Introduction

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.

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.

Carbon flows and food webs in deep-sea 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. Nevertheless, 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). Also, the network analysis developed from the information theory has been applied to solve information involved in a complex network (e.g., a food web) and then condense this information into interpretable indices (Fath and Patten, 1999; Ulanowicz, 2004).

Related food-web studies in submarine canyons

　　To the best of our knowledge, only two studies have attempted to construct a comprehensive benthic carbon food web in the submarine canyons so far. The first study was conducted 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-slopes. A single species of amphipod dominated the Mississippi Canyon head, resulting in extremely high macrofauna abundance (> 20,000 individual m-2) and biomass (> 400 mg Cm-2) (Wei et al., 2012). Therefore, based on the secondary production estimates and total sediment community oxygen consumption (SCOC), considerable carbon was cycled mainly through the macrofauna stock, while the OC remineralization of bacteria and meiofauna was reduced in the canyon. On the other hand, because the production of the amphipods was considered as a food source for larger invertebrates and fishes, the diversity and biomass of megafauna and fishes were relatively higher than that on the upper continental slopes. In Rowe et al. (2008) food-web model, the particulate organic carbon (POC) input was two times higher than the required amount to support the calculated demand (i.e. sum of total respiration, production, and export), suggesting almost 40% of POC rain was exported down the canyon. While the carbon demand at the continental slope was greater than the estimated POC input, indicating the organic resources in the community were supplemented from the basin margin.

　　In the other study, carbon food-web models were contrasted within three sections of the Nazaré Canyon (eastern Atlantic Ocean) off Portugal's coast (van Oevelen et al., 2011), including upper (300–750 m water depth), middle (2700–3500 m) and a lower section (4000–5000 m) of the canyon. In comparison to Rowe et al. (2008), the models were constructed with linear inverse modeling, which combined the biomass, data of carbon processes, and the general physiological constraints from literature, to examine how the food web was influenced by the characteristics of different sections of the canyon. The environmental conditions were notably differed between sections, especially for OM input and hydrodynamic activity, resulting in strongly affected the food web structure. van Oevelen et al. (2011) found that prokaryotes uptake of DOC and its respiration to DIC dominated the upper section, with a significant meiofaunal and smaller macrofaunal contribution. The high densities of meiofauna suggested that the conditions of the upper canyon, such as high current speeds and sediment resuspension, favor the meiofauna. In the middle canyon section, the megafauna (holothurians) benefited from the high OM input and accreted sediments, showing a megafaunal hotspot in the deep sea. In contrast, prokaryotes uptake of DIC dominated the carbon cycling and all carbon flows diminished in the lower section of the canyon, therefore, the food web structure resembled that of lower slope and abyssal plain sediments.

Aim of this study

**First LIM model apply in GPSC**

Considering the GPSC’s high energy setting (Liu et al., 2016, 2013) and peculiar biological community strucuture(Chen, 2018; Liao et al., 2020, 2017), 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).

**Difference in carbon flow between GC1 and GS1**

**Compare with other submarine canyons**