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 (Harris & Whiteway, 2011), showing abundant and ubiquitous submarine canyons crossing continental margins globally.

Though the benthic community structure and productivity have been poorly studied in submarine canyons, some findings suggest that the elevated benthic biomass and diversity in the canyon can be attributed to the high habitat heterogeneity (De Leo et al., 2014; McClain & Barry, 2010). For example, habitat heterogeneity among sampling localities may enhence meiofauna trophic complexity in the sedimentary environment (Ramalho et al., 2014). Moreover, commercially-important rockfishes benefit from the natural refuge provided by the Soquel Submarine Canyon in Monterey Bay, because the high-relief structures of boulders and rock outcrops in narrow deep-water canyons are less accessible to fishing activities (Yoklavich et al., 2000). Other remarkable ecological and physical characteristics of submarine canyons have also been reported. For example, submarine canyons may reflect and focus internal waves and lead to strong bottom currents (Hall & Carter, 2011). The interactions between canyons and coastal ecosystems may lead to seasonal upwelling and contribute to high productivity (Sobarzo et al., 2001). Submarine canyons may also trap dense aggregation of diel vertical migrators and their predators (Greene et al., 1988; Maycas et al., 1999).

These unusual ecological and physical characteristics might be attributed to the complex topographic features in submarine canyons. A great variety of hypotheses had been proposed to explain the origin of submarine canyons, but the most important factors in the development of canyons are the erosion triggered by turbidity currents (Shepard,1981) and the mass failures during sea-level low stands (Walsh et al., 2007). The sediment transport efficiency of canyons is partly controlled by how distant the canyon head extent from the shelf. When the distance between the canyon head and the shore is short, terrestrial sediment and organic carbon can be efficiently transported to the deep ocean (Covault et al., 2007; Galy et al., 2007), and the canyon stays active. There are many examples of these shore-connected canyons, which frequently occur along the Californian coast, the Indian-Ocean coast of the Arabic Peninsula, and the Eastern Black Sea (Bernhardt & Schwanghart, 2021). The connection between river and canyon is not the only factor involved in the activity of a submarine canyon. Some canyons, such as the Monterey Canyon, La Jolla, and Hueneme canyons, can capture longshore-transported sediments to feed their canyon head through the bottom currents (Covault & Graham, 2010). A total of 4633 heads of submarine canyons in the world’s oceans were examined by Bernhardt and Schwanghart (2021). Most canyons were classified as slope canyons (60%) and shelf-incising canyons (37%), while only 183 canyons were shore-connected. The submarine canyons around Taiwan have also been studied. In contrast to the world’s canyons, Chiang & Yu (2022) identifies that Taiwan's margin is dominated by the shore-connected canyons (n=7, 54%). Six of the shore-connected canyons locates in the East Taiwan margin, which receives sufficient input of terrestrial material and erodes headward at a rate comparable with the Holocene's millennial-scale sea-level rise. The rest shore-connected canyons around the Taiwan margin is the Gaoping submarine canyon (GPSC) off southwest Taiwan. Because of the wider shelf and lack of other major rivers delivering sediment, there are fewer shore-connected canyons on the west margin than on the east margin. The GPSC is deeply incised into the Gaoping Shelf, and the canyon head is near the mouth of Gaoping River (GPR). The GPR is a typical small mountain river (SMR) with a steep gradient over a short distance from its headwaters to its confluence or mouth (Lin et al., 2016). With only 1 km from the canyon head to the shoreline, high suspended sediment discharge from the GPR (49 MT/yr) is delivered to the head of the GPSC. The frequent earthquake and typhoon events, such as the 2006 Pingtung Earthquake and 2009 Typhoon Morakot, also lead to the recurring turbidity and episodic gravity-driven sediment flows in GPSC, which allows for the continual erosion of the canyon floor and sediment transportation (Gavey et al., 2017; Ikehara et al., 2020; Chiang et al., 2020). Because of the event-caused sediment flows and the extremely high discharge from the GPR, the canyon head of GPSC remains active as a conduit for terrestrial sediment from Mt. Jade to the deep South China Sea (SCS). It has been suggested that these oceanographic physical settings inside the submarine canyons increase the concentration of suspended particulate matter and the transport of sediment (Keller et al., 1973; Puig et al., 2008; Gaudin et al., 2009). Such an increase in 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). The annual sediment discharge into the GPSC is approximately 30–80% of the Mississippi's annual export (Meade and Moody, 2010), the world's third-largest river. It is remarkable given that Taiwan represents less than 0.02% of the Earth's land surface. The highly correlated relationship between sediment load and POC flux revealed the importance of carbon cycling in this area. For example, Liu et al. (2016) reported that the daily transport of particulate organic carbon (POC) through the GPR–GPSC system is estimated to be 5.98 × 106 g C/d in the dry season and 1.25–276 × 106 g C/d in the flood season. In the past few decades, many researchers have investigated the source, spatial and temporal variations of riverine carbon fluxes under increasing global climate change and intensifying anthropogenic perturbations (Huang et al., 2012; Zhang et al., 2013; Li et al., 2017). However, little is known about the process of carbon cycling after entering and accumulating in canyons. Hence, we focused on the carbon cycling of the head of GPSC) and Gaoping Slope (GS) off southwestern Taiwan.

Compare GPSC with GS in terms of physical conditions and community structure

Gaoping River-Canyon system is the most extensive sediment dispersal system in SW Taiwan, including the Gaoping River drainage basin, the Gaoping Shelf, the Gaoping Slope, the Gaoping submarine canyon, and the Manila Trench in the northeast margin of the SCS. The Gaoping slope (GS) continues from the narrow (<10 km) continental shelf, extending southwest toward the northern SCS. The slope can be divided into upper and lower parts by 1000 to 1200-m water depth (Yu et al., 2009). Embedded within the GS, the Gaoping submarine canyon (GPSC) extends 260 km from the Gaoping River (GPR) mouth, crossing through the continental shelf and slope and merging into the Manila trench (Liu et al., 2016). The canyon comprises three geographically distinct segments. The upper section meanders southwestward from 126 to 1750 m in water depth, featured in great relief. The middle reach runs southeastward along an elongate escarpment and then makes a sharp turn to the southwest, covering the water depths between 1750 and 2800 m. The lower canyon spans 2800 to 3600 m in water depths and finally connects to the northern opening of the trench (Yu et al., 2009).

The physical settings and topographic features are markedly different between the GPSC and GS. Hsu et al. (2013) suggested that the “filling-and-spilling” plays a key role in the sediment deposition across the GS, whereas other processes such as tectonic activities, mass wasting events, and canyon and channel feedings diversify the sediment transport dynamics from the inner to outer slopes. The bedding geometries in the slope basin revealed a competition between local basin flank uplift rate and sediment deposition rate. As such, the upper GS tends to have higher accommodation rates and relatively slower deposition rates than the lower GS (Hsu et al., 2013). In contrast, much more complex sediment deposition and transport processes occur in submarine canyons. For example, gravity currents such as turbidity and hyperpycnal flows may erode the surface sediment in the submarine canyons (Mulder et al., 2001). The erosion processes may be more pronounced in the canyons like GPSC subjected to frequent gravity currents (refs) and strong internal tides from the Luzon and southeastern Taiwan Strait (Chiou et al., 2011; Jan et al., 2008). Accompanying the semidiurnal tides (M2), the head-ward propagation of the internal waves and bottom currents converges in beam patterns that move parallel to the canyon thalweg (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 GPSC seafloor, a benthic nepheloid layer (BNL) thicker than 100 m with suspended sediment concentration (SSC) exceeding 30 mg/l was documented and likely maintained by current-induced resuspension (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 organic matter (OM) deposition from the water column to the seafloor. Meanwhile, because the nitrogen consumption rate is higher than carbon (Danovaro, 2010; Meyers, 1994), the TOC to nitrogen (C/N) ratio can estimate the aging and sources of OM. Generally, the benthic population densities decline with depth because of the declinature of sinking particulate organic matter (POM) flux (McClain and Rex, 2015; Wei et al., 2010), while higher population densities are expected in the submarine canyon head and near the shelf break due to the higher concentration of OM. Liao et al. (2017) compared the TOC contents and C/N ratios between the surface sediment from GPSC and GC. However, they found that the TOC was negatively related to the bottom current velocity, resulting in a lower faunal abundance and diversity in the surface sediments due to stronger bed flows near the canyon head. In comparison, the TOC increased toward the GS and resulted in higher benthos population density, indicating significant influences of food supplies on benthic community structure.

The benthic macrofaunal and meiofaunal community structures in the GPSC and GS were thoroughly studied by Liao et al. (2017, 2020). Unlike previously mentioned high productivity submarine canyons, the upper GPSC was severely impacted by physical disturbance triggered by internal tides and gravity flows. The biological responses, such as reduction and loss in species richness or total abundance, alteration of taxonomic composition, and the dominance of deep-dwelling burrowing infauna, showed that the benthic communities underwent intense physical disturbances in the GPSC (Liao et al., 2017). Moreover, distinct nematodes assemblages were identified between the GPSC and GS (Liao et al., 2020). They also found that the nematodes species, functional and trophic diversity, and community maturity were severely depressed in the GPSC. These physical extremes, such as strong near-bottom currents and lower TOC due to sediment erosion, likely overwhelmed the effect of OM accumulation and possibly the high food delivery in the active submarine canyons like GPSC. Liao et al. (2020) also attributed the distinct nematode assemblages in the GPSC to the species filtering by the environmental stresses in the canyon. As a result, the nematode assemblages in the GPSC were dominated by r-strategist and non-selective deposit feeders with clavate tails. In contrast, the species with longer lifespans, diverse feeding strategies, and tail shapes coexisted on the GS. Though environmental filtering was the primary mechanism structuring the benthic community between the GPSC and GS, the nestedness patterns (Baselga, 2010; 2012) were also evident, indicating that species immigration and local extinction might also occupy crucial roles in shaping the species composition in the canyon.

Carbon flows and food webs in deep-sea environment

　　Despite the unique geology and community structure between the GPSC and GS, their effects on the sediment biogeochemical cycles and ecosystem functioning remain unknown. The biogeochemical cycles in aquatic sediments depend on coupled reactions and transport processes, including diffusion, advection, and biologically induced transport (Meile et al., 2001). For example, macrobenthos burrowing (i.e., bioturbation and bioirrigation activities) enhances solute transport between the sediment and water interface. In the sediment with high macrofauna densities (e.g., Hammond and Fuller 1979; Archer and Devol 1992), the fluxes across the sediment-water interface are mainly attributed to bioirrigation instead of diffusion. 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 exporting from the Gaoping Rivers into the GPSC ranges from 45.6 to 110 MT (Hsu et al., 2014). This quantity is about 30-80% of the sediment transported b the Mississippi River (~145 MT yr-1, Meade and Moody, 2010). However, the sediment accumulation rates were 2-12 MT yr-1 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. It may lead to an erroneous estimate of OC cycling on the seafloor (Snelgrove et al., 2018).

Previous studies suggested the higher quality of sedimentary OC from relatively rapid transport in the active canyon compared 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 that the unfavorable physical disturbance in the GPSC may severely impact the benthic communities, how the carbon cycling within the canyon food web may be affected 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) and suggested that the entire benthic systems 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. A comprehensive understanding of the benthic ecosystem structure is needed to evaluate the carbon cycle within the food web.

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 food supplies with metabolic activities, such as growth and reproduction, consume the remaining detritus deposited on the seafloor (Tyler et al., 1982; 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 difficult, even for relatively well-studied shallow-water benthic ecosystems (e.g., van Oevelen et al., 2006), not to mention the undersampled deep sea. Nevertheless, a linear inverse model (LIM) has been developed and applied to marine food-web studies to deal with data limitations (Vézina and Platt, 1988). Also, network analysis developed from the information theory has been used to solve information 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 our knowledge, only two studies have attempted to construct a comprehensive benthic carbon food web in the submarine canyons. 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 C/ m2) (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. At the same time, the OC remineralization of bacteria and meiofauna was reduced in the canyon. Because the production of the amphipods was considered a food source for larger invertebrates and fishes, the diversity and biomass of megafauna and fishes were relatively higher in the Mississippi Canyon than on the upper continental slopes. Notably, the particulate organic carbon (POC) input was two times higher than the required amount to support the calculated biological demand (i.e., the sum of total respiration, production, and export), suggesting almost 40% of POC rain was exported through the Mississippi Canyon (Rowe et al., 2008). In contrast, the carbon demand at the continental slope was greater than the estimated POC input, indicating that the organic resources required by the community were supplemented from the basin margin (Rowe et al., 2008).

　　In the other study, carbon food-web models were contrasted within the three sections of the Nazaré Canyon (eastern Atlantic Ocean) off Portugal's coast (van Oevelen et al., 2011), including the upper (300–750 m water depth), middle (2700–3500 m) and a lower sections (4000–5000 m) of the canyon. Compared to Rowe et al. (2008), the food webs 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 characteristics of different canyon sections may influence the food webs. The environmental conditions, especially OM input and hydrodynamic activity, vary significantly along the canyon, resulting in distinct food web structures at different canyon sections. For example, the prokaryote uptake of DOC and its respiration to DIC dominated the carbon flows in the upper canyon food web. The meiofauna also has a higher density and contributes more to the carbon flows than the macrofauna, suggesting that the meifauna may tolerate the high current speeds and sediment resuspension in the upper canyon better than the macrofauna. In the mid canyon, holothurians benefited from the high OM inputs and accreted sediments, resulting in a megafaunal hotspot. In the low canyon, all carbon flows diminished, but the prokaryote uptake of DIC dominated the food web, resembling the food web of the lower slope and abyssal plain sediments.

Aim of this study

In this study, the carbon stocks of biota and abiota were estimated in the upper GPSC and adjacent slope off SW Taiwan. Firstly, if the seasonality difference exists is examined. Then, combining the biogeochemical data from references with our *in situ* data, LIM models are constructed to quantify carbon flows in the simplified food webs structure of the two study sites. Finally, the selected network indices are examined as a function of the characteristics of the system. This study follows Liao et al. (2017; 2020), attempting to contribute to knowledge gaps by quantifying the carbon cycling in an SMR-fed submarine canyon ecosystem.