

Trophic structure of megabenthic food webs along depth gradients in the South China Sea and off northeastern Taiwan

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ABSTRACT: Food web structure along depth gradients in the South China Sea and off northeastern Taiwan were investigated by analyzing stable isotopic compositions of demersal fish, benthic megafauna invertebrates and fish stomach contents. Various prey items were found in fish stomach contents, which covered a wide range of $\delta^{13}\text{C}$ values; however, most fish had empty stomachs at catch. Cnidarians and ophiuroids had relatively low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, while asteroids had higher values for both isotopic compositions. Molluscs and decapods showed the widest ranges for $\delta^{13}\text{C}$ (–25 to –15‰) and $\delta^{15}\text{N}$ (2 to 16‰), indicating feeding on different food sources and trophic niche expansion in deep-sea environments. A positive relationship between depth and $\delta^{15}\text{N}$ was found in cnidarians, molluscs and fish. In addition, depth was negatively related to $\delta^{13}\text{C}$ of cnidarians, decapods and fish. This disparity can be explained by different degrees of biological reworking of particulate organic matter (POM) along depth gradients, and a variety of food sources, e.g. phytodetritus, terrigenous matter, chemosynthetic matter and wood falls, used by different taxonomic groups. At the continental shelf and upper slopes, phytodetritus from surface phytoplankton production was the main food source for consumers, while reworked POM including both marine and terrestrial organic matter might contribute to food sources for consumers in the deep-sea basin. Other food sources, e.g. organic material synthesized in hydrothermal vents, could have provided nutrients to the surveyed site in the southern Okinawa Trough since the base consumer (shrimp) and top predators (fish) all showed $\delta^{13}\text{C}$ values (between –24 and –26‰) lower than those found in sinking POM and surficial sediments (between –23 and –21‰).

KEY WORDS: Deep sea · Megafauna · Food web · Stable isotope

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INTRODUCTION

A typical feature of deep-sea food webs is the lack of *in situ* primary production, except for at cold seep and hydrothermal vent systems (Gage & Tyler 1991). The food resources of a deep-sea community come from vertical input of phytodetritus from surface waters (Billett et al. 1983, Graf 1989), large animal carcasses falling to the depths (Smith 1994, Witte 1999) and advective input from river discharge or nepheloid layer formation (Sanchez-Vidal et al. 2009, Fanelli et al. 2011). Although the deep sea is thought

to be a vast sink for oceanic and terrestrial material, only about 1–10% (Klages et al. 2003) or 20–50% (Buesseler et al. 2007) of the organic material produced from the ocean surface reaches the deep-sea floor.

The analysis of stomach contents is commonly used to study food webs and trophic levels (e.g. Mauchline & Gordon 1985). However, this approach has disadvantages for the study of deep-sea food web structure. Many deep-sea fish show evidence of long starvation or have their stomach everted by expanding swim bladders when brought to the sea surface

(Stowasser et al. 2009). Stomach contents are also often in the latter stages of digestion, becoming too difficult to be identified. Furthermore, stomach contents only represent a snapshot of the diet a short time before capture.

Stable isotope analysis is an alternative way to study food webs. Stable carbon and nitrogen isotopes in biological tissue can reflect the food sources and trophic level of the organism for a long period of time, thus providing time-integrated dietary information (Peterson & Fry 1987). Laboratory research and field observations show a rise in isotopic signatures with an increasing trophic level by approximately 2–5‰ and 0.3–2‰ for nitrogen and carbon, respectively, as a result of isotopic fractionation associated with respiration and excretion (DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984). This fractionation makes the nitrogen isotope particularly useful in determining trophic levels (Hobson & Welch 1992, Post 2002) and the carbon isotopes useful in distinguishing between food sources with different $\delta^{13}\text{C}$ values (Peterson & Fry 1987).

The South China Sea (SCS) is the largest marginal sea except for the Arctic Ocean (Sverdrup et al. 1942). The semi-enclosed SCS connects to the western Pacific Ocean through the Luzon Strait and has wide continental shelves, slopes and deep-sea basins with a maximal depth of around 5000 m in southwest Luzon. It is an oligotrophic ocean with a typical chlorophyll *a* (chl *a*) concentration of 0.05–0.08 mg m⁻³ with the primary production between 120–170 g C m⁻² yr⁻¹ mainly regulated by East Asian monsoons (Tseng et al. 2005). The strong northeast monsoon in the winter enhances primary production by cooling surface waters and promoting vertical mixing in the water column (Tseng et al. 2005). Tropical cyclones and eddies also increase chl *a* concentration about 30-fold from <0.1 mg m⁻³ to >3 mg m⁻³ and 5-fold increases from <0.1 mg m⁻³ to ~0.4 mg m⁻³, respectively, in this tropical sea (Lin et al. 2003, 2010). In the central SCS, the isotopic composition of sinking particulate organic matter (sPOM) varies seasonally (–25 to –22.5‰ for $\delta^{13}\text{C}$, 3 to 5.5‰ for $\delta^{15}\text{N}$) in the photic zone, gradually decreasing with depth and reaching a mean (\pm SD) value of about $-24 \pm 1.5\%$ for $\delta^{13}\text{C}$ and $3 \pm 1.7\%$ for $\delta^{15}\text{N}$ near the deep-sea floor of 3500 m (Liu et al. 2007).

The northeastern coast of Taiwan has a narrow continental shelf and a sharp bathymetric gradient. The north-to-south topography is characterized by the East China Sea slope, Okinawa Trough, Ryukyu Island Arc and Ho-ping basin. At least 4 types of water masses can be identified there: China coastal current, Taiwan warm current, upwelled water and

the Kuroshio (Hung et al. 2003). Lipid distributions in sediments show that the river discharges from eastern Taiwan are a significant contributor of organic matter to the sea floor (Jeng et al. 2003). Upwelled water, cold cyclonic eddies and cold domes bring nutrient deep water to the surface and enhance the primary production in the fronts between the Kuroshio and the East China Sea, with seasonal variations (Hsin et al. 2011). The complex interaction between different marine water masses and freshwater discharges can produce multiple-sources of organic materials to be incorporated into the deep-sea food web system. Extensive studies have focused on hydrological and geochemical characteristics of the SCS and the northeastern coast of Taiwan, but knowledge of biological interactions and the food web structure remains scarce.

Deep-sea food webs share common features such as long food chains, a broad trophic spectrum, different trophic relationships along depth gradients and seasonal variations (Iken et al. 2005, Jeffreys et al. 2009, Fanelli et al. 2011). Deep-sea communities are closely influenced by resource availability and different food sources (Gage & Tyler 1991). Particulate organic matter (POM) plays an important role in the bathymetric zonation of benthic fauna, which influences species composition and abundance (Hessler & Jumars 1974, Wei et al. 2010). The sPOM collected from shallower depths (<200 m) in the central SCS is predominantly of marine origin (Liu et al. 2007). However, low surface primary production and a permanent thermocline decrease food availability as well as the POM sinking rate to deep regions of the oligotrophic SCS. On the other hand, considerable terrigenous organic matter (TOM) was found on the continental slopes (450–1300 m depth) of the northern SCS (Liu et al. 2007) and on the continental margin of the southwestern coast of Taiwan (Kao et al. 2006). The sedimentary organic matter (SOM) in the Southern Okinawa Trough mostly originates from the inner shelf of the East China Sea (Kao et al. 2003). In addition, organics produced from hydrothermal vents have been reported in the Okinawa Trough (Ohta & Kim 2001, Hsu et al. 2003). Food resources with different origins may contribute to the deep-sea food web in the SCS and northeastern coast of Taiwan. However, very few studies have been conducted to investigate the trophic dynamics in these areas.

The objective of this study is to understand the food web structure in the SCS and northeastern coast of Taiwan by investigating the trophic ecology of benthic megafauna across a depth gradient, and compar-

Table 1. Sampling information for the benthic megafauna with Stns 1–6 located in the South China Sea and Stns 7–8 off the northeastern coast of Taiwan (see Fig. 1). BWT: bottom water temperature; towing time: duration of the trawl on the sea floor

Site	Depth collected (m)	BWT (°C)	Towing time (min)	Sampling date	Latitude (N)	Longitude (E)
Stn 1	1442	3.4	30	Jun 2, 2008	19°49.91'	116°18.94'
Stn 2	342	11.5	30	Jun 2, 2008	20°59.28'	116°58.95'
Stn 3	3458	2.4	30	Oct 2, 2008	20°31.61'	120°00.22'
Stn 4	91	20.3	30	Oct 5, 2008	22°29.94'	119°00.73'
Stn 5	595	7.5	60	Oct 7, 2010	22°25.57'	120°06.03'
Stn 6	803	5.5	60	Oct 9, 2010	22°10.14'	120°15.64'
Stn 7	1525	2.7	60	Jul 15, 2009	24°52.80'	122°33.29'
Stn 8	1242	3.0	60	Jul 16, 2009	24°22.83'	122°13.88'

ing the food web structure of the SCS with previous studies conducted in (1) oligotrophic regions, e.g. the Mediterranean Sea; (2) eutrophic regions, e.g. North Atlantic, North Pacific, Arabian Sea, and polar regions with higher primary production. We hypothesize that food sources among the continental shelf, the slope and deep-sea basin are different and the food chain in the SCS oligotrophic region deep-sea community will be longer due to limited food availability.

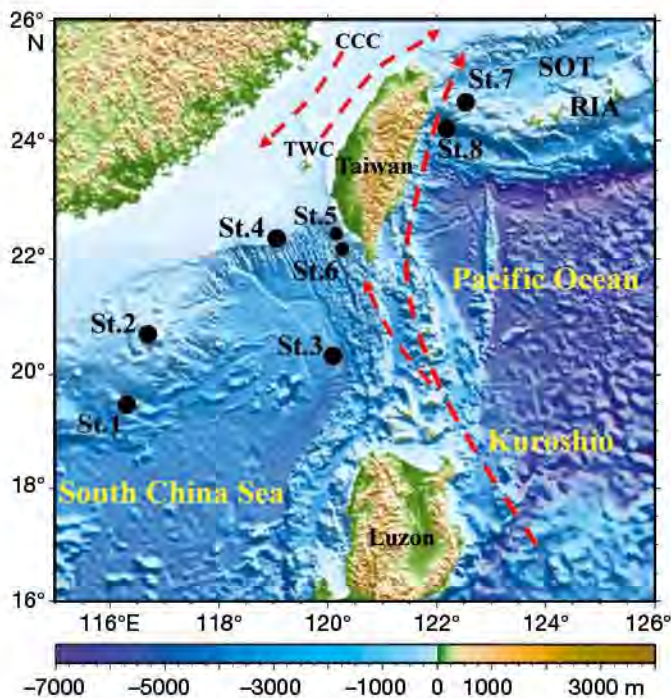


Fig. 1. Sampling sites (solid circles) for benthic megafauna with Stns 1–6 in the South China Sea and Stns 7–8 off northeastern Taiwan. The dashed lines represent the currents for the Taiwan warm current (TWC), China coastal current (CCC) and Kuroshio. SOT: Southern Okinawa Trough; RIA: Ryukyu Island Arc

MATERIALS AND METHODS

Study sites and sample collection

Biological samples were collected from the SCS and the northeastern coast of Taiwan in June, July and October from 2008 to 2010 (Table 1). Stns 1–6 were situated along bathymetric gradients from the outer continental shelf (depth: 91 m, Stn 1) to the deep-sea floor (depth: 3458 m, Stn 3) at 6 different depths in the SCS (Fig. 1, Table 1). Two other study sites (Stn 7 and Stn 8) off the northeastern coast of Taiwan were investigated for comparison. Stn 7 (depth: 1525 m) was located in the deep-sea basin of the southern Okinawa Trough and Stn 8 (depth: 1242 m) was located at the Ho-ping Basin south of the Ryukyu Island Arc. Hydrological data, including vertical salinity and temperature profiles, were measured by a SeaBird CTD recorder (SBE 9/11 plus, SeaBird), except at Stn 7 where the water temperature was obtained from archival summer data (from Aug 21, 1996) provided by Taiwan's ocean databank (www.odt.ntu.edu.tw/?lang=en). The megafauna for stable isotope analysis were collected with a bottom beam trawl (4.7 × 0.28 m, mesh size 15 mm²). One trawl was conducted at each station and the duration of each haul was 30 or 60 min (Table 1) with an average ship speed of 2.5 knots (1 knot = 1.852 km h⁻¹). The trawled samples were frozen on board immediately and the species were identified in a laboratory. A total of 2602 individual specimens were collected, of which 126 species were identified and 265 individual specimens were analyzed for their isotopic compositions. Feeding types of the fish and crustaceans were classified into either zooplankton feeders or benthic feeders, determined from the literature, information obtained from the Fishbase database (www.fishbase.org) and stomach contents examined in this study.

Stable isotope analysis

The stomach contents (from the anterior alimentary canal) of the fish (58 species) and the echinoderms were carefully transferred to Petri dishes and examined under a light microscope. The stomach contents of the fish were identified and pooled into several categories, e.g. chyme (unidentified organic matter), fish, crustaceans and molluscs. The stomach contents

and muscles of the organisms were carefully taken to avoid viscera, gonads, bones and exoskeletons (invertebrates) for isotopic analysis. Muscles were extracted from the tube feet of asteroids, central body disks of ophiuroids, body walls of holothurians, chelipeds and cephalothoraxes of decapods and dorsal parts of fish. Muscles were not collected from specific parts of the body of other taxonomic groups, e.g. cnidarians and molluscs. All selected samples were rinsed first in distilled water and dried at 60°C for 24 h. To remove calcium carbonate (CaCO₃), the stomach contents were acid-treated with 1 M HCl and then washed and dried again for at least 24 h. Muscle tissues were not acid-treated with HCl. All samples were ground to powder and subsamples of 1.1–1.3 mg were packed in tin capsules for further analysis. Although some authors suggest that the lipid content in tissues should be removed due to lower δ¹³C in lipids relative to proteins (Sweeting et al. 2006, Logan & Lutcavage 2008), this significantly alters the δ¹⁵N value (Logan & Lutcavage 2008) making it unsuitable for trophic level estimates (Mintenbeck et al. 2008). Moreover, Caut et al. (2009) indicated that no significant differences were found in both carbon and nitrogen discrimination factors with lipid extraction. Therefore, lipid extraction was not performed in this study. Total contents of carbon and nitrogen and their isotopic compositions were determined with an isotope ratio mass spectrometer (Thermo Finnigan Deltaplus Advantage) system connected to an automatic elemental analyzer (Carlo-Erba EA 2100). Analyzed results are expressed in standard δ notation with the isotopic ratios of carbon and nitrogen presented as follows: $\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where X is either ¹³C or ¹⁵N and R is either (¹³C:¹²C) or (¹⁵N:¹⁴N), respectively. The reference standards for carbon and nitrogen were Pee Dee Belemnite (PDB) and atmospheric nitrogen, respectively. The US Geological Survey standard #40 (L-glutamic acid), which has certified δ¹³C (−26.2‰) and δ¹⁵N (−4.5‰) and acetanilide (Merck) with δ¹³C (−29.8‰) and δ¹⁵N (−1.5‰) were used as working standards. The best precision and accuracy for nitrogen isotopic composition is when the absolute nitrogen content is >20 μg N. At this level of nitrogen, organic C in the tissue is always sufficient for dual isotope analysis. Therefore, we took the absolute amount of N as criteria for weighing. All samples including working standards were weighted to produce ~50–100 μg N and, therefore, no correction was needed. The standard deviations of C and N isotopic compositions of our working standard were ±0.15 for a total of 48 working standards in 6 batches for this

study. The long-term (10 yr; >3000 runs) standard deviations of lab working standard are <0.25‰ after discarding bad numbers (<1%) while instrumental condition is known to be improper. Accordingly, both precision and accuracy are good enough to discern the isotopic differences among the samples. Most samples were only analyzed once, except 2 fish at Stn 7 that showed extremely negative δ¹³C values that were analyzed twice. Duplicated measurements showed consistent δ¹³C values (−25.2‰, −26.4‰) for *Alepocephalus umbriceps* and (−25.9‰, −25.7‰) for *Aldrovandia affinis*.

Data analysis

Since the trophic enrichment factors for δ¹⁵N and δ¹³C vary but generally range between 2.5–4.5‰ (Minagawa & Wada 1984, Post 2002) and 1–2‰ (Wada et al. 1991), respectively, both the maximum and minimum trophic enrichment values were considered to demarcate the lenient ranges of marine plankton (Loick et al. 2007), the sPOM in the SCS (Liu et al. 2007, Table 2), SOM off northeastern Taiwan (Kao et al. 2003, 2006, Hu et al. 2006, Table 2), the hydrothermal vent clams *Calyptogena magnifica* (Fisher et al. 1994) and mussels *Bathymodiolus* sp. (McKinness et al. 2005) in the Pacific Ocean on the δ¹³C and δ¹⁵N biplot.

In order to investigate whether the isotopic signatures of the organisms are different among bathymetric gradients and taxonomic groups, the δ¹³C and δ¹⁵N values of the organisms were compared with 1-way ANOVA on ranks and multiple comparison tests (Dunn's test) due to unequal data group variances. Non-linear regression was used to evaluate the possible relationship between isotopic values and depth gradients after natural log transformation of depth.

RESULTS

Stomach contents and isotopic values

Most fish had empty stomachs or their food was fully digested into unidentified chyme. Prey items from only one third of stomach samples could be identified by the otoliths of fish, exoskeletons of crustaceans and beaks of cephalopods. The δ¹³C varied from the lowest values of −25 to −26.6‰ for the stomach contents of blackbelly tonguesole *Symphurus strictus* at Stn 5, Gilbert's halosaurid fish *Aldro-*

Table 2. Mean and range of isotopic values and C/N ratios of phytoplankton (^{phy}), sinking particle organic matter (^{sPOM}), sediment organic matter (^{SOM}) and hydrothermal vent mussels/clams (^{mc}) used to estimate the food sources of the megafauna at each station as shown in Fig. 2. SOT: Southern Okinawa Trough. Kao et al. (2006) and Liu et al. (2007) measured $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of SOM and sPOM and only reported $\delta^{13}\text{C}$ data in their papers

Station (this study)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	C/N ratio	Collected period/depth (m)	Sources
01–06	2.9 (^{phy}) (1.4 to 8.8)	−20.9 (^{phy}) (−21.6 to −20.3)	7.4 ± 0.8 (^{phy})	Jul 2003 <100 m	>42 km from the coast Loick et al. (2007)
1	3.4 (^{sPOM}) (2.3 to 4.5)	−23.2 (^{sPOM}) (−23.7 to −22.6)	9.9 (^{sPOM}) (7.7 to 12.2)	Dec 2001–Apr 2002 1248 m	Site: M2S Liu et al. (2007)
2, 4	4.3 (^{SOM}) (4.1 to 4.7)	−22.5 (^{SOM}) (−22.9 to −22.2)	5.3 (^{SOM}) (4.1 to 7.4)	Jul 02 85 m	Sites: A8, C10, D7 Hu et al. (2006)
3	4.4 (^{SOM})	−21.5 (^{SOM})	6.8 (^{SOM})	Dec 1994 2890 m	Site: No.15 Kao et al. (2006)
5, 6	3.6 (^{SOM}) (3.4 to 3.8)	−23.3 (^{SOM}) (−23.4 to −23.1)	7.4 (^{SOM}) (5.8 to 8.4)	Dec 1994 620–812 m	Sites: No. 8, 25, 26 Kao et al. (2006)
7, 8	3.7 (^{SOM}) (3.5 to 3.9)	−21.3 (^{SOM}) (−21.1 to −21.5)	7.4 (^{SOM}) (6.7 to 8.0)	1992–1996 1303–1630 m	Site: SOT Kao et al. (2003)
7	5.2 (^{mc}) 1.4 (−0.9 to 4.5)	−26.6 (^{mc}) −33.4 (−34.9 to −32.0)		Aug 1999/2200 m 1988	McKiness et al. (2005) Fisher et al. (1994)

vandia affinis and the slickhead *Alepocephalus umbriceps* both at Stn 7 to −17.7‰ for yellowfin scorpionfish *Scorpaenopsis neglecta* at Stn 4. The $\delta^{15}\text{N}$ values ranged from 5.6‰ for the stomach contents of spearnose whiptail *Coelorinchus acutirostris* at Stn 2 to 13.6‰ for Kaup's arrowtooth eel *Synaphobranchus kaupii* at Stn 8. The differences between muscle tissues and stomach contents were 2.7 ± 1.3 ‰ (mean ± SD) in $\Delta\delta^{13}\text{C}$ and 3.2 ± 1.8 ‰ in $\Delta\delta^{15}\text{N}$ (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m501p053_supp.pdf).

Isotopic values of megafauna

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of analyzed muscle samples varied considerably. $\delta^{15}\text{N}$ values varied from 2.4‰ for limpets (*Bathycmaea* sp.) to 15.9‰ for bivalves (*Pseudomalletia* sp.) both at Stn 3, and the $\delta^{13}\text{C}$ values ranged from −26.4‰ for the slickhead *Alepocephalus umbriceps* at Stn 7 to −14.1‰ for asteroids at Stn 8 (see Table S2 in the Supplement). Isotopic ranges also varied among different sites with the largest range found at Stn 7 ($\delta^{13}\text{C}$ range: 7.6‰) and Stn 3 ($\delta^{15}\text{N}$ range: 13.5‰) and the narrowest range found at Stn 6 ($\delta^{13}\text{C}$ range: 1.0‰ and $\delta^{15}\text{N}$ range: 2.0‰) probably a result of the small number of species analyzed (Fig. 2). Sampling sites with larger ranges of $\delta^{13}\text{C}$ usually were accompanied by larger ranges of $\delta^{15}\text{N}$ except at Stn 7. Significant differences were observed among sites for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

($H = 61.3, 69.2$, respectively, $df = 7$, $p < 0.001$, Kruskal-Wallis 1-way ANOVA on ranks), with lower $\delta^{15}\text{N}$ found at the shallowest station, Stn 4 (depth: 91 m), than at Stns 1, 3, 5 and 8 (Dunn's test, $p < 0.05$). The $\delta^{13}\text{C}$ values at Stn 4 were significantly larger than the isotopic values at Stns 1, 2, 3, 5 and 7 (Dunn's test, $p < 0.05$). Significant differences were also observed among taxonomic groups for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($H = 50.6, 45.7$, respectively, $df = 4$, $p < 0.001$, Kruskal-Wallis 1-way ANOVA on ranks), with higher $\delta^{15}\text{N}$ in molluscs than in cnidarians and decapods (Dunn's test, $p < 0.05$). The $\delta^{13}\text{C}$ of cnidarians and decapods were significantly lower than molluscs, echinoderms and fish (Dunn's test, $p < 0.05$).

In the SCS, most species at Stn 2 and Stn 4 had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values within the range appropriate for marine phytoplankton as the food source. At deeper sites, e.g. Stn 1, Stn 3, Stn 5 and Stn 6, the $\delta^{13}\text{C}$ values of most megafauna moved toward the overlapped range of sPOM, SOM and phytoplankton, indicating mixed diets from different sources (Fig. 2). The isotopic values of some species, e.g. *Bathycmaea* sp., at Stn 3 were not situated in the funnel-shaped areas extending from SOM or phytoplankton, suggesting alternative food sources used by these animals. The majority of species at Stn 8 had isotope values within the range of surficial SOM, but the isotopic values of the megafauna at Stn 7 (except for a crustacean *Gnathophausia* sp.) indicated that their carbon sources came from carbon fixation fueled by chemosynthetic pathways (Fig. 2).

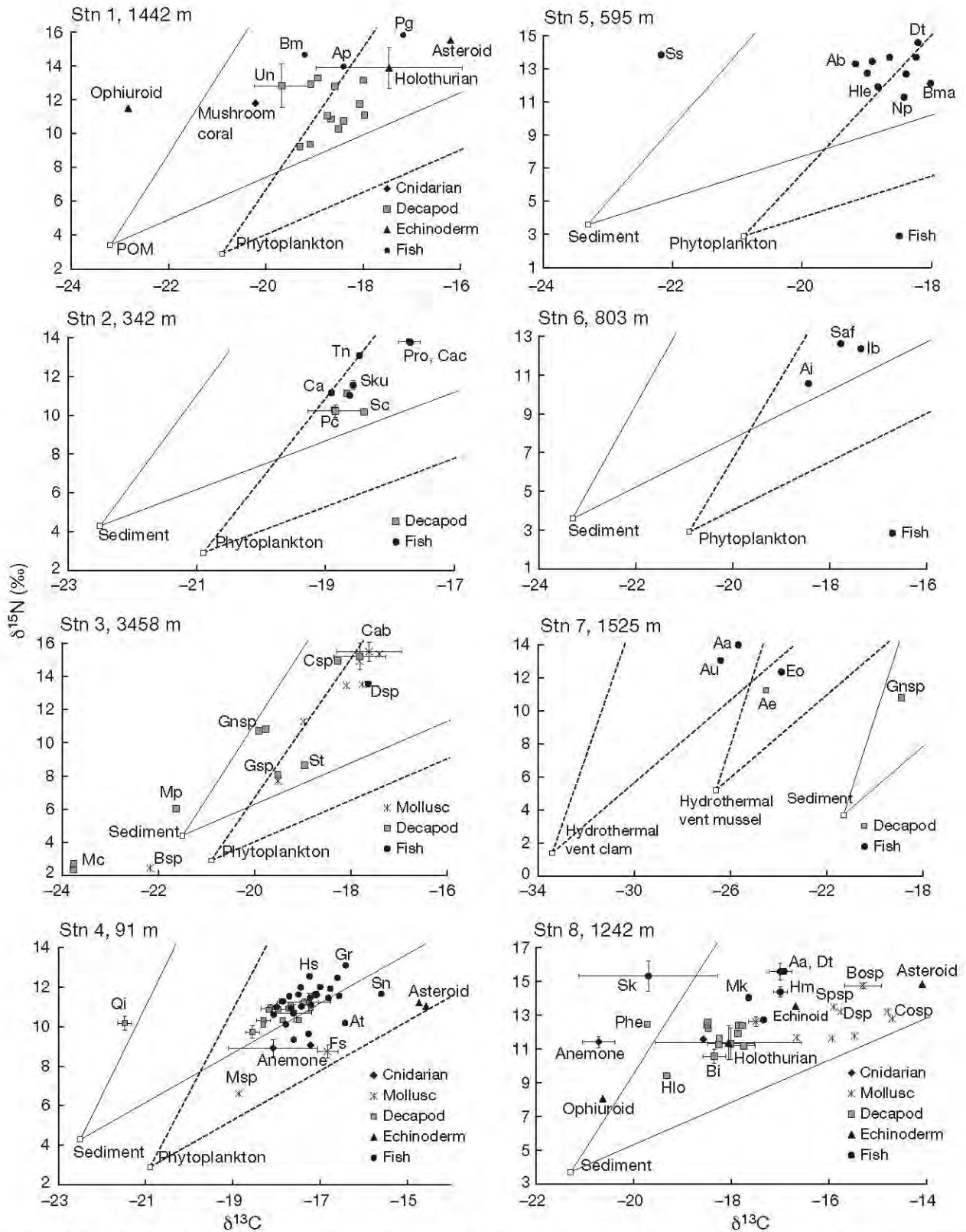


Fig. 2. Biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the megafauna. Funnel-shaped areas show the potential isotopic ranges of consumers that fed on different food sources, considering trophic enrichment of +1‰ in $\delta^{13}\text{C}$ with +4.5‰ in $\delta^{15}\text{N}$ (upper boundary) and of +2‰ in $\delta^{13}\text{C}$ with +2.5‰ in $\delta^{15}\text{N}$ (lower boundary). Mean isotopic values (\pm SD) were shown for the species having more than 3 individuals analyzed. See Table 2 for the sources of baseline data and Table S2 in the Supplement for species codes

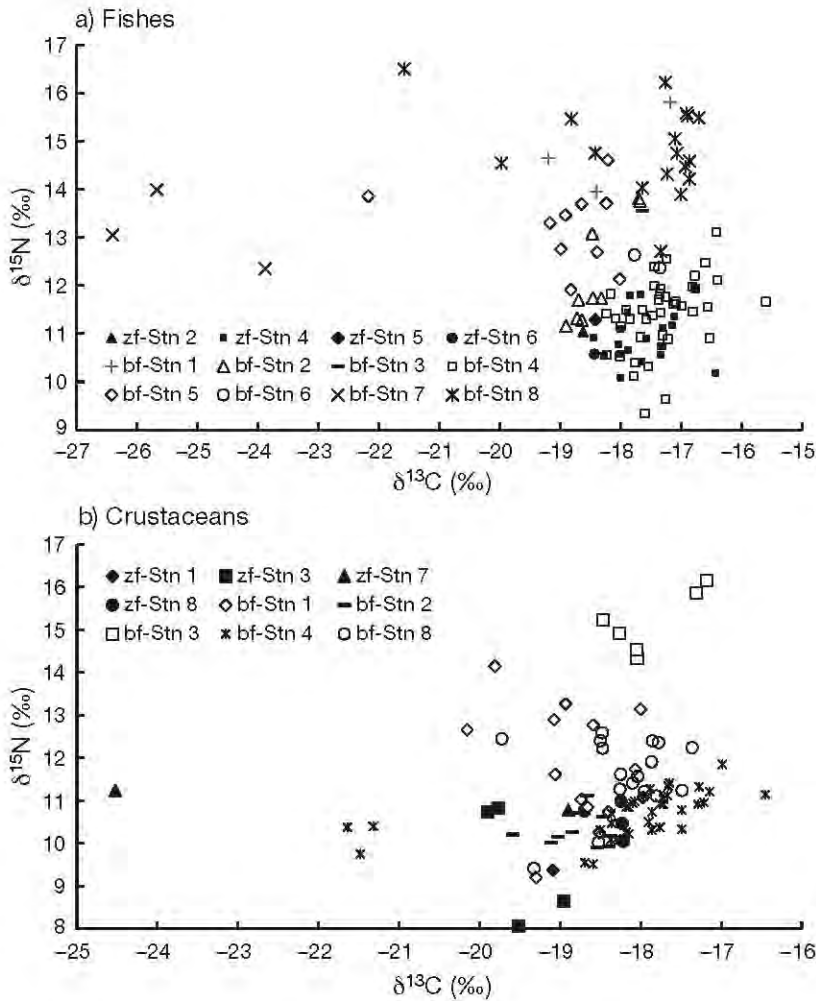


Fig. 3. Muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of (a) fish and (b) crustaceans shown by station (Stns 1–8) and feeding type (zf: zooplankton feeders; bf: benthic feeders)

Cnidarians (anemones and a mushroom coral) had relatively low isotopic mean values for $\delta^{13}\text{C}$ (-17.2 to -20.2‰) and $\delta^{15}\text{N}$ (8.8 to 11.8‰). Molluscs and decapods showed the widest isotopic ranges of $\delta^{13}\text{C}$ (-14.7 to -22.2‰ and -16.5 to -24.5‰ , respectively) and $\delta^{15}\text{N}$ (2.4 to 16.0‰ and 2.3 to 16.1‰ , respectively). Most fish had relatively higher isotopic mean values for $\delta^{13}\text{C}$ (-15.6 to -19.7‰) and $\delta^{15}\text{N}$ (9.5 to 15.6‰), except 3 fish species (*Aldrovandia affinis*, *Alepocephalus umbriceps*, *Elassodiscus obscurus*) with the lowest $\delta^{13}\text{C}$ between -23.9 to -26.4‰ at Stn 7. A significant but weak correlation ($r = 0.41$, $p < 0.0001$, Pearson's correlation) between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was observed after combining all samples except for Stn 7, which had distinct and isotopically light $\delta^{13}\text{C}$ values. Stronger Pearson's correlations between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were found for cnidarians ($r = -0.84$, $p = 0.002$), molluscs ($r = 0.50$, $p = 0.004$), decapods ($r =$

0.60 , $p < 0.0001$) and echinoderms ($r = 0.51$, $p = 0.03$). No correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was observed in any of the fish species ($p = 0.12$).

Isotopic values between different trophic guilds

Zooplankton-feeding fish were only identified at Stn 2 (1 species), Stn 4 (5 species), Stn 5 (1 species) and Stn 6 (1 species). The remaining 45 fish species were classified as benthic feeders (Table S2). Zooplankton feeders ($n = 23$) had lower $\delta^{15}\text{N}$ values ranging from 10.1 to 12.0‰ with a mean value of $10.9 \pm 0.5\text{‰}$, and the benthic-feeding fish ($n = 86$) showed larger $\delta^{15}\text{N}$ values with a wider range between 9.3 and 16.5‰ and with a mean value of $12.6 \pm 1.6\text{‰}$ (Fig. 3a). There were significant differences in $\delta^{15}\text{N}$ values between these 2 trophic guilds ($F_{1,107} = 23.7$, $p < 0.0001$, 1-way ANOVA); however, $\delta^{13}\text{C}$ values were not significantly different between these 2 groups ($F_{1,107} = 0.64$, $p = 0.43$, 1-way ANOVA). The $\delta^{15}\text{N}$ values of fish muscle were positively related to the natural log-transformed total length of the fish ($r = 0.68$, Pearson's correlation, $p < 0.001$).

Zooplankton-feeding decapods were identified at Stn 1 (1 species), Stn 3 (3 species), Stn 7 (2 species) and Stn 8 (1 species). The mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of these 11 samples were $10.2 \pm 1.0\text{‰}$ and $-19.5 \pm 1.8\text{‰}$, respectively. The remaining 83 decapod samples were benthic feeders and had a mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ value of $11.3 \pm 1.4\text{‰}$ and $-18.3 \pm 0.9\text{‰}$, respectively. Significant differences were found in the isotopic values between these 2 feeding guilds ($F_{1,92} = 6.9$, 11.6 , $p = 0.01$, 0.001 for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, 1-way ANOVA; Fig. 3b).

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ patterns along depth gradients

The $\delta^{15}\text{N}$ values of all megafauna gradually increased with depth, with a weak non-linear regression fit ($r = 0.37$, $p < 0.0001$) or relative higher fit ($r = 0.52$, $p < 0.0001$, Pearson's correlation) when data

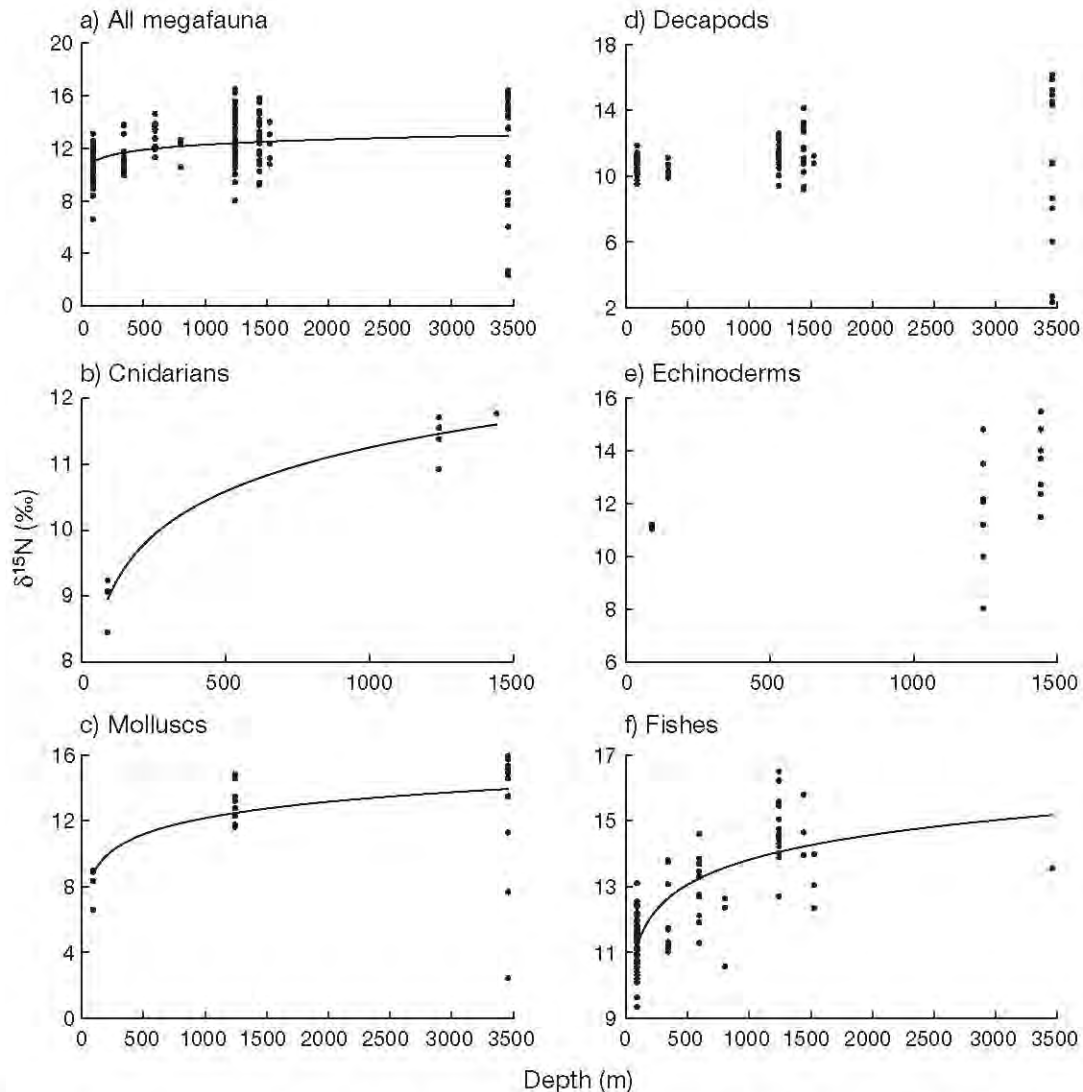


Fig. 4. Relationship between $\delta^{15}\text{N}$ values and depth for (a) all megafauna, $\delta^{15}\text{N} = 0.56 \times \ln(\text{Depth}) + 8.37$, $r = 0.37$, $p < 0.0001$; (b) cnidarians, $\delta^{15}\text{N} = 0.96 \times \ln(\text{Depth}) + 4.62$, $r = 0.98$, $p < 0.0001$; (c) molluscs, $\delta^{15}\text{N} = 1.42 \times \ln(\text{Depth}) + 2.32$, $r = 0.52$, $p = 0.002$; (d) decapods, not statistically significant; (e) echinoderms, not statistically significant; (f) fish, $\delta^{15}\text{N} = 1.09 \times \ln(\text{Depth}) + 6.26$, $r = 0.79$, $p < 0.0001$. Each black dot represents an individual sample

from the deepest site were removed (Fig. 4a). However, a disparity in $\delta^{15}\text{N}$ patterns with depth was found among taxonomic groups. The $\delta^{15}\text{N}$ values of decapods and echinoderms were not correlated with depth ($p = 0.20$, 0.22 , respectively, Pearson's correlation). On the other hand, $\delta^{15}\text{N}$ values of cnidarians ($r = 0.98$, $p < 0.001$), molluscs ($r = 0.52$, $p = 0.002$) and fish ($r = 0.79$, $p < 0.001$) increased significantly with depth (Fig. 4).

Molluscs, decapods and echinoderms had larger ranges of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values at deeper sites (Figs. 4 & 5). The $\delta^{13}\text{C}$ values of all megafauna were negatively related to depth ($r = 0.24$, $p < 0.001$; Fig. 5a). Among them, cnidarians ($r = 0.82$, $p = 0.003$),

decapods ($r = 0.31$, $p = 0.002$) and fish ($r = 0.40$, $p < 0.001$) showed a significant and negative relationship with depth; however, no significant relationship was observed with depth for either molluscs ($p = 0.22$) or echinoderms ($p = 0.07$, Pearson's correlation; Fig. 5).

DISCUSSION

Food sources of benthic megafauna

Carbon and nitrogen isotope values and C/N ratios can be used to distinguish between marine and terrigenous organic matter (TOM). Values for marine

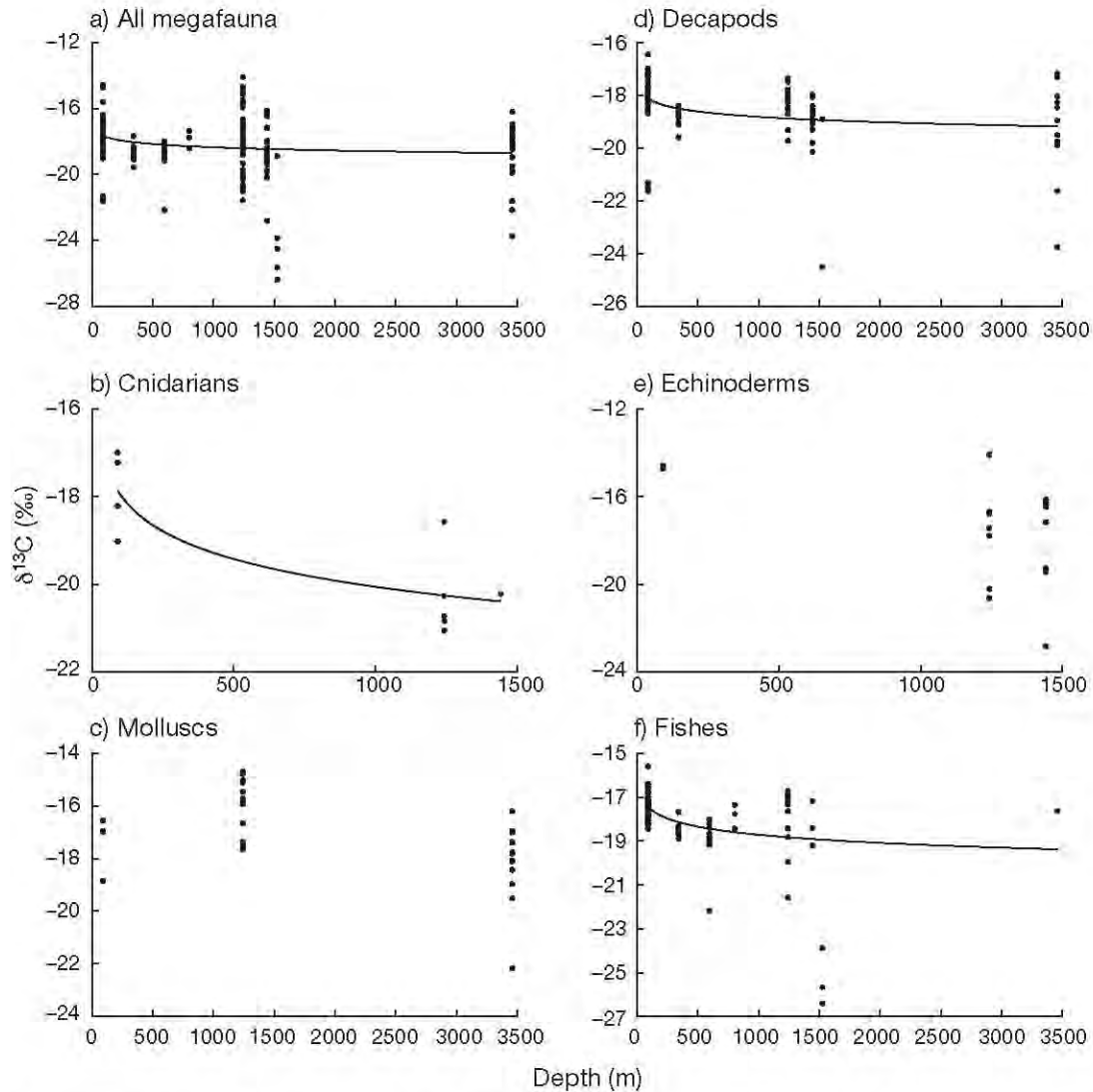


Fig. 5. Relationship between $\delta^{13}\text{C}$ values and depth for (a) all megafauna, $\delta^{13}\text{C} = -0.29 \times \ln(\text{Depth}) - 16.37$, $r = 0.24$, $p < 0.0001$; (b) cnidarians, $\delta^{13}\text{C} = -0.91 \times \ln(\text{Depth}) - 13.75$, $r = 0.82$, $p < 0.003$; (c) molluscs, not statistically significant; (d) decapods, $\delta^{13}\text{C} = -0.29 \times \ln(\text{Depth}) - 16.8$, $r = 0.31$, $p = 0.002$; (e) echinoderms, not statistically significant; (f) fish, $\delta^{15}\text{N} = -0.53 \times \ln(\text{Depth}) - 15.03$, $r = 0.40$, $p < 0.0001$. Each black dot represents an individual sample

phytoplankton $\delta^{13}\text{C}$ are between -22 and -19% (Peterson & Fry 1987). TOM has $\delta^{13}\text{C}$ values of -28 to -25% if C3 plants are dominant and -15 to -12% if C4 plants are dominant (Hedges et al. 1997). Terrestrial plants and marine nitrogen fixers use atmospheric N_2 as a nitrogen source ($\delta^{15}\text{N} \sim 0\%$); however, marine phytoplankton assimilate dissolved nitrogen ($\delta^{15}\text{N} \sim 4.8\%$, Sigman et al. 2000). C/N ratios for marine organic matter range from 5–7 while C/N ratios for terrestrial plants may exceed 20 (Hedges et al. 1988). $\delta^{13}\text{C}$ values and C/N ratios of sPOM and SOM in the SCS are within the range reported for marine phytoplankton. The higher C/N ratios (up to 12) of sPOM found in the northern SCS suggest minor con-

tributions of TOM in this region (Liu et al. 2007). The $\delta^{15}\text{N}$ values of sPOM and SOM in the SCS are low, ranging from 2.7 to 3.6‰ (Gaye et al. 2009), compared with other studies, e.g. 8.2‰ at the Porcupine Abyssal Plain (Iken et al. 2001), 5.8 to 7.4‰ at the West Antarctic Peninsula Shelf (Mincks et al. 2008) and 8.1 to 9.3‰ at the Pakistan Margin (Jeffreys et al. 2009). The low $\delta^{15}\text{N}$ values of sPOM and SOM suggest fixation of newly dissolved N_2 by cyanobacteria such as *Trichodesmium*, *Richelia* and some unicellular species in the SCS (Chou et al. 2006). In the summer, stratified water prohibits the transport of nitrate from deeper waters to the euphotic zone. Therefore, atmospheric nitrogen fixation ($\delta^{15}\text{N} \sim 0\%$)

by phytoplankton becomes the dominant N source. POM with lower $\delta^{15}\text{N}$ values can be transferred to higher consumers through the food chain (Aberle et al. 2010). This biogeochemical process may explain the lower $\delta^{15}\text{N}$ values in deep-sea sPOM and SOM observed in the SCS, relative to that in other oceans.

The megafauna from most surveyed locations showed higher $\delta^{13}\text{C}$ values mostly between -21 and -15% , indicating that *in situ* primary production in the surface euphotic zone, sPOM and SOM were the main contributors to their food sources. At Stn 7, one shrimp (*Acanthephyra eximia*) and 3 fish species (*Aldrovandia affinis*, *Alepocephalus umbriceps*, *Elasmodiscus obscurus*) showed the lowest $\delta^{13}\text{C}$ values (-26 to -24%) among all analyzed samples and the values were even lower than that for the sPOM (-24 to -23% , Sheu et al. 1999) and surficial SOM (-21% , Kao et al. 2003) in the Southern Okinawa Trough. These results suggested that *in situ* primary production in the euphotic zone, sPOM and surficial SOM were not the main nutrients providing the C source for the shrimp or the top predators, the fish, at Stn 7. Chemosynthesis associated with hydrothermal vents might be a possible nutrient source for the deep-sea ecosystem at Stn 7. Numerous deep-sea hydrothermal vents and chemosynthetic communities have been discovered in the middle to southern Okinawa Trough (e.g. Chan et al. 2000, Ohta & Kim 2001). Therefore, the low $\delta^{13}\text{C}$ values ($<-30\%$, Fisher et al. 1994; -26.6% , McKiness et al. 2005) of symbiont-bearing organisms might be delivered to top predators through the food chain. Different lipid contents in tissues among species could also influence $\delta^{13}\text{C}$ values (Sweeting et al. 2006, Logan & Lutcavage 2008). However, all the fish tissues analyzed for isotopes in this study were collected from the same type of muscle tissue and, for that reason, should contain similar proportions of lipids. Therefore, deep-sea fish with low $\delta^{13}\text{C}$ values (-26 to -24%) collected at Stn 7 may feed on prey consuming mixed carbon sources derived from photosynthetic and chemosynthetic production. Different carbon sources more likely explained the large difference in isotope values of the same fish species (*Aldrovandia affinis*) collected at Stn 7 and Stn 8.

Trophic dynamics of the SCS food web

Cnidarians are typical suspension feeders that predominantly feed on a number of different floating organic particles, including zooplankton. Two species of anemones collected at the euphotic zone

(Stn 4) showed the lowest $\delta^{15}\text{N}$ values other than the gastropod grazers, suggesting their main food sources were from fresh phytodetritus. In contrast, the $\delta^{15}\text{N}$ values of the cnidarians increased approximately 3% at the deep-sea Stn 1 and Stn 8. Cnidarians such as mushroom corals might opportunistically feed on small zooplankton by using their nematocysts due to a more limited food supply on the deep-sea floor, consequently increasing their $\delta^{15}\text{N}$ values.

In Echinodermata, ophiuroids cover a larger spectrum of feeding types including suspension, deposit, omnivorous, scavenging and carnivorous feeding modes. We observed stomachs full of sediments inside the central body disk of the ophiuroids, strongly indicating the deposit-feeding behavior of these species. This inference was supported by the low isotopic values and trophic levels of the ophiuroids. Iken et al. (2001) and Jeffrey et al. (2009) suggest the low isotopic values in some ophiuroids might be caused by a fresh POM feeding type in these species. In contrast, asteroids are generalist predators with some species as detritivores or even specialized suspension feeders. We found chyme but not sediments in the stomach of asteroids, suggesting that these species are carnivorous predators. This observation supports asteroids at higher trophic levels and their isotopic values were even higher than many fish at Stn 1, Stn 4 and Stn 8. Asteroids occupied the highest trophic level at the Porcupine Abyssal Plain (Iken et al. 2001) and the Arctic Basin (Bergmann et al. 2009). The holothurians had isotopic values between ophiuroids and asteroids suggesting niche expansion from feeding on SOM to preying on small crustaceans and polychaetes, as shown by Iken et al. (2001). The largest variations of isotopic values, especially the $\delta^{13}\text{C}$ values, were observed in the holothurians, suggesting feeding on multiple food sources with marine and terrestrial origins or ingesting various debris on the seafloor for holothurians.

To reduce competition pressure, species might evolve to specialize or expand into different trophic niches. We found that zooplankton feeding fish and crustaceans had relatively lower $\delta^{15}\text{N}$ values than fish that preyed on benthic organisms. These findings are supported by other studies (Iken et al. 2001, Boyle et al. 2012, Papiol et al. 2013). In general, zooplankton-feeding fish, e.g. the duck-billed eel *Nettastoma parviceps*, have small mouths, limiting predation to smaller organisms, e.g. shrimps (Saldanha et al. 1995), thus accumulating lower $\delta^{15}\text{N}$ values. However, benthic-feeding fish are usually predators or scavengers feeding on diverse food items from ben-

thic invertebrates to other fish, therefore expanding their $\delta^{15}\text{N}$ values and trophic levels. For example, a fleshy-lipped spikefish *Tydemania navigatoris* mainly feeds on the scales of different fish (Mok 1978) and showed higher $\delta^{15}\text{N}$ values than other benthic-feeding fish and decapods at Stn 2. However, the lowest $\delta^{15}\text{N}$ values were observed in flounders (*Psettina iijimae* and *Laeops tungkongensis*) that were classified as benthic-feeding fish. This result was attributed to the small sizes of the *P. iijimae* (2 cm), whose diet may shift during ontogenetic development (Stowasser et al. 2009), or to the specialized feeding of *L. tungkongensis* on low trophic prey.

Bathymetric variations in isotopic values

Most megafauna at the shallower Stns 2 and 4 had a lower and narrower $\delta^{15}\text{N}$ range. This suggests a single food source of oceanic origin and a shorter settling time for biogeochemical fractionation in the POM that nourishes the benthic fauna. In contrast, a larger range of $\delta^{15}\text{N}$ in molluscs and decapods suggests different food sources and wider trophic levels under low food availability at the sites below 1000 m (aphotic zone). For example, an isotopically depleted limpet *Bathycyma* sp. ($\delta^{15}\text{N}$: 2.4‰, $\delta^{13}\text{C}$: -22.2‰) may use chemosynthetic nutrients as found in *Bathycyma secunda* (Sasaki et al. 2003). In addition, galatheid crabs (*Munidopsis ceutrina* and *M. profunda*), which are known to feed on wood falls and their associated biofilms (Hoyoux et al. 2009, 2012), had much lower values in both isotopes ($\delta^{15}\text{N}$: 2.5‰, $\delta^{13}\text{C}$: -23.80‰; $\delta^{15}\text{N}$: 6.0‰, $\delta^{13}\text{C}$: -21.6‰, respectively). Other decapods with a pelagic diet (genus *Gennadas*, Heffernan & Hopkins 1981) or a mixed diet of benthic and pelagic prey (slipper lobsters *Scyllarus martensii*, Sekiguchi et al. 2007) also had lower $\delta^{15}\text{N}$ values. The highest $\delta^{15}\text{N}$ values (15 to 16‰) observed in shrimp (*Parastylodactylus* sp.) and bivalves (*Cetoconcha* sp., *Cuspidaria abyssopificica*, *Pseudomalletia* sp) at the deepest station, Stn 3, was comparable to the $\delta^{15}\text{N}$ values of 13 to 17‰ in other bivalve species (Iken et al. 2001, 2005). Feeding on reworked POM, carrion of high trophic fish (Cartes 1993), carnivorous habit (e.g. genus *Cuspidaria*, Reid & Reid 1974) or long starvation under a food limitation condition might increase the $\delta^{15}\text{N}$ values of these invertebrates (Hobson et al. 1993).

Non-linear relationships were found between bathymetric gradients and the $\delta^{15}\text{N}$ levels of some taxonomic groups. Non-linear relationships are commonly observed in many environmental and

biological factors along depth gradients. Mintenbeck et al. (2007) also used a non-linear model for studying the relationship between the $\delta^{15}\text{N}$ levels of organisms and depths. We found no significant relationship between decapods' $\delta^{15}\text{N}$ levels and depth. This result is consistent with the findings of Mintenbeck et al. (2007). Most decapods and molluscs feed on sPOM, including large and fast-sinking POM which usually have lower $\delta^{15}\text{N}$ values as well as the small, reworked POM that can be higher in $\delta^{15}\text{N}$ values (Rau et al. 1990, Wakeham et al. 2009). Morphology, mobility, digestive properties and food selectivity on freshly deposited matter or reworked material in the subsurface might explain various $\delta^{15}\text{N}$ values found in molluscs and decapods (Iken et al. 2001, 2005, Bergmann et al. 2009). In contrast, cnidarians as typical suspension feeders have increasing $\delta^{15}\text{N}$ values along depth gradients and the same phenomena was found in the Weddell Sea (Mintenbeck et al. 2007) and in the Fram Strait (Bergmann et al. 2009). Several mechanisms control the isotopic level of deposit-feeding molluscs, decapods and suspension-feeding cnidarian along depth gradients. First, suspension feeders utilize smaller suspended particles which have a longer residence time in the water column and, therefore, undergo a higher level of microbial fractionation (Mintenbeck et al. 2007). Second, deposit feeders might use particles advected from the shelf to the deep-sea basin or resuspended sediments due to low food availability. Third, nutrient stress and starvation can also cause enrichment of $\delta^{15}\text{N}$ levels in animal tissues (Adams & Sterner 2000).

Comparison with other deep-sea food webs

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the deep-sea megafauna in the East China Sea, Sulu Sea, Celebes Sea and Philippine Sea ranged from 7 to 15‰ and -21 to -14‰, respectively (Asante et al. 2008, 2010). These values are generally similar to the isotopic ranges of the megafauna from the SCS and the northeastern coast of Taiwan. In the deeper water of the East China Sea, the crustaceans have larger variations of $\delta^{15}\text{N}$ (7 to 14‰) compared with other phyla (Asante et al. 2008). However, in the Porcupine Abyssal Plain and the Arctic basin, the crustaceans show a narrow range of $\delta^{15}\text{N}$ from 12 to 16‰ (Iken et al. 2001) and 13 to 15‰ (Bergmann et al. 2009), respectively. The decapods and molluscs at 3458 m of depth in the SCS show a large range of $\delta^{15}\text{N}$ (2 to 16‰). The isotopic data from this and previous studies suggest a wider

trophic spectrum in the decapod and mollusc species in the tropical deep seas than in the temperate and arctic deep seas. Benthos-feeding, scavenging and feeding on reworked organic matter could enrich $\delta^{15}\text{N}$ values (Iken et al. 2001, Mintenbeck et al. 2007, Bergmann et al. 2009), contributing to the elevated trophic levels of the deep-sea megafauna. In contrast, decapods and molluscs depleted in $\delta^{15}\text{N}$ might exploit less-energetic resources such as undifferentiated detritus, small meiofauna or wood falls because of the limited resources available on deep-sea floors (Cartes & Carrassón 2004). These mechanisms can explain the broader range of $\delta^{15}\text{N}$ values and trophic niches for the decapods and molluscs found at the deeper site of the SCS.

We found that zooplankton-feeding fish were distributed only on the continental shelf and the upper slope while benthic-feeding fish occupied the deep-sea floors. This result is in agreement with Serrano et al. (2011) and Yeh & Drazen (2011) who found that zooplankton-feeding fish predominantly live on the upper slope of the Northern Span and more scavenging fish live at deeper sites on the California slope. More species at high trophic levels and longer food chains at deeper sites might reflect the limited contribution of phytodetritus to the deep-sea food web.

Based on the $\delta^{15}\text{N}$ values of the megafauna, the food web in the SCS deeper than 1000 m might cover 5 trophic levels using a mollusc grazer as the baseline (data not shown). The food chain of 4 to 5 trophic levels were also reported in the Arctic deep-sea environments (Iken et al. 2005, Bergmann et al. 2009) and in the bathyal Mediterranean (Polunin et al. 2001). However, Iken et al. (2001) and Mincks et al. (2008) found only 3 trophic levels of the food chain at the Porcupine Abyssal Plain and West Antarctic Peninsula, respectively. Our results together with published data suggest that oligotrophic seas, such as the SCS and Arctic deep-sea environment, have longer food chains while eutrophic seas, e.g. the Northeastern Atlantic Ocean and the Antarctic Sea, have shorter food chains. Low surface productivity and scarce food supply to the deep-sea floor might enhance the trophic niche expansion, thus resulting in longer food chains in the oligotrophic SCS.

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