Between the GPSC and adjacent slope, the internal tide flushing and episodic submarine geohazards (e.g., turbidity currents and debris flows) are the main drivers for variation in benthic community structure (Liao et al., 2020, 2017). The sediment erosions by bottom currents sync with the tidal cycles and likely have long-term, recurrence, and pressing effects on seafloor communities (Harris, 2014; Okey, 1997). In contrast, the mass wasting events are unpreditable and occur on longer timescales (e.g., seasonal, annual, or decadal) but likely have devastating effects (Hsu et al., 2008; Huh et al., 2009; Liu et al., 2013, 2012; Su et al., 2012). Such contrasting environmental and biological properties provide a unique opportunity to study the cumulative impacts and recovery of benthic communities, and more importantly, the effect on their ecosystem functioning (Snelgrove et al., 2014; Thrush and Lohrer, 2012). By textbook definition, the ecosystem functioning is the flow of matter and energy transferring within or between trophic levels or ecosystems (Danovaro et al., 2008; Loreau, 2008). For example, the sediment reworking and irrigation by burrowing infauna and epifauna may affect microbial carbon remineralization, sediment oxygen penetration, carbon storage, and nutrient regenerations (Lohrer et al., 2004). The feeding, predation, growth, and mortality of the benthos also directly affect the productivity, carbon sequestration, nutrient cycling, and organic matter decomposition on the seafloor (Snelgrove et al., 2014). Off the SW Taiwan, the GPSC received 14-49 MT of sediments from the Gaoping Rivers each year (Hsu et al., 2014). On average, more than 27 g m-2 d-1 of sediments may be 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). Assuming the equal amount of organic carbon (OC) in both estimates, most of the OC is likely exported down 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 sediment benthos' role, which likely remineralizes the OC through their feeding, burrowing, respiration, and predation activates and may lead to erroneous estimates of the OC cycling on the seafloor (Snelgrove et al., 2017).

This project will measure and contrast benthic carbon stocks and carbon cycling of the heterogeneous seafloor off SW Taiwan. 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. 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); however, to the best of our knowledge, only two studies so far attempt to construct comprehensive benthic carbon food web in the submarine canyons. In the northern Gulf of Mexico, the carbon food webs were contrasted between the head of the Mississippi Canyon and the adjacent mid-slope (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 Gulf of Mexico, extremely high abundance (> 20,000 individual m-1) and biomass (> 10 g m-1) of macrofauna were found at the head of the Mississippi Canyon (Wei et al., 2012). As a result, the relative role of bacteria and meiofauna in the total OC remineralization was reduced in the canyon. Almost 40% of POC rain was exported down the canyon (Rowe et al., 2008). 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).

**Sediment carbon budget:**

In the deep-sea sediments, the total inventory of organic carbon (OC) can be partitioned into the living and non-living components (Fig. 10). The living component of OC is mainly contributed by the biomass of prokaryotes (mainly bacteria), protozoan (mainly foraminifera), meiofauna (> 0.04 mm in length) and macrofauna (> 0.3 mm in length) (Rex et al., 2006; Rowe, 1983; Wei et al., 2010). The non-living component of OC includes labile (i.e., fresh phytodetritus or chlorophyll-a contents), semi-labile (i.e., lipid, protein, and carbohydrate), and refractory OC (i.e., humic and fulvic acids, structural carbohydrates, and “black” carbon) (Danovaro, 2010). The source of OC is mainly supplied by the slow rain of particulate organic carbon (POC) from the euphotic zone or lateral advection of POC from terrestrial or marine organics. The loss of OC balances the source through carbon remineralization (SCOC), biological utilization of labile OC, the predation among living components of OC, long-term burial of the refractory OC and down-slope OC export (i.e., by turbidity currents).

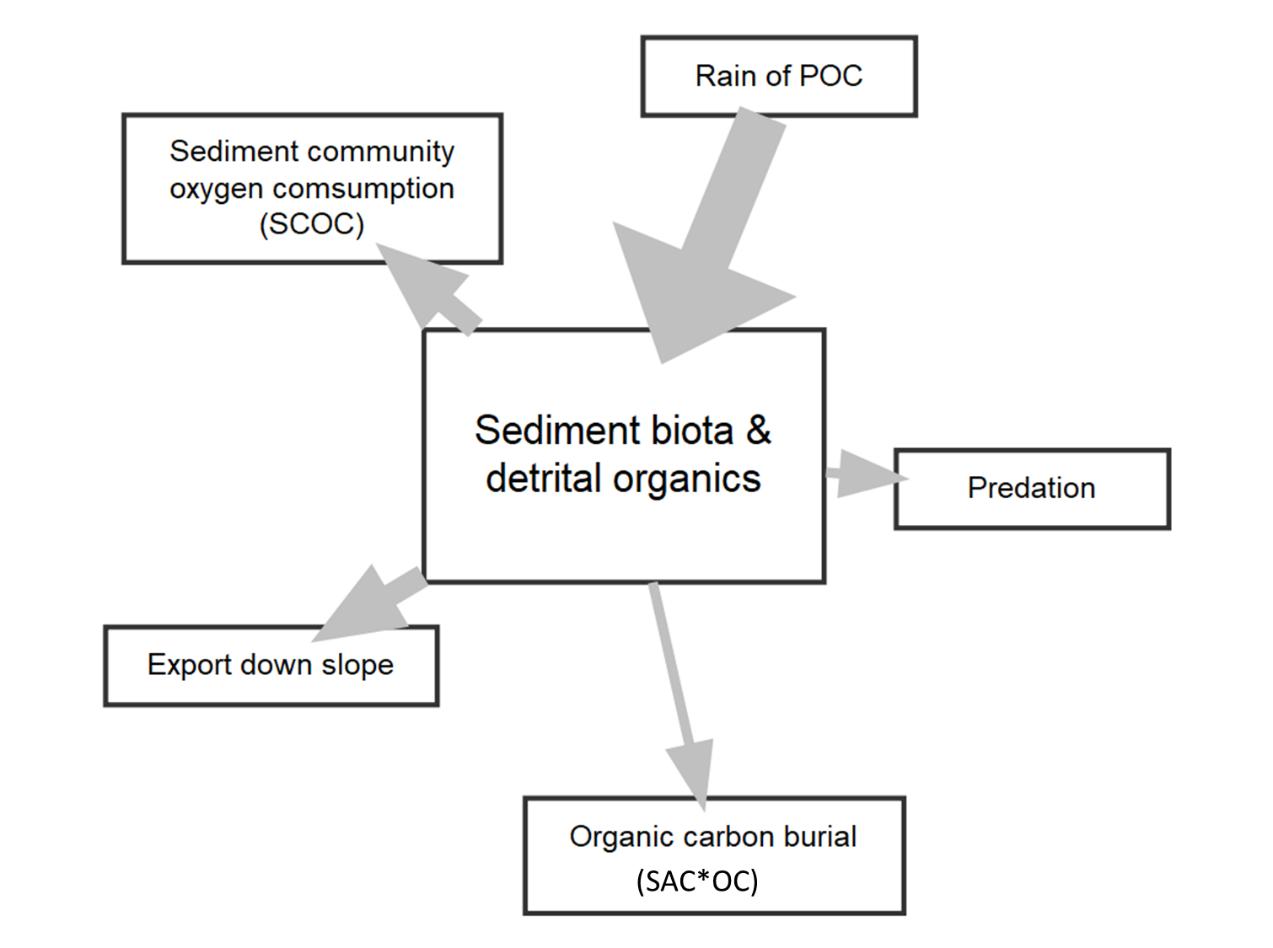


Fig. 10. Carbon budget and cycling in the deep-sea sediment. The conceptual model is modified from Rowe et al. (2008). For example, the mass flux at the head of GPSC likely exceeds 700-800 g m-2 d-1, which is equivalent to 3200 mg C m-2 d-1, assuming 0.4% organic carbon (Liu et al., 2009, 2006; Liu and Lin, 2004). The export POC flux on the shelf break of the northern South China Sea was estimated to be 48 ± 6 mg C m-2 d-1 (Hung and Gong, 2010). The contrasted POC input and physical condition between the canyon and slope habitats likely contribute to distinctively different carbon budgets and cycling.

**Sediment biota and detrital organic**

**Prokaryote biomass:** A cutoff 10-ml sterile syringe (i.d. 15 mm) will take subsamples from the top 1-cm of sediments within a core tube. Similar to the operation of a piston core, the syringe plunger will be held fixed at the sediment surface, and then the barrel will be pushed into the sediment to take 2 mL of the sample. The syringe sample will be added to a 15-mL polyethylene centrifuge tube containing 2 mL of pre-filtered PBS solution. Approximately 0.3 mL of 16% formaldehyde will also be added to the centrifuge tube until the sample reaching a final concentration of 2% formalin and then stored at 4˚C fridge. In the lab, the sediment samples will be further diluted by 500- or 1000-fold in PBS solution depending on the number of potentially interfering particles, treated with Triton-X detergent to loosen attached or aggregated cells, centrifuged through Nycodenz® and then placed on a 0.2-µm pore size filter, stained with SYBR Green and DAPI stains, and mounted on a slide for enumeration (Deming and Carpenter, 2008; Kallmeyer et al., 2008). The prokaryote abundance will be determined by epifluorescence microscopy, and the cellular dimensions in each slide will be estimated from an image taken by a CCD digital camera. The mean biovolume of cell sizes in each sample will be calculated assuming each cell is a sphere [(4/3) r3× π]. The biomass will be converted from biovolume using a conversion factor of 310 fg C µm−3 (Fry, 1990).

**Foraminifera biomass:** Only the top 1-cm of sediment will be retained due to most of the living foraminifera inhabiting near the surface (Rathburn and Corliss, 1994). An equal volume of 10% buffered formalin (with borax, sodium tetraborate Na2B4O7, and 1 g L-1 rose bengal) will be added to the sediment samples to make a final concentration of 5% formalin and allowed to stain for a least one week. In the lab, the sediment samples will be freeze-dried and then wet sieved through a 63-µm sieve. The dry coarse fraction (particle size > 63µm) will be sieved again by 150 µm sieve before picking. Both the individuals are intensively pink or red-stained (living individuals), and non-stained (dead individuals) will be counted, picked out, and sorted for identification seperatedly. The organic carbon biomass will be converted from abundance multiplying average carbon biomass per individual from Bernhard et al. (2008).

**Meiofauna biomass:** A cutoff 10-ml sterile syringe (i.d. 15 mm) will take subsamples from the top 5-cm of sediments as suggested by Montagna (2017). The syringe plunger will be held fixed at the sediment surface, and then the barrel will be pushed into the sediments to create vacuum suction to draw the sediment samples into a 250-ml specimen jar. An equal volume of 10% buffered formalin (with borax, sodium tetraborate Na2B4O7, and 1 g L-1 Rose Bengal) will be added to sediment samples to make a final concentration of 5% formalin. Upon returning to the lab, the sediment samples will be wet sieved through a 1000-µm sieve with a 40-µm sieve underneath and then transferred to 70% ethanol. The meiobenthos specimens will be extracted from the sediments using Ludox HS40 solution (gravity = 1.18 g/cm3) and centrifuged for 10 min at 8,000 rpm (repeated three times) to extract meiofauna (Danovaro, 2010; Montagna et al., 2017) and enumerated to major taxonomic groups under a high power stereomicroscope (Olympus® SZX16; 0.7-11.5 X zoom). The body volume of meiofauna specimens will be calculated with the formula: V = L x W2 x C, where V is the volume, L is the length, W is the width, and C is the taxon-specific conversion factors (Feller and Warwick, 1988; Rachor, 1975; Warwick and Gee, 1984). The biovolume will be converted into wet weight, assuming a specific gravity of 1.13 (Warwick and Gee, 1984), and organic carbon using the conversion factor of 12% (Baguley et al., 2004).

**Macrofauna biomass:** Once the sample is recovered, the supernatant water above the sediment surface will be siphoned carefully through a 300-µm sieve. The top 10 cm of the sediments will be extruded (by an extruder) and washed with filter seawater (with a 5-µm filter) through the same 300-µm sieve as suggested by Montagna (2017). In our previous surveys, we also found that most macrofauna was in the top 10 cm of the sediments (Liao et al., 2017). The remaining sediments will be kept in a 250-mL specimen jar. An equal volume of 10% buffered formalin (with borax, sodium tetraborate Na2B4O7, and 1 g L-1 Rose Bengal) will be added into the sampling jars to fix the samples for at least 24 hours (yielding a final 5% of formalin solution) and then transfer to 70% ethanol for permanent preservation. Macrobenthos samples will be sorted and enumerated into major taxonomic groups and polychaete genus using a stereo sorting microscope (Olympus® SZ61; 0.67-4.5X zoom) and then permanently preserved in 70% ethanol. The body volume of macrofauna specimens will be estimated by the same length-width relationship (V = L x W2 x C) based on images taken by a digital camera and analyzed by image analysis software ImageJ. For the taxa whose conversion factors are not available, the biovolume was calculated from length and width using the nearest geometric shapes (e.g., scaphopods - cone; aplacophorans - cylinder; sipunculans - cylinder; ophiuroids - ellipsoid or cylinder; asteroids - ellipsoid; nemerteans - cylinder). The biovolume will be converted into wet weight assuming a specific gravity of 1.13 (Warwick and Gee, 1984) and then multiplied by 4.3 % to obtain the organic carbon content (Rowe, 1983).

**Detrital organic carbon:** Surface sediment will be taken and stored in 50-ml centrifuge tube in -20°C freezer. In the lab, an aliquot of frozen sediment (up to 2 g) will be extracted (12 h at 4 °C in the dark) with 8 ml of 90% acetone. A fluorometer will measure the chlorophyll a and phaeopigments in the extract (after acidification with HCl). The chlorophyll a concentration will be converted to carbon, assuming a carbon: chlorophyll-a ratio of 40 in phytoplankton (Stephens et al., 1997). The sediment samples will be freeze-dried for 3 to 5 days to measure wet weight (before freeze-drying), dry weight (after freeze-drying), water content, and porosity, assuming the sediment bulk density of 2.65 g cm-3 (Eleftheriou, 2013). An aliquot of freeze-drying sediment (~0.3 g) will be centrifuged (4500rpm / 5min) with distilled water to remove the salt. The cement and carbonates will be removed by adding 10% of 12N hydrochloride (HCl), and the organic matter will be removed by adding 15% hydrogen peroxide (H2O2) for 1-2 days. Sodium hexametaphosphate (Na(PO3)6) will be added to deflocculate and disperse sediment particles and then analyze for grain size with laser diffraction particle size analyzer (Beckman Coulter LS13 320). Another aliquot of freeze-drying sediment (~0.4 g) will be acidified with HCl to remove calcium carbonate, combusted at 1000˚C with pure oxygen, and analyzed with a Flash EA 1112 elemental analyzer for total organic carbon (TOC) and total nitrogen (TN). The combusted sample (CO2) will also be analyzed for organic carbon isotopic composition using a mass spectrometer. Extensive data on sedimentary chlorophyll-a, phaeopigment, and TOC in the proximity of our sampling site will be extracted from published values for comparison (Chen, 2012; Hsu et al., 2014; Kao et al., 2006).

**Sediment community oxygen consumption (SCOC)**

**In-situ incubation:** We have constructed a prototype of plexiglass dark and light chambers based on the design by Rowe et al. (1994) and Warnken et al. (2000) (Fig. 11a). The *in-situ* benthic flux chamber (BFC) each enclosed a volume of 6.8 liters of water and covered an area of 0.09 m2, with a collar on the outside of each chamber to assure precise penetration depth into the sediments (Fig. 11a). A one-way valve on each plexiglass chamber's lid will soon be designed (not done yet) and installed to release the excess of water caused by the chamber's insertion into the sediment, ensuring a gentle placement on the seafloor. The chambers are continuously stirred by a pair of inductively driven magnetic stirs (i.e., at 60 rmp), directing flow from near the sediment-water interface out over the top of the chambers. This general flow pattern has been confirmed with the use of dyes (Rowe 1994) and the same chamber design has participated in an extensive inter-calibration with chambers of other designs (Tengberg et al., 2004).

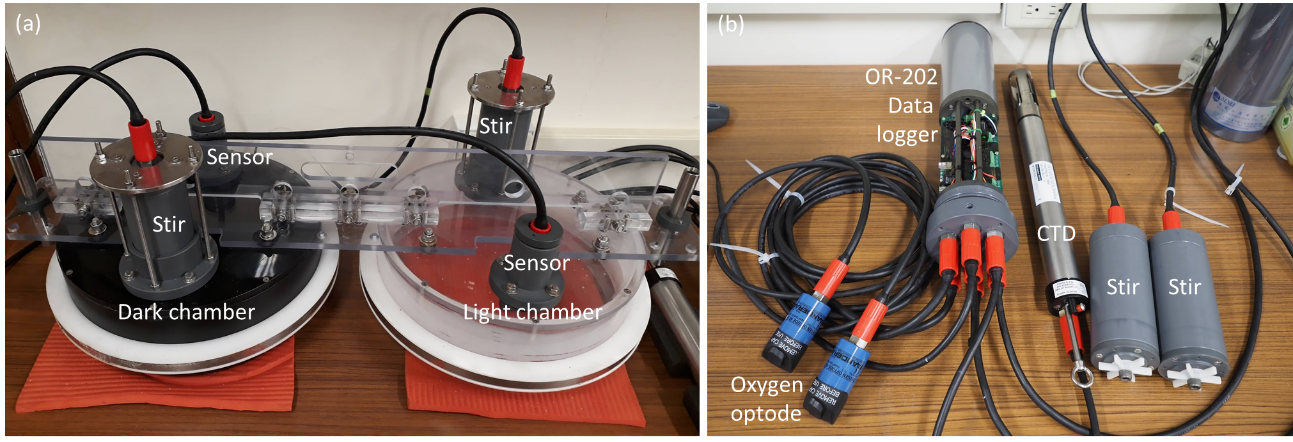


Fig. 11. Custom-build benthic flux chamber (BFC) system. (a) Paired light and dark benthic chambers (each enclosed 8.6 litters of volume and 0.09 m2 of the area). (b) Custom-built data logger/controller (OR-202) for BFC system.

The sensing system is composed of two Aanderaa oxygen optode 4330 and Idronaut Ocean Seven 304 CTD. A custom-built data acquisition computer (OR-202) powered by Alkaline battery pack can record the hydrographic data and control stirring motors. OR-202 can communicate with a laptop through a USB 3.0 cable and software OrTalk. The starting time, cast interval, stirring duration, and sampling delay can be programmed in OrTalk. The data can be download from a micro SD card on OR-202 or from a USB cable directly. Currently, OR-202 and the two stirring motors are enclosed in high-density polyethylene (HDPE) housings, allowing them to be submerged to 500-m water depth. We proposed to replace the HDPE with titanium housing to enable the chamber to be depth-rated down to 6000-m. The new BFC system is self-sustained and lightweight enough (7 kg in water) to be deployed by SCUBA Diver or remotely operated vehicle (ROV).

This proposed project will deploy the newly designed BFC from an autonomous benthic lander (ABL) or an ROV (when possible) to measure in-situ SCOC. The ABL is constructed by combining two square 1.4 x 1.4 m stainless-steel frames (Fig. 2). It carries: (1) acoustically controlled disposable anchors; (2) 12 floatation spheres providing 300 kg of buoyancy; (3) primary and redundant acoustically commanded release mechanism to control anchor release; (4) electronic timed-release system to implant (or release) chambers to the bottom; (5) power supply; (6) time-lapse video camera and deep-sea light (Fig. 3); (7) two oxygen optodes, CTD, and data acquisition system; and (8) additional environmental sensor (Aanderaa Seaguard II) to record basic hydrographic properties outside the chambers over time. The time-lapse video camera and deep-sea light are custom-built by the OR1 instrumentation center. The Aanderaa Seaguard II data logger will equip with Aanderaa oxygen (4330), turbidity (4112), pressure (4117), and conductivity (4319) sensors. The fluxes of oxygen into or out of the sediments will be calculated as Flux = [Change in concentration x Volume of overlying water] / [Chamber area x Time]. The dissolved inorganic carbon produced by the respiration will be calculated by the flux of oxygen in moles multiplying a respiratory quotient of 0.85.

**Ship-board incubation:** Three core tubes from a megacorer (assigned to measure SCOC) will be incubated in the dark at *in-situ* temperature in a temperature-controlled water bath (Fig. 7b). If the supernatant water is not enough to fill the core tube, the sediment core will be carefully topped with bottom water collected from the CTD rosette. The sediments will be allowed to acclimate for approximately 6 hours until the flocculent materials settle and the overlying water is clear. The tube will be closed hermetically with a custom-built HDPE lid, and air bubbles will be removed. A magnetically driven impeller (60–80 rpm) attached to the core lid will gently circulate the water during the incubation. The dissolved oxygen concentration will be measured every 8 hours with a miniature oxygen optode (i.d. 2 mm) through a sampling port on the core lid (PreSens® Microx 4). Dissolved oxygen will be measured until the concentrations decreased by 15% of the initial concentration, according to Glud (2008) to prevent hypoxic stress. The fluxes of oxygen into or out of the sediments will be calculated as Flux = [Change in concentration x Volume of overlying water] / [Core area x Time]. The dissolved inorganic carbon produced by the respiration will be calculated by the flux of oxygen in moles multiplying a respiratory quotient of 0.85.

**Sediment oxygen profiling:** After the shipboard incubation, three oxygen microelectrode (100-µm tip size) will be inserted simultaneously into sediments at 100-µm increments using Unisense® Field Microprofiling System (Fig. 7c). The diffusive oxygen fluxes through the sediment–water interface will be calculated using Unisense® Profile software according to the Fick’s first law of diffusion based on oxygen porewater profile concentration, sediment porosity, and initial concentrations in the overlying water and oxygen diffusion coefficient corrected by temperature (Berg et al., 1998; Glud, 2008). The oxygen penetration depth (OPD) will be determined by the depth where dissolved oxygen concentration < 5 µmol L-1.The diffusive carbon remineralization will be calculated by the flux of oxygen in moles multiplying a respiratory quotient of 0.85. In general, the sediment oxygen profile concentrations measure the diffusive oxygen utilization (DOU) mainly contributed by aerobic respiration of microorganisms through slow diffusion of oxygen molecules. In contrast, the sediment incubation experiment (e.g., shipboard or ABL) measures the total oxygen utilization (or TOU). Therefore, in addition to DOU, the TOU also accounts for benthos' respiration and the benthos-mediated oxygen utilization through their bioirrigation and bioturbation activities (Glud, 2008; Lichtschlag et al., 2015; Wenzhöfer and Glud, 2004). The difference between the TOU and DOU is the benthos-mediated oxygen utilization (BMU), characterizing benthos' contribution to sediment oxygen dynamics.

**Organic carbon burial**

The rate of organic carbon burial will be estimated by multiplying sediment accumulation rate (SAR) with total organic carbon (TOC)(Jahnke, 1996). Extensive SAR data and empirical relationships between SAR and depth in our study are available from Hsu et al. (2014), Huh et al. (2009) and Kao et al. (2006). SAR will also be deterimed by 210Pb activity using a α-spectrometer via the granddaughter nuclide 210Po through collaboration with FATES co-PIs 林玉詩 and 蘇志杰 (IONTU).

**Rain of POC**

The rain of POC will be estimated in two different ways. First, the mass flux of sediment or export POC flux will be derived from the previous sediment trap measurements from the FATES project (Liu et al., 2006; Liu and Lin, 2004) or other published data (Chung et al., 2004; Hung and Gong, 2010; Wei et al., 2017). Second, if we consider the seafloor as an ultimate sediment trap, the rain of POC will equal to the sum of organic carbon burial and sediment community oxygen consumption (SCOC) (Jahnke, 2001, 1996).

**Food web modeling**

The deep-sea benthic ecosystems depend on food supply of detritus derived from primary production in the euphotic zone. Before detritus becomes a part of the sediment, it is first consumed by suspension feeders which filter organic matter from the overlying bottom water (Gage and Tyler, 1996) or by deposit feeders (Blair et al., 1996). The remains are then ingested by bacteria (Lochte and Turley, 1988) and sediment-inhabiting organisms of several sizes, which respond rapidly to the change of food supply with metabolic activity, such as growth and reproduction (Tyler et al., 1982; C.R. Smith et al., 2008). Then, the detritivores are predated by lager animals such as megafauna and fish. The waste products of all consumers become food for deposit-feeders or bacteria again or are exchanged with the water column as DIC or nutrients. In brief, the food web comprises the abiotic (detritus, DIC, etc.), biotic compartments and the linkage of flows between one and another. While the identification and quantification of these energy flows are the basic elements to understand the functional interactions in the food web, direct measurement and experimentation are notoriously difficult, even for relatively well-studied shallow-water benthic ecosystem (e.g. van Oevelen et al., 2006), not to mention undersampled deep water systems. To deal with data limitations and extract as much information from previous studies as possible, linear inverse model (LIM) has been developed and applied to marine ecosystem studies (Ve´zina and Platt, 1988).

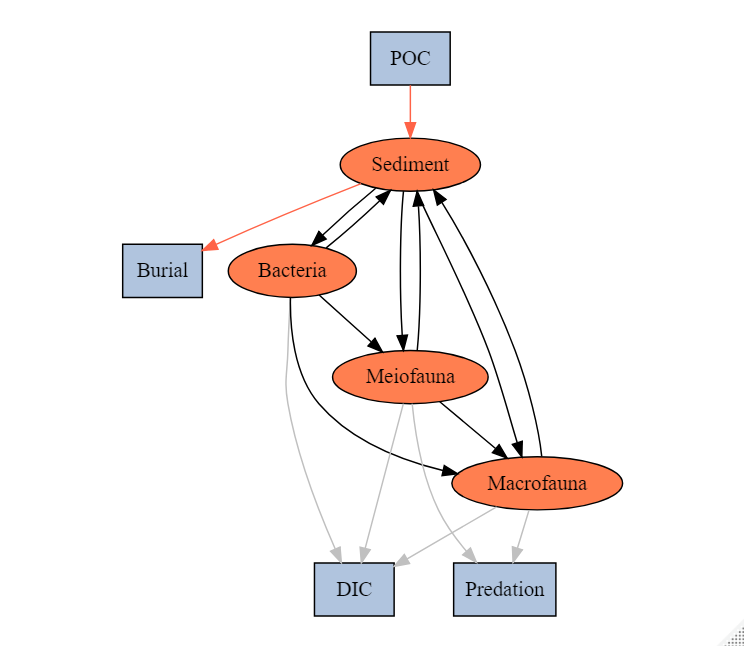
**Establishing the topological food web structure:** Linear inverse modelling starts with choosing relevant abiotic and biotic compartments, and specifying the links between them. Take the schematic fig.12 for example, we assumed that the influx POC as a complex assemblage of organic matter derived from the water column, while a portion of sediment flows out the system through the process of burial and/or export (orange flows). Then, it is assumed 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), and the macrofauna stocks will be divided into surface deposit-feeders, 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 the loss of carbon as the feces and as consumed by benthopelagic/pelagic predators (fig. 12). In this LIM model, the compartments with orange color are part of the food web model, whereas compartments with blue color were only considered as carbon influx or efflux, but were not directly modeled.

Fig. 12. Conceptual benthic food web model off SW Taiwan

**Physiological and behavioral constraints:** A broadly accepted physical constraint is that, for each chemical element, mass is conserved. 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:

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indicating that the temporal mass change of a compartment(X) is equals to difference between the incoming( and outgoing( flows. Therefore, if is larger than , X will increase in time. Base 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:

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Furthermore, this mass balance principle can also be applied to organisms’ physiological behaviors. Take ingestion process for example, when organisms ingest food, only part of the food is assimilated, and the rest is expelled as feces. And the assimilated food is used for 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:

,

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 compartment are tightly linked. For instance, if species A feeds on species B, not only an increase flow flows into A, but a loss of the same magnitude flow out B. As a result, the direction of the flows matters, and we can simply take the mass-balanced equation as sums and subtractions of these unknown quantities of flows. Here, we classify this type of linear mass balance equation as “equality equation” , and it can be expressed with matrix notation in the general form:, in which x is a vector consisted of unknown flows, b is a vector consisted of changed rates of the component. Also, because the flows are non-negative quantities, .

On the other hand, the physiology and behavior of organisms impose 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 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 apply 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 min-max 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 min-max 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.

***In situ* measurements:** The data types mentioned above are derived from the general principles which can be applied to most ecosystem. To deal with a food web model of a specific location, the *in situ* data is necessary. 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 in site-specific measurements, this type of data is generally implemented as equality equations: , where f represents the vector contains *in situ* data.

**Model Solution:** Finally, we combine three types of data together to achieve our entire model, which consists of 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 solution which 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. Early modeling studies usually selected one solution from this solution space. The principle of parsimony had often been applied as the selection criterion (Vézina and Platt, 1988), implying that the flow set with the minimal sum of squared value is selected. While the parsimonious food web often takes the 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, in which the mean values and standard deviations of the flow values are calculated from the solution set (Kones et al., 2006). The *LIM* package (Soetaert and Herman, 2009; van Oevelen et al., 2010) in R (R Development Core Team 2020) will be used to set up and solved the conceptual model in Fig. 12.

**Network flow indices of ecosystems:** While the food web can be solved with linear inverse methods, the subsequent network analysis is indispensable. Network analysis helps us better understand the structural properties and transformations that occur in ecosystem. To compare the complex interactions between compartments for the different food webs, several network indices were calculated from the results of LIM-solved flows with MCMC algorithm, which serve as robust estimators of food web functioning even in the face of food web uncertainty (Kones et al., 2009).

The descriptions of symbols used in network indices calculations are shown in Table 1 and Table 2. 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 total system through flow () is the sum of cycled flow in all through flows (Finn, 1976). The proportion of and is referred to the Finn cycling index (), which summarized the fraction of the material/energy that is generated by recycling process (Allesina and Ulanowicz, 2004). Finally, the index average mutual information () based on communication theory measure the average amount of constraint placed on an arbitrary unit of flow from any 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).

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| --- | --- |
| 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. 1. Nomenclature of symbols used in calculation of network indices.

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

Table. 2. Algorithms for the calculation of the network indices.

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