deepened dwelling distribution of the burrowing infauna in sediment, showed the communities were undergoing intense disturbance (Liao et al., 2017). Moreover, significantly distinct two nematodes assemblages were identified in the GPSC and GS (Liao et al., 2020). The nematodes species, maturity, functional and trophic diversity were severely depressed in the GPSC, corresponding to the environmental indicators such as strong near-bottom currents speed and lower TOC. The distinction of nematodes species composition was attributed to the species replacement resulting from environmental filtering. In the GPSC, nematodes assemblages were dominated by r-strategist non-selective deposit feeders with clavate tails, whereas the species with longer lifespans, diverse feeding strategies, and tail shapes coexisted on the slope area. Though environmental filtering was considered as the main mechanism, the nestedness patterns (Baselga, 2010; 2012) indicated that species immigration and local extinction may also occupy crucial roles in shaping the species composition in the canyon.

* 1. **Carbon flows and food webs in deepsea environment**

　　Despite that the unique geology and biological community structure in the GPSC and GS were relatively well studied, the biogeochemical cycles in the sediment and the environmental effect on ecosystem functioning remain unknown. Biogeochemical cycles in aquatic sediments depend on coupled reaction and several transport processes, including diffusion, advection, and biologically induced transport (Meile et al., 2001). For example, macrobenthos enhance solute transport with water from the sediment-water interface through burrowing activities (i.e. bioirrigation). In sediment where with high macrofauna densities (e.g., Hammond and Fuller 1979; Archer and Devol 1992), bioirrigation-increased fluxes exchange rather than diffusion mainly attributed the measured benthic fluxes across the sediment-water interface. On the other hand, ecosystem functioning is defined as the flow of matter and energy transfer within or between different trophic levels or ecosystems (Danovaro et al., 2008; Loreau, 2008). For instance, burrowing infauna and epifauna may affect microbial carbon remineralization, sediment oxygen penetration, carbon storage, and nutrient regenerations through reworking sediment and bioirrigation (Lohrer et al., 2004). In addition, the feeding, growth, predation, and mortality of the benthos directly affect the productivity, nutrient cycling, organic matter decomposition, and carbon sequestration on the seafloor (Snelgrove et al., 2014).

　　The estimate of annual sediment transporting from the Gaoping Rivers into the GPSC ranged from 45.6 to 110 MT (Hsu et al., 2014). This quantity is about 30-80% of the sediment transport in the Mississippi River (~145 MT yr-1, Meade and Moody, 2010). However, the annual accumulation fluxes were 2-12 MT yr-1 of sediments in the Gaoping shelf and slope area (Hsu et al., 2014; Huh et al., 2009), which is approximately 4 to 55 times less than the transporting mass flux. Thus, most of the sediment, especially the organic carbon (OC) content, is likely exported down through the GPSC and buried in the deep South China Sea (Hsu et al., 2014; Kao et al., 2014; Liu et al., 2016, 2013). However, this view completely ignores the role of benthos, which likely remineralizes the OC through their feeding, respiration, burrowing, and predation activities, and may lead to an erroneous estimate of OC cycling on the seafloor (Snelgrove et al., 2018).

Previous studies suggested that the quality of sedimentary OC results from relatively rapid transport in the active canyon were higher in comparison to the slope sediments at similar depth (Garcia et al., 2007; Pusceddu et al., 2010; Vetter and Dayton, 1999). These high quantities and quality of the OM in submarine canyons enhanced the carbon oxidation rates (Epping et al., 2002; Rabouille et al., 2009), benthic standing stocks of nematodes (Ingels et al., 2009), and deposit-feeding holothurians (Amaro et al., 2009; De Leo et al., 2010; Vetter and Dayton, 1999), indicating the extensive carbon cycling in the benthic food web. Though we have already known the benthic community structures showed an opposite trend in the GPSC due to unfavorable physical disturbance, how the carbon partitioning within the food web is affected by canyon conditions remains unclear. In addition, most of the marine benthic studies focused on the individual components of the food web (e.g. Ramirez‐Llodra et al., 2010; Bianchelli et al., 2010), which suggested that different components may be benefited from the increased OM flux into the canyons. However, these comparisons were only based on single biomass-to-biomass or process-by-process comparisons. To evaluate the carbon cycle inside the whole system, a comprehensive understanding of the benthic ecosystem structure is needed.

The deep-sea benthic ecosystems depend on the slow sinking of detritus derived from primary production in the euphotic zone. Before detritus settle 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 notorious, 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 (Vézina and Platt, 1988).

* 1. **Linear inverse modelling and related studies in submarine canyons**

To the best of our knowledge, only two studies so far attempt to construct comprehensive benthic carbon food web in the submarine canyons.

The first one was conducted in in the northern Gulf of Mexico (Rowe et al., 2008). The carbon food webs were contrasted between the head of the Mississippi Canyon and the adjacent mid-slope, and the extremely high macrofauna abundance (> 20,000 individual m-1) and biomass (> 10 g m-1) were found at the head of the Mississippi Canyon (Wei et al., 2012). Consequently, the relative minor role of bacteria and meiofauna in the OC remineralization was reduced in the canyon. Almost 40% of POC rain was exported down the canyon (Rowe et al., 2008)

In another study, the carbon food web was contrasted within three sections of the Nazaré Canyon off Portugal's coast (van Oevelen et al., 2011). In the Nazaré Canyon, the prokaryotic uptake of DOC and its respiration to DIC, nonselective feeding by meiofauna, and predation and scavenging by macrofauna dominated the carbon cycling in the upper canyon. In contrast, the megafauna deposit-feeders dominated the carbon cycling in the mid-canyon, and all carbon flows diminished in the lower canyon (van Oevelen et al., 2011).

Nevertheless, we expected that carbon cycling in the submarine canyons off the SW Taiwan would be drastically different from that of the Mississippi or Nazaré Canyons (Rowe et al., 2008; van Oevelen et al., 2011) due to the GPSC’s high energy setting (Liu et al., 2016, 2013) and peculiar biology (Chen, 2018; Liao et al., 2020, 2017).

The studies of carbon cycling in the deep sea have spurred recent interests (Bell et al., 2017; Dunlop et al., 2016; Snelgrove et al., 2018; Stratmann et al., 2018; van Oevelen et al., 2012, 2011);

Here in this study, we measure the benthic carbon stocks and carbon cycling of the heterogeneous seafloor off SW Taiwan.

* however,

1. **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**

The carbon flows entering the system, between the stocks, and leaving the system will be measured by shipboard experiment or derived from literature to evaluate the carbon cycle

(i.e., one of the most crucial seafloor ecosystem functions) on the heterogeneous seafloor habitats.

* + **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 |  |  |

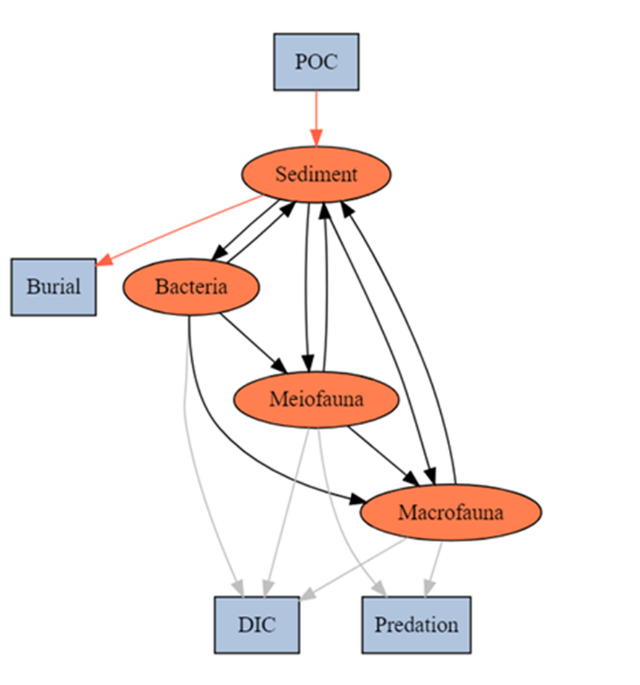
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Fig. 14. Conceptual benthic food web model off SW Taiwan