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Spatial dietary shift in bivalves from embayment with river discharge and mariculture activities to outer seagrass beds in northwestern Philippines

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Abstract To investigate the spatial variation in bivalve food sources along a pollution gradient and assess bivalve contribution to biogeochemical cycles in tropical coastal ecosystems, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bivalves and their potential food sources were studied in northwestern Philippines. In a semi-enclosed embayment affected by river discharge and mariculture activities, bivalves depended primarily on ^{13}C -depleted suspended particulate organic matter such as phytoplankton and/or fish feeds. However, toward the relatively oligotrophic seagrass beds, the bivalve food source gradually shifted to more ^{13}C -enriched resuspended and/or settled particles. Furthermore, in the outer

seagrass beds exposed to the open ocean, bivalves mainly relied on similar food sources, such as detritus of microalgae, regardless of the distance from the embayment. These trends appear to reflect the ready availability of the food sources. Especially in the outer seagrass beds, a semi-closed material cycle within the vicinity of the sea bottom likely emerged between bivalves and algae, but not between the phytoplankton in the overlying water column. This resulted in a relatively weak benthic-pelagic coupling for bivalves. These cycles would need to be taken into account when estimating the biogeochemical cycles in eutrophicated coastal areas.

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Introduction

Bivalves often dominate the macrobenthos in coastal marine communities. Their high biofiltering activity plays a key role in biogeochemical cycles, including food webs, and estimating their contribution is essential for evaluating the material cycles in coastal ecosystems. Bivalves take up suspended materials from the overlying water column with high efficiency (Bayne and Newell 1983; Bayne and Hawkins 1992). After particle selection (e.g., Ward and Shumway 2004) and assimilation, they deposit the particulate materials to sediments as pseudofeces and feces, respectively (biodepositon; Haven and Morales-Alamo 1966; Dame 2011). They excrete ammonium and phosphate into the ambient and sediment-pore water after digesting particulate organic nitrogen and particulate phosphorus, respectively, which are inaccessible to aquatic primary producers (Kautsky and Evans 1987; Peterson and Heck 1999). This contributes to benthic-pelagic coupling (e.g., Dame 2011) where suspension feeding and nutrient release can control phytoplankton abundance via top-down

and bottom-up control, respectively (Asmus and Asmus 1991; Newell 2004). The biofiltering contributes to water purification, especially in coastal areas threatened by water quality deterioration from human activities such as aquaculture (Lefebvre et al. 2000; MacDonald et al. 2011) and increased river load (Riera and Richard 1997; Kasai et al. 2004).

Bivalves have two feeding modes, suspension-feeding and deposit-feeding (mainly surface deposit-feeding), and these modes can be either obligatory or facultative (i.e., switching between the two modes; Hummel 1985; Ólafsson 1986). Bivalves generally prefer phytoplankton, but sometimes shift their preference depending on the availability of favorable foods. Even obligatory suspension-feeders can assimilate various sources of nutrition from the water column via resuspension. Kanaya et al. (2008) reported that *Laternula marilina* assimilated both marine particulate organic matter (POM) and resuspended benthic diatoms at a highly productive site, whereas it relied on terrestrial plant detritus at a less productive and river-dominated site. This was attributed to ability of *L. marilina* to assimilate refractory organic materials, probably using digestive enzymes (cellulase). In addition, some bivalve species have a photo-autotrophic relationship (e.g., *Tridacna*) with zooxanthellae and chemo-autotrophic relationship (e.g., Lucinidae) with sulfide-/methane-oxidizing bacteria (Gosling 2015). The stable carbon isotope ratio ($\delta^{13}\text{C}$) of bulk organic shell matrices are more depleted in symbiotic bivalves than in non-symbiotic bivalves (Dreier et al. 2014), and the bivalve–sulfide-oxidizer symbiosis is advantageous to both bivalves and tropical seagrass beds (van der Heide et al. 2012). For studies on biogeochemical cycles, it is important to evaluate which materials are incorporated into the food web by bivalves, because they represent the primary consumer level. However, diverse food preferences across species and trophic plasticity make this complicated. The application of $\delta^{13}\text{C}$ and the nitrogen isotope ratio ($\delta^{15}\text{N}$) can elucidate this by comparing bivalves and their potential food sources.

Seagrass beds are highly productive ecosystems (Duarte and Chiscano 1999), and provide habitat and food to various organisms directly or indirectly (e.g., Larkum et al. 2006). Some animals such as herbivorous fish and sea urchins feed on seagrass (McClanahan et al. 1994; Eklöf et al. 2008). However, many macrobenthos, including bivalves, do not prefer seagrass due to its low nutrient quality (Cebrián 1999) and high contents of indigestible lignin and inhibitory polyphenols (Harrison 1982). Organic sources that support seagrass food webs are still under discussion (Lebreton et al. 2011). For bivalves, several food sources are reported, such as phytoplankton, epiphytes on seagrass blades, detritus derived from them, macroalgae and seagrasses, and

bacteria (e.g., Moncreiff and Sullivan 2001; Rossi et al. 2015). Recently, the importance of microphytobenthos has been increasingly recognized due to the development of new isolation techniques (Moncreiff and Sullivan 2001; Lebreton et al. 2011). Even within a single seagrass-bed site, various bivalve species sometimes use different food sources. Kharlamenko et al. (2001) suggested that the dominant mollusk, *Macoma incongrua*, which is relatively ^{13}C -enriched ($-11.0\text{\textperthousand}$), relied mainly on detritus of various phytoplankton, epiphytes, and seagrasses. In contrast, *Ruditapes philippinarum* is ^{13}C -depleted ($-19.4\text{\textperthousand}$), reflecting its preference for phytoplankton. Although a relatively large amount of information is available for food webs in temperate seagrass beds, there have been very few studies performed on tropical and subtropical seagrass beds, which are typically surrounded by coral reefs. Furthermore, previous bivalve studies have been completed only at a limited number of stations per site. Hence, the spatial relationship between the environment and bivalve food sources across different ecosystems has not been clarified, and bivalve contribution to material cycles cannot be comprehensively described in coastal areas.

Bolinao, northwestern Philippines, is an intriguing area to investigate the spatial variation of bivalve food sources, as there is a continuous and wide environmental gradient from polluted waters caused by mariculture and river discharge to the seagrass beds surrounded by coral reefs. Along this gradient, there has been a decline in the species richness of seagrass (Fortes et al. 2012; Tanaka et al. 2014) and macrofauna (Leopardas et al. 2016), seagrass cover and shoot density of *Thalassia hemprichii* (Fortes et al. 2012), growth rate of the goatfish *Parupeneus barberinus* (Watai et al. 2015), and survival, growth, and reproduction of the coral *Pocillopora damicornis* (Villanueva et al. 2006) with increasing pollution. In contrast, an increase in the abundance of macrofauna, dominated by mollusks (mainly gastropods; Leopardas et al. 2016), and the coverage and shoot density of the seagrass *Enhalus acoroides* (Fortes et al. 2012) have been observed in seagrass beds affected by polluted waters.

The objective of the present study was to investigate the effects of the pollution gradient in Bolinao on the feeding ecology of bivalves using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of bivalves ($\delta^{13}\text{C}_{\text{bivalve}}$ and $\delta^{15}\text{N}_{\text{bivalve}}$), focusing on which food sources bivalves utilized, and how far particles in the polluted embayment spread and supported bivalves in the outer seagrass beds. Water quality parameters and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of potential food sources were also determined. A bivalve transplantation experiment was conducted to compare bivalve response to their food source across seasons and sites.

Materials and methods

Study site

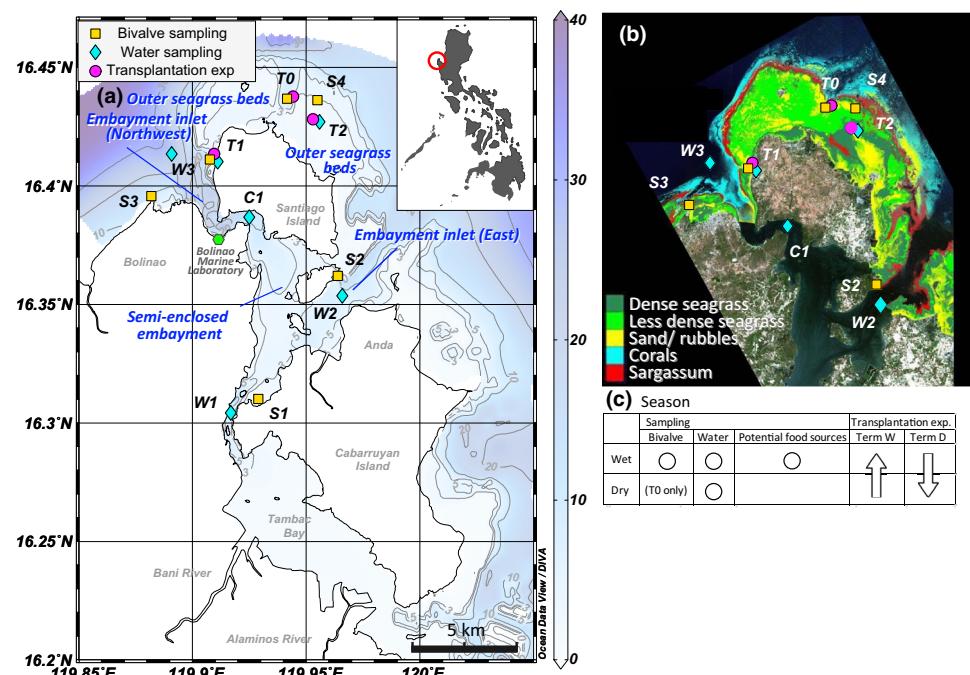
The study was conducted in Bolinao, Pangasinan, northwestern Philippines ($16^{\circ}18'–26' N$, $119^{\circ}53'–58' E$; Fig. 1). In the semi-enclosed embayment located between Bolinao and Santiago and Cabarruyan Islands, fish cages/pens culturing milkfish (*Chanos chanos*) are densely deployed. The allowable number of fish cages/pens (~544) was established for Bolinao in 2000, but has not been determined for Anda, where the number of structures has increased (Bolinao/Anda: 384/328 in 2003, 351/588 in 2014; Ferrera et al. 2016). Oyster and mussel farms also operate in the embayment (White 2009). The embayment is severely eutrophicated (San Diego-McGlone et al. 2008; Ferrera et al. 2016), and fish kill events have repeatedly occurred (David et al. 2014) due to phytoplankton blooms followed by hypoxia (Azanza et al. 2005; San Diego-McGlone et al. 2008). The Bani River is the largest river discharging into the embayment through Tambac Bay. Along the northwest, north, and east side of Santiago Island, shallow seagrass beds occur widely, being exposed to the open ocean and dominated by *T. hemprichii*, *Cymodocea rotundata*, and *Enhalus acoroides* (Fortes et al. 2012; Tanaka et al. 2014). From the outer seagrass beds to the embayment, there is a clear pollution gradient with respect to dissolved inorganic nitrogen (DIN , $NO_3^- + NO_2^- + NH_4^+$, from ~8 to ~30 μM), phosphate (~1 to ~3 μM), and chlorophyll *a* (Chl *a*, ~3 to ~16 $\mu g/L$) with salinity (to 14~; Fortes et al. 2012; Watai et al. 2015; Ferrera et al. 2016). Rainfall occurs mainly in

the wet season from June to September (monthly mean precipitation: 736 mm; Ferrera et al. 2016) during the southwest monsoon, while little precipitation is observed in the dry season from November to March (23 mm) during the northeast monsoon. Water exchange in the embayment is affected by tides, and the direction of residual current in the surface layer is almost similar to the wind direction, i.e., from Tambac Bay to the east and northwest inlets (openings) in the wet season, and from the east to northwest inlet and Tambac Bay in the dry season (Yoshikai 2016). In contrast, the residual current in the bottom layer is opposite to the surface layer in the wet season (i.e., from east and northwest inlets to Tambac Bay), and the same as the surface layer in the dry season. The surface embayment water is flushed to the outer seagrass beds surrounding Santiago Island, especially in the wet season.

Sampling

Bivalves were collected from one site in the embayment (S1), one site in the embayment inlet (S2), and four sites in the outer seagrass beds around Santiago Island (S3, S4, T0, T1) in September 2011 (wet season; except T0) and March and September 2012 (T0, dry and wet seasons) by snorkeling (Fig. 1). S1 is located near a narrow strait connecting the embayment and Tambac Bay. S2 is on the east embayment inlet connecting the embayment and the outer seagrass beds, and located at the southern edge of the seagrass beds. The other four sites were inside the wide outer seagrass beds, and the distance from the inlet increased in the order of $T1 > S3 > T0 > S4$. The common

Fig. 1 **a** Locations of bivalve ($S1–S4$, $T0$, $T1$) and water (spatial survey: $W1–W3$, $C1$, $T1$; 24 h continuous observation: $C1$, $T2$) sampling sites and transplantation experiment sites (from $T0$ to $T1$ and $T2$) in Bolinao area. Bathymetry data are from GEBCO 08. Depth contours are in meters. **b** Benthic cover map of Bolinao area based on multispectral satellite image analysis (described in detail in Tamondong et al. 2013). Sampling sites of this study are indicated in the map. **c** Sampling seasons for bivalves, water, and potential food sources, and terms (Term *W* and *D*) for the transplantation experiment



species of bivalves were randomly sampled. After sampling, the adductor muscle and the mantle were dissected (whole soft tissue was used for small bivalves) and stored at $<-20^{\circ}\text{C}$.

To evaluate the spatial and seasonal variations of water quality, water samples were collected near the bivalve sampling sites (W1, W2, T1, W3) and at C1 for spatial survey on September 15 and 16, 2010 (wet season) and March 1 and 7, 2011 (dry season; except T1). In addition, 24 h continuous observation was conducted on September 19–20, 2011 (wet season) and March 2–3, 2012 (dry season) at C1 and T2 monitoring sites with a floating platform. Salinity was measured by the CTD-type profiler AAQ-RINKO (JFE Advantech). Water samples were collected from the surface using a bucket, and from the bottom using either a Van Dorn (10 L) or a Niskin (5 L) water sampler. Only surface water was collected at the shallow sites, T1 and T2. Samples for DIN were filtered on board through syringe filters (DISMIC-25CS, cellulose-acetate membrane, 0.8 μm , ADVANTEC), packed in 10-mL acrylic tubes, and temporarily stored on ice. Samples for particulate organic carbon (POC), particulate nitrogen (PN), and their stable isotope ratios were prescreened on board through a 250- μm sieve and stored temporarily in 10-L polyethylene containers. After transporting to the Bolinao Marine Laboratory, the samples for POM were filtered through precombusted (450°C , 3 h) glass microfiber filters (GF/F, 47-mm diameter, Whatman). All the water and filter samples were then stored at $<-20^{\circ}\text{C}$ until analysis. A portion (100–500 mL) of samples collected for POM was filtered (25-mm diameter), and the filter was soaked in *N,N*-dimethylformamide in polypropylene tubes covered with aluminum foil and stored at $<-20^{\circ}\text{C}$ for later determination of Chl *a*.

As potential food sources for bivalves, the isotopic signatures of suspended POM, sedimentary organic matter (SOM), sinking particles (SP), seagrasses collected at/near several of the bivalve sampling sites (distance from the sites ~1.85 km) in the wet season, and fish feeds were also determined. Samples for SOM and seagrasses were collected and analyzed based on methods described in Miyajima et al. (2015) and Tanaka et al. (2008), respectively. Samples for SP were collected by deploying sediment traps. The trap consisted of a PVC pipe (7 cm diameter and 30 cm height) with a narrow bottom and a 1-cm² wire mesh cover on its open mouth. Replicated traps were deployed 1 m above the bottom at each site for 1 week. After retrieval, the contents of the trap were collected carefully, making sure that algae growing on the walls of the trap were not included, and filtered through precombusted GF/F filter (47-mm diameter, Whatman). The filter was stored at $<-20^{\circ}\text{C}$. Six types of fish feeds (dry pellets) used in mariculture farms were obtained from fish cage/pen caretakers and stored at $<-20^{\circ}\text{C}$.

Transplantation experiment

To determine whether $\delta^{13}\text{C}_{\text{bivalve}}$ and $\delta^{15}\text{N}_{\text{bivalve}}$ reflect changes in food sources from the different environments across seasons and sites, a bivalve transplantation experiment was conducted. The bivalve *Anadara antiquata*, which is a common species in seagrass beds in the present study area, was collected at site T0 and transplanted to T1 and T2 between March and September 2012 (Term W, from dry to wet season), and between September 2012 and March 2013 (Term D, from wet to dry season). Each bivalve was randomly placed in a separated rectangular parallelepiped room (side length: 5–12 cm) of plastic net cage (opening: ~1.5 cm) following a checkerboard pattern with alternating bivalve rooms and vacant rooms to avoid interactions among bivalves. Cages were placed at the sea bottom under the marine protected area guard structure (T1) and monitoring floating platform (T2). After 6 months, the bivalves were retrieved, and their longest diameter and thickness of shells were measured using a digital caliper. The bivalves were treated in the same way as described in “Sampling” section.

Sample analysis

DIN concentration was determined using an autoanalyzer AAC-III (BLAN+LUEBBE). The filters for POM were lyophilized and fumed with 12 N HCl for 2 days to remove the inorganic carbon. Excess HCl was removed using a vacuum desiccator with NaOH tablets for at least 1 week. The concentration and stable isotope ratio of POC and PN were determined using an elemental analyzer/isotope ratio mass spectrometer (FLASH EA/Conflo IV/DELTA V Advantage, Thermo Fisher Scientific). Chl *a* concentration was determined using a fluorometer (10AU, Turner Designs).

Bivalve tissues were lyophilized and ground using an agate mortar and pestle into a homogeneous and fine powder. Their C and N contents and isotope ratios were also quantified using the elemental analyzer/isotope ratio mass spectrometer.

The C and N contents and isotope ratios of potential food sources were quantified using the elemental analyzer/isotope ratio mass spectrometer as well, after the following procedure: filters with SP were dried at 60°C , and fumed with 12 N HCl to remove inorganic carbon. Excess HCl was removed in a vacuum desiccator with NaOH tablets. Fish feeds were lyophilized and ground in the same way as bivalves.

Bivalve species were identified using the WoRMS database (WoRMS 2016).

Statistical analyses were performed using one-way ANOVA followed by Tukey’s HSD test. The significance of Pearson’s correlation coefficient was checked using *t* test.

Results

Water quality

Salinity was low, especially in surface waters during the wet season (surface 15.7~32.2, bottom 27.8~33.9), while it was spatially homogeneous during the dry season (surface 33.0~34.4, bottom 33.1~34.5; Table 1). Vertical distribution of density σ_t (data not shown) indicated stratification in the wet season, whereas well vertical-mixing in the dry season. Salinity was lowest at W1, and gradually increased with distance from the Bani River mouth in the wet season. DIN, POC, and Chl *a* were generally higher in the embayment (W1, C1) and the eastern embayment inlet (W2) than in the outer seagrass beds (T1, T2). POC and Chl *a* were higher in the wet season than in the dry season at each site except at C1 in the 24 h sampling.

In the 24 h sampling, DIN, POC, and Chl *a* changed with a significant negative correlation to salinity at T2 in the wet season ($p < 0.01$). POC and Chl *a* were significantly positively correlated in surface waters at C1 in both wet and dry seasons, and at T2 in the wet season ($p < 0.0001$).

The POC/PN ratio was approximately 5–7, and slightly increased to 10 in the surface layer of the embayment in the wet season. POC/Chl *a* weight ratio varied, and was low (<200) in the wet season, except at W3 (bottom), while high values (>200) were often observed in the dry season.

Spatiotemporal variation of $\delta^{13}\text{C}_{\text{POC}}$ and $\delta^{15}\text{N}_{\text{PN}}$

The $\delta^{13}\text{C}_{\text{POC}}$ values were lower in the wet season (−19.7 to −27.8‰) than in the dry season (−19.4 to −22.6‰) at each site, and increased gradually with distance from the Bani River mouth in the wet season. The $\delta^{15}\text{N}_{\text{PN}}$ values

Table 1 Spatiotemporal variation in water quality from 24 h sampling and spatial survey

Site	Layer	Salinity	DIN (μM)	POC (μM)	$\delta^{13}\text{C}_{\text{POC}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{PN}} (\text{\textperthousand})$	POC/PN	Chl <i>a</i> (μg/l)	POC/Chl <i>a</i>
Wet season									
24 h sampling									
C1	S	19.2±0.7 (10)	8.0±1.7 (13)	85.5±25.4	−27.8±0.4	2.3±1.7	5.4±0.5 (13)	21.3±7.1 (13)	49.1±6.1
	B	31.4±0.1 (11)	6.5±1.8 (13)	14.0±4.3	−23.7±1.1	−1.2±1.8	5.5±0.4 (13)	1.1±0.3 (13)	154±47
T2	S	27.4±2.0 (22)	1.0±0.6 (24)	18.3±7.2	−19.9±1.7	3.1±0.4	5.8±0.4 (13)	1.7±2.0 (13)	184±71
Spatial survey									
W1	S	15.7±2.2 (2)	4.4 (1)	156.9	−25.4	2.2	6.8 (1)	19.4 (1)	97.3
	B	27.8 (1)	4.1 (1)	89.9	−24.1	2.7	6.2 (1)	14.1 (1)	76.3
W2	S	27.7±0.2 (2)	2.1 (1)	159.0	−24.4	1.8	9.8 (1)	25.0 (1)	76.3
	B	32.6±0.0 (2)	1.4 (1)	62.0	−23.8	2.6	6.6 (1)	6.1 (1)	122
C1	S	28.2±0.8 (2)	0.8 (1)	99.4	−24.6	1.4	10.0 (1)	12.5 (1)	95.3
	B	32.9±0.2 (2)	6.6 (1)	78.1	−23.2	1.9	6.5 (1)	9.2 (1)	102
W3	S	30.7±0.5 (2)	0.2 (1)	100.0	−23.5	2.1	9.3 (1)	19.5 (1)	61.7
	B	33.9±0.4 (2)	0.4 (1)	13.7	−26.2	5.6	6.0 (1)	0.2 (1)	801
T1	S	32.2 (1)	1.3 (1)	22.1	−19.7	3.4	6.8 (1)	—	—
Dry season									
24 h sampling									
C1	S	33.3±0.0 (12)	5.8±1.5 (13)	45.9±15.5	−21.3±0.4	1.0±1.4	5.8±0.5 (13)	24.2±13.6 (13)	25.9±8.0
	B	33.1±0.1 (12)	5.5±2.1 (13)	31.1±7.4	−21.7±0.4	−0.4±1.0	6.6±0.7 (13)	4.3±1.7 (13)	98.6±38.4
T2	S	33.5±0.1 (25)	0.5±0.3 (25)	10.0±1.3	−19.4±0.8	2.9±1.0	7.2±0.5 (25)	0.4±0.2 (25)	410±197
Spatial survey									
W1	S	34.4±0.4 (2)	17.0±1.6 (2)	76.2±2.2	−22.6±1.5	−1.0±2.1	6.3±0.5 (2)	2.6 (1)	360
	B	34.5±0.5 (2)	17.1±3.5 (2)	67.7±16.6	−22.6±1.3	−1.2±0.3	6.5±0.0 (2)	—	—
W2	S	33.5±0.2 (2)	4.3±4.1 (2)	15.1±3.3	−21.5±1.4	1.2±4.0	5.7±0.3 (2)	0.5 (1)	445
	B	33.6±0.1 (2)	5.3±4.8 (2)	27.0±9.8	−21.6±1.3	1.9±3.9	5.9±0.3 (2)	1.7 (1)	236
C1	S	33.5±0.1 (2)	7.4±2.9 (2)	57.3±16.9	−21.2±1.2	−0.7±1.1	6.1±0.4 (2)	—	—
	B	33.9±0.0 (2)	13.0±2.0 (2)	37.8±4.6	−21.6±1.0	−0.7±1.2	5.8±0.4 (2)	—	—
W3	S	33.0±0.0 (2)	0.3±0.1 (2)	10.3±6.5	−22.4±0.2	4.9±2.0	6.1±0.4 (2)	1.9 (1)	93.4
	B	33.2±0.0 (2)	0.7±0.0 (2)	4.3	−22.6	4.0	6.0 (1)	—	—
T1	S	—	—	—	—	—	—	—	—

Data are means ± SD (n). Samples were collected from the surface (S) and bottom (B) layers

were higher in the wet season (-1.2 to 5.6‰) than in the dry season (-1.2 to 4.9‰) at each site except for C1 (24 h sampling, bottom) and W3 (spatial survey, surface). The $\delta^{13}\text{C}_{\text{POC}}$ values in the 24 h sampling changed with a significant positive correlation to salinity at T2 in the wet season ($p < 0.01$).

Bivalves sampled from the field

Sampled bivalve species and sites are as follows: *Septifer virgatus* (S1), *Saccostrea* sp. (S1), *Perna perna* (S1, S2), *Megacardita ferruginosa* (S2), *Macridiscus aequilatera* (S2), *Anadara antiquata* (S2, T1, S3, T0 including dry season), *Globivenus orientalis* (T1), *Isognomon isognomum* (T1), *Arca* sp. (T1), *Pinna atropurpurea* (T1), *Malleus albus* (T1), *Spondylus* sp. (T1), *Placuna placenta* (S3), *Vasticardium pectiniforme* (S3), and *Pinctada margaritifera* (S4). Their $\delta^{13}\text{C}_{\text{bivalve}}$ varied spatially, with lowest values at S1, followed by S2, and similar or overlapping values at the outer seagrass-bed sites (T1, S3, T0, S4; Fig. 2a). In contrast, $\delta^{15}\text{N}_{\text{bivalve}}$ varied within species and site, and overlapped between sites. Generally, bivalves were ^{15}N -depleted at S1 and S2, and ^{15}N -enriched for several species in the seagrass-bed sites. C/N ratio was high at S1 and S2, compared with the outer seagrass-bed sites (Fig. 2b).

Transplanted bivalves

The $\delta^{13}\text{C}_{\text{bivalve}}$ of *A. antiquata* transplanted to T1 significantly decreased in Term W (average: -2.4‰) compared to that in the original samples collected at T0 ($F_{2,10} =$

31.52 , $p < 0.0001$, Fig. 3a), while that of the transplanted samples to T2 significantly increased in Term D ($+0.5\text{‰}$) compared to that in the original samples (T0; $F_{2,14} = 24.67$, $p < 0.0001$, Fig. 3b). $\delta^{15}\text{N}_{\text{bivalve}}$ showed no significant change at both T1 and T2 compared to T0 for Terms W and D ($p > 0.05$, Fig. 3a, b). C/N_{bivalve} ratio increased significantly at T1 ($+0.3$) compared to T0 in Term W ($F_{2,10} = 20.29$, $p < 0.001$, Fig. 3c), and decreased at T1 (-0.1) and T2 (-0.2) compared to T0 in Term D ($F_{2,14} = 31.98$, $p < 0.0001$, Fig. 3d).

Shell growth rate (longest diameter \times thickness, ratio of after/before transplantation) was significantly higher at T1 (average: 1.05) and T2 (1.02) in Term W than at T1 and T2 (1.00) in Term D ($F_{3,32} = 18.58$, $p < 0.0001$).

Potential food sources

The $\delta^{13}\text{C}$ value of potential food sources was generally lowest at S1, followed by S2 (Fig. 4b). Attached algae (mostly macroalgae) that grew on the artificial substrates placed ca. 30 cm above the sediment (Umezawa et al.; unpubl data) were also compared. The increasing order of $\delta^{13}\text{C}$ of potential food sources is as follows: fish feeds (mean \pm SD: $-24.7 \pm 2.2\text{‰}$), POM (mean at all sites, $-20.9 \pm 2.4\text{‰}$), attached algae ($-20.7 \pm 3.0\text{‰}$), SP captured by sediment trap ($-18.9 \pm 3.9\text{‰}$), SOM ($-14.7 \pm 3.2\text{‰}$), and seagrass ($-7.3 \pm 1.5\text{‰}$). Unlike $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values did not show a clear spatial pattern (Fig. 4d). Seagrass and SP showed relatively higher $\delta^{15}\text{N}$ at S1 and S2 than in the outer seagrass-bed sites. The range of C/N ratio did not overlap between bivalves (≤ 3.8) and any of the potential food sources (≥ 5.8 ;

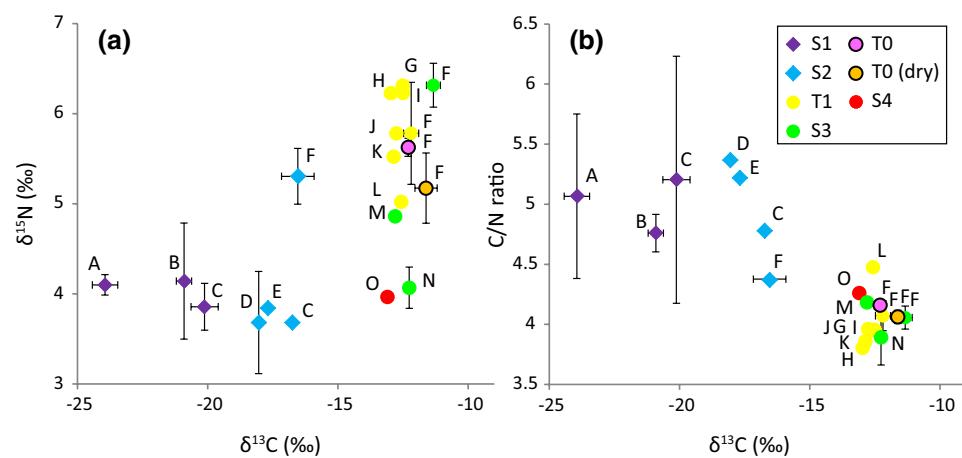


Fig. 2 $\delta^{13}\text{C}$ and **a** $\delta^{15}\text{N}$ values and **b** C/N ratios of bivalves sampled at each site. Bars indicate \pm SD. Samples were collected in the wet season and only at T0 in the dry season. Different letters indicate sample species as follows (sample numbers are shown in parentheses): A: *Septifer virgatus* (3), B: *Saccostrea* sp. (3), C: *Perna perna* (S1: 2, S2: 1), D: *Megacardita ferruginosa* (2), E: *Macridiscus aequilatera* (1), F: *Anadara antiquata* (S2: 2, T1: 4, S3: 7, T0:

5, T0 (dry): 7), G: *Globivenus orientalis* (1), H: *Isognomon isognomum* (1), I: *Arca* sp. (1), J: *Pinna atropurpurea* (1), K: *Malleus albus* (1), L: *Spondylus* sp. (1), M: *Placuna placenta* (1), N: *Vasticardium pectiniforme* (2), O: *Pinctada margaritifera* (1). Adductor muscle and mantle were used for analysis, but the whole body was used for A, D, and E

Fig. 3 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in Terms **a** W and **b** D, and C/N ratios in Terms **c** W and **d** D of transplanted bivalves at each site. Bars indicate $\pm \text{SD}$. Term W is dry to wet season (6 months), and Term D is wet to dry season (6 months). Bivalves were collected at T0, and transplanted to T1 and T2. Different small letters indicate significant differences for $\delta^{13}\text{C}$ (top), $\delta^{15}\text{N}$ (bottom), and C/N ratio in each Term. Sample numbers are as follows (shown in parentheses): Term W: T0 (7), T1 (2), and T2 (4), Term D: T0 (5), T1 (5), and T2 (7)

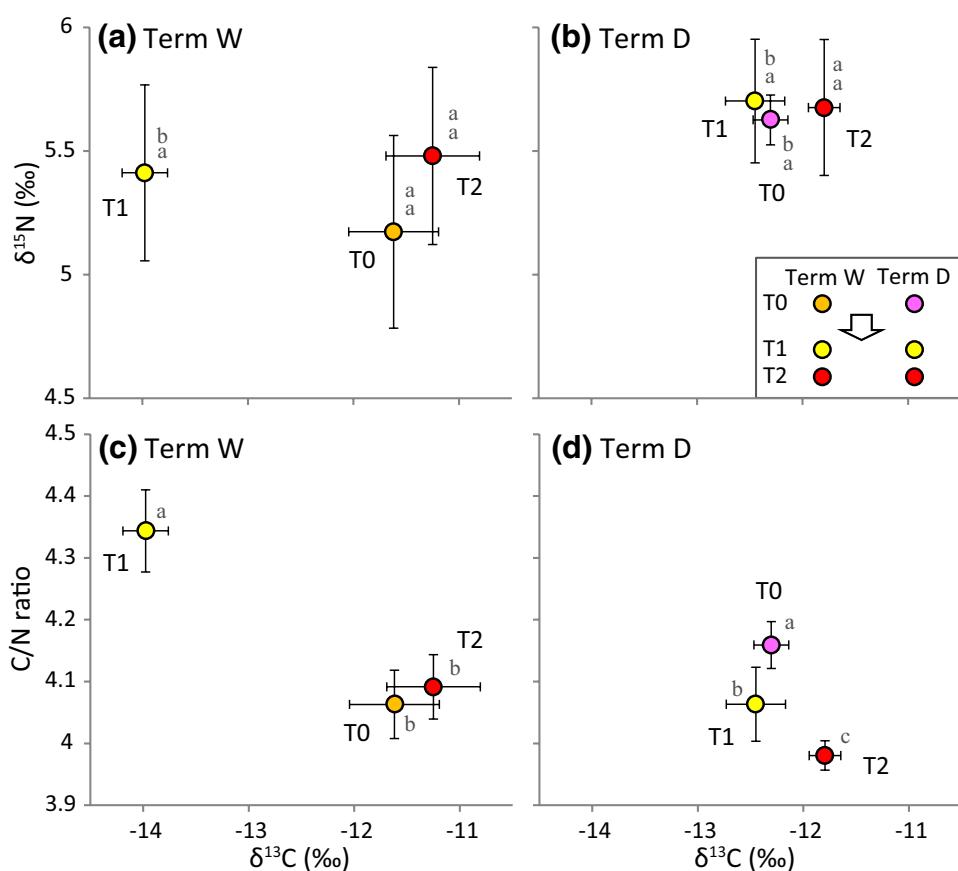


Fig. 4e, f). The C/N ratio of seagrasses was higher than the other sources at each site.

Discussion

The observed spatial trend in the $\delta^{13}\text{C}_{\text{bivalve}}$ values (Fig. 2a) suggests the occurrence of a dietary shift for the bivalves along an environmental gradient in the study area.

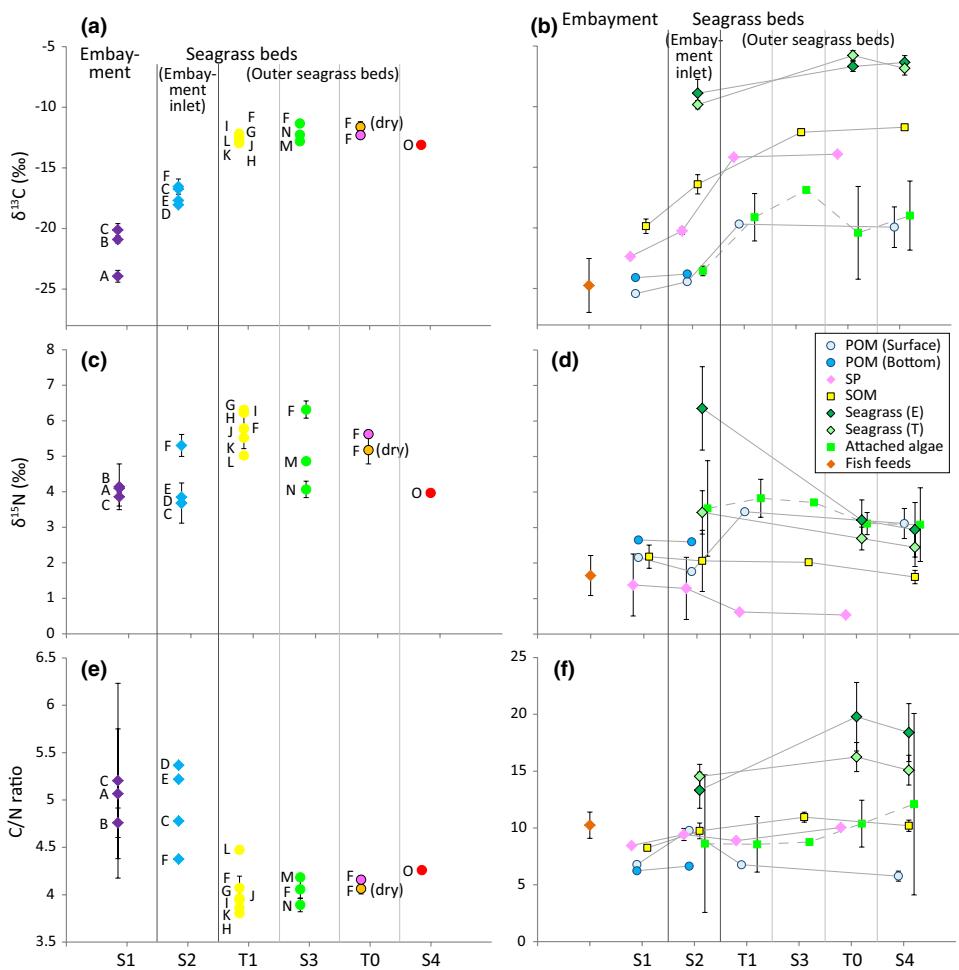
Spatiotemporal variation and the characteristics of POM

Suspended POM is considered a predominant food source for bivalves. As seen in the salinity and $\delta^{13}\text{C}_{\text{POC}}$ values, river discharge created a clear spatial gradient in this semi-enclosed embayment during the wet season. In the outer seagrass beds, positive correlation of $\delta^{13}\text{C}_{\text{POC}}$ and negative correlation of DIN, POC, and Chl *a* with salinity during the 24-h sampling at T2 implies that the eutrophic embayment waters have spread with the tidal current and reached even T2, resulting in poor water quality in the outer seagrass beds. According to Yoshikai (2016), the embayment water is extensively flushed from the east and northwest embayment inlets into the outer seagrass beds, especially during

the wet season. In the spatial survey, strong linear correlation between salinity and $\delta^{13}\text{C}_{\text{POC}}$ of surface waters at the embayment sites (W1–W3, C1, $R^2=0.78$) allowed estimation of the riverine end-member $\delta^{13}\text{C}_{\text{POC}}$ of $-27.2\text{\textperthousand}$ at $S=0$, which is considered one of the potential food sources for bivalves. The relatively low POC/Chl ratio (<200) during the wet season suggests that POM was dominated by phytoplankton (Parsons et al. 1984; Cifuentes et al. 1988). The high POC/PN ratio (>8) of surface waters observed at several of the embayment sites (W2, C1, W3) implies that a fraction of terrestrial material is contained in POM (Parsons et al. 1984; Cifuentes et al. 1988).

In the dry season, the river discharge was minimal. Therefore, poor water quality such as high DIN and POC in the embayment (Table 1) is primarily due to mariculture activities. The dense mariculture structures in the embayment most likely limited water exchange with the outer ocean, which accelerated the accumulation of mariculture- and river-derived pollutants. The slightly lower $\delta^{13}\text{C}_{\text{POC}}$ values at the embayment sites (-21.2 to $-22.6\text{\textperthousand}$) than at the outer seagrass-bed sites ($-19.4\text{\textperthousand}$) might be attributed to ^{13}C -depleted phytoplankton, fish feeds ($-24.7\text{\textperthousand}$), and feces. The phytoplankton in the embayment most likely utilize the ^{13}C -depleted DIC owing to the mixing of CO_2 generated by remineralization of fish feeds and feces. The

Fig. 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and C/N ratios of bivalves (**a**, **c**, **e**, respectively) and potential food sources (**b**, **d**, **f**, respectively) sampled at/near each site. Bars indicate $\pm \text{SD}$. Potential food sources are POM in the surface and bottom waters, SP captured by sediment trap, SOM, the seagrasses *Enhalus acoroides* (E) and *Thalassia hemprichii* (T), and fish feeds. Data of attached algae growing on artificial plate (Umezawa et al.; unpubl data, set for 5 days in September 2011) were also added. Different capital letters (in **a**, **c**, **e**) indicate bivalve species (see Fig. 2)



$\delta^{13}\text{C}$ of fish feces is generally even lower than that of fish feeds (Franco-Nava et al. 2004; Yokoyama et al. 2006). The relatively high POC/Chl ratio (>200) and low POC/PN ratio (<8) of POM in the dry season indicate that the POM was depleted of phytoplankton and often dominated by fish feed-/feces-derived particles and/or aged plankton/plant detritus heavily colonized by bacteria.

Estimation of bivalve food sources

Similar spatial and seasonal patterns were observed in the field samples and the transplantation experiment. The $\delta^{13}\text{C}_{\text{bivalve}}$ values and $\text{C/N}_{\text{bivalve}}$ ratios collected in the embayment (S1) and its inlet (S2) were lower and higher, respectively, than those in the outer seagrass beds (T1, S3, T0, S4) in the field samples (Fig. 2a, b). In the transplantation experiment, the $\delta^{13}\text{C}_{\text{bivalve}}$ and $\text{C/N}_{\text{bivalve}}$ ratio at T1, which is closer to the northwest embayment inlet than T0 and T2, significantly decreased and increased, respectively, in the wet season compared to T0 collected in the dry season (Fig. 3a, c). These low/decreased $\delta^{13}\text{C}_{\text{bivalve}}$ values and high/increased $\text{C/N}_{\text{bivalve}}$ ratios could be due to the

influence of embayment water. As transplanted cages were placed at the sea bottom, the effect of embayment water might have been enhanced in the caged bivalves, compared with natural bivalves dwelling in the sediment.

Before estimating the bivalve food sources, studies comparing bivalves and potential organic sources in other seagrass beds were reviewed (Table 2). The majority of the $\delta^{13}\text{C}_{\text{bivalve}}$ values listed ranged from -16 to $-21\text{\textperthousand}$, which overlap with the values at S2 (-16.5 to $-18.0\text{\textperthousand}$), but is lower than the values at the outer seagrass-bed sites (-11.3 to $-13.1\text{\textperthousand}$). The $\delta^{13}\text{C}_{\text{bivalve}}$ of *R. philippinarum* and *Scrobicularia plana* reported in Lebreton et al. (2011) was appreciably higher (-15.4 and $-13.5\text{\textperthousand}$, respectively) than that of *R. philippinarum* ($-19.4\text{\textperthousand}$) stated by Kharlamenko et al. (2001) and *S. plana* ($-16.6\text{\textperthousand}$) in Rossi et al. (2015). Flagellates and diatoms in microphytobenthos were suggested as the main food source for the suspension feeder *R. philippinarum* and the facultative deposit feeder *S. plana*, respectively, in the study by Lebreton et al. (2011). Their site was in a semi-enclosed bay, receiving river discharge and with oyster farms in the vicinity, where microphytobenthos dominated the

Table 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bivalves and their possible food sources in seagrass beds

Seagrass and epi-phyte	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Microphytobenthos, SOM, POM and macroalgae	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Bivalve	Feeding mode	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Thayer et al. (1978), North Carolina, USA									
Live <i>Zostera marina</i>	-10.2±0.75		Grass bed sediment	-18.7±0.94		<i>Ameritella versicolor</i>	S/SF	-17.3	
Dead <i>Zostera marina</i>	-10.6±0.55		Suspended particulates (from <i>Zostera</i> bed)	-19.4±0.29		<i>Macoma tenta</i>	S/SF	-17.8	
Epiphytes on blades	-16.0±1.94		Suspended particulates (from estuary)	-20.0±1.55		<i>Eontia ponderosa</i>	S/SF	-18.3	
			Suspended particulates (Ocean particulates)	-22.2±1.60		<i>Macoma balthica</i>	S/SF	-18.6	
Fry (1984), Florida, USA									
<i>Syringodium filiforme</i> (rhizomes)	-7.5±0.8 (Oct 81) -5.9±0.5 (Feb 82)		Sediments	-17.2±0.2 (Feb 82)		<i>Ensis minor</i>	FF	-11.3 (Feb 82)	
<i>Syringodium filiforme</i> (leaves)	-9.2±1.4 (Oct 81) -7.1±0.6 (Feb 82)		Dissolved organic carbon	-22.3±0.6 (Oct 81)		<i>Chione cancellata</i>	FF	-18.0±0.6 (Feb 82)	
Dead plant debris (from cores)	-13.2±1.6 (Oct 81) -13.4±5.5 (Feb 82)		Particulate organic carbon	-23.9±2.4 (Oct 81) -20.1±0.8 (Feb 82)		<i>Mercenaria mercenaria</i>	FF	-18.7±0.9 (Oct 81)	
Epiphytes on <i>Syringodium filiforme</i>	-22.1±1.9 (Oct 81) -16.9±0.8 (Feb 82)					<i>Mytilus edulis</i>	FF	-19.6 (Oct 81)	
						<i>Crassostrea virginica</i>	FF	-20.5±0.5 (Oct 81)	
Lepoint et al. (2000), Corsica									
<i>Posidonia oceanica</i> (living leaves)	-13.9±1.0		Macroalgae (Weighted averages)	-18.3	1.8	<i>Emarginula</i> sp	G/DF	-16.2	4.1
<i>Posidonia</i> leaf epifauna	-18.6±1.9	3.0±0.9	Organic suspended particulate matter	-22.5±0.8	1.9±0.5	<i>Pecten</i> sp	SF	-19.5±1.4	5.3±0.3
<i>Posidonia</i> leaf epifauna (fixed epifauna)	-19.4±0.8	3.4±0.6							

Table 2 (continued)

Seagrass and epiphyte	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Microphytobenthos, SOM, POM and macroalgae	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Bivalve	Feeding mode	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Kharlamenko et al. (2001), Russia									
<i>Zostera marina</i> (Green leaves)	-6.7±0.1		Sedimentary organic matter	-15.2		<i>Macoma incongrua</i>	SDF/FF	-11.0±0.3	
<i>Zostera marina</i> (Senescent brown leaves)	-7.9		Benthic POM	-15.5		<i>Ruditapes philippinarum</i>	FF	-19.4±0.2	
<i>Zostera marina</i> (Fallen decomposing leaves)	-6.9		Phytoplankton (mainly <i>Chaetoceros</i> spp.)	-20.7		<i>Pilucina pistidium</i> (Body)	FF/Sy	-26.2±0.3	
<i>Zostera marina</i> (Rhizomes)	-8.9±0.1		Suspended POM (zooplankton)	-20.9±0.3		<i>Pilucina pistidium</i> (Gills)		-27.8±0.1	
Epiphytic algae (diatoms + <i>Pneophyllum lejolii</i>)	-13.5±0.3								
Moncreiff and Sullivan (2001), Mississippi, USA									
<i>Halodule wrightii</i>	-12.2±1.2	6.0±1.1	Sand microflora proxies (Diatom-rich sea-grass substrate)	-14.7	7.8	<i>Mercenaria campechiensis</i>		-18.5	10.8
Epiphytic algae	-17.5±1.7	5.9±0.9	Sand microflora proxies (<i>Mellita quinquesperforata</i>)	-16.9	6.7	<i>Tellina alternata</i>		-19.2	7.5
			Macroalgae	-16.8±0.5	7.0±2.8				
			Phytoplankton	-21.8±0.7	9.9±0.9				
Jaschinski et al. (2008), Germany									
<i>Zostera marina</i>	-9.64±0.65	8.04±0.32	Red algae (<i>Alnifelia plicata</i>)	-16.87±1.03	10.30±0.93	<i>Mytilus edulis</i>	FF	-21.81±0.41	8.40±0.19
Epiphytes on <i>Zostera marina</i>	-11.31±0.81	6.99±0.28	Red algae (<i>Ceramium rubrum</i>)	-17.43±0.15	8.00±0.13				
			Red algae (<i>Polysiphonia fibrillosa</i>)	-24.61±0.17	7.23±0.17				
			Red algae (<i>Dulsella sanguinea</i>)	-34.85±1.02	8.05±0.85				
			Sediment microflora	-20.04±0.23	6.00±0.42				
			Phytoplankton, 20 µm	-22.56±0.06	7.55±0.06				

Table 2 (continued)

Seagrass and epi- phyte	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Microphytobenthos, SOM, POM and macroalgae	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Bivalve	Feeding mode	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Lebreton et al. (2011), France									
<i>Zostera noltii</i> (roots)	-9.7±0.4	7.8±1.9	Microphytobenthos	-15.4±0.9	6.9±0.1	<i>Scrobicularia plana</i>	SDF	-13.5±0.5	10.2±1.6
<i>Zostera noltii</i> (leaves)	-9.9±0.7	7.8±2.2	Sediment surface organic matter	-17.9±1.4	6.1±1.0	<i>Ruditapes philippi-</i> <i>narium</i>	SF	-15.4±0.8	9.3±0.8
<i>Zostera noltii</i> (fresh detrital matter)	-10.4±0.8	8.4±1.8	Suspended POM	-22.0±2.3	-	<i>Cerastoderma edule</i>	SF	-15.7±2.2	9.5±0.7
<i>Zostera noltii</i> (degraded detrital matter)	-12.8±0.9	7.5±0.8							
Epiphytes	-12.8±<0.1	6.3±0.3							
Rossi et al. (2015), Portugal									
<i>Zostera noltii</i> (leaves)	-12.4±0.3	8.9±0.4	Floating macroalgae (<i>Upha</i> sp.)	-12.6±0.4	10.2±0.2	<i>Scrobicularia plana</i>	FDF	-16.64±0.18	11.00±0.26
<i>Zostera noltii</i> (roots)	-12.9±0.4	8.7±0.3	Floating macroalgae (<i>Gracilaria</i> sp.)	-17.4±1.1	10.5±0.6				
			SOM	-21.9±0.1	6.2±0.2				
			POM	-22.5±0.4	5.7±0.3				
This study, Philippines									
Outer seagrass beds (T1, S3, T0, S4)									
<i>Thalassia hemprichii</i>	-6.3±0.7	2.6±0.5	SOM	-12.2±0.5	2.2±0.7	<i>Anadara antiquata</i>		-11.8±0.5	5.7±0.6
<i>Enhalus acoroides</i>	-6.5±0.5	3.1±0.7	Sinking particles cap- tured by sediment traps	-14.0±0.2	0.6±0.1	<i>Vasticardium pectini-</i> <i>forme</i>		-12.3±0.1	4.1±0.2
			Algae growing on artificial plates	-18.9±2.4	3.4±0.7	<i>Arcia</i> sp		-12.5	6.2
			POM (surface)	-19.9±1.6	3.1±0.4	<i>Globivenus orientalis</i>		-12.5	6.3
						<i>Spondylus</i> sp		-12.6	5.0
						<i>Placuna placenta</i>		-12.8	4.9
						<i>Pinnna atropurpurea</i>		-12.8	5.8
						<i>Malleus albus</i>		-12.9	5.5
						<i>Pinctada margaritifera</i>		-13.1	4.0
						<i>Iognomon isognom-</i> <i>mum</i>		-13.9	6.2

Table 2 (continued)

Seagrass and epiphyte	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Microphytobenthos, SOM, POM and macroalgae	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Bivalve	Feeding mode	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Embayment inlet (S2)									
<i>Enhalus acoroides</i>	-8.9±1.1	6.4±1.2	SOM	-16.4±0.8	2.1±0.9	<i>Anadara antiquata</i>	-16.5±0.6	5.3±0.3	
<i>Thalassia hemprichii</i>	-9.8±0.3	3.4±0.6	Sinking particles captured by sediment traps	-20.2±0.3	1.3±0.9	<i>Perna perna</i>	-16.7	3.7	
			Algae growing on artificial plates	-23.5±0.4	3.5±1.3	<i>Macridiscus aequilatera</i>	-17.7		
			POM (surface)	-24.4	1.8	<i>Megacardita ferruginea</i>	-18.0±0.0	3.7±0.6	
			POM (bottom)	-23.8	2.6				

Species name was modified to the latest one, following the WoRMS database (WoRMS 2016). Data are means±SD, but SE for Rossi et al. (2015). Feeding mode categorized in each study are as follows: S/SF suspension/surface feeder, FF filter-feeder, SF suspension feeder, G/DF grazer and/or fauna feeding on plants detritus, Sy symbiotroph, SDF suspension deposit feeder, FDF facultative deposit-feeder

SOM. Moncreiff and Sullivan (2001) suggested that eutrophic conditions would favor the food web of seagrass beds based on algae. Thus, it might be likely that eutrophication caused the predominance of ^{13}C -enriched benthic microphytobenthos in the bivalve food source at their site. Comparison of potential food sources in Table 2 shows that the $\delta^{13}\text{C}$ values of the macroalgae varied widely. However, with the exception of epiphytes in Moncreiff and Sullivan (2001), the other source $\delta^{13}\text{C}$ values follow this order: phytoplankton, POM, and suspended matter< SOM and sediment< microphytobenthos and sand/sediment microflora< epiphytes on seagrass blade< seagrass. Furthermore, the $\delta^{13}\text{C}$ value of dead plant and detritus was lower than that of the original plants as seen in Lehmann et al. (2002).

In food web analysis, trophic enrichment factors commonly used for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are 0.8‰ (DeNiro and Epstein 1978) and 3.4‰ (Minagawa and Wada 1984), respectively. However, these values can vary, with $\delta^{15}\text{N}$ showing larger variation than $\delta^{13}\text{C}$ (e.g., Vander Zanden and Rasmussen 2001). Based on feeding experiments for bivalves, trophic enrichment factors of 0.6–2.0‰ for $\delta^{13}\text{C}$ and 3.4–3.6‰ for $\delta^{15}\text{N}$ (Yokoyama et al. 2005; Dubois et al. 2007) were assumed in the present study.

Comparison of the available $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between bivalves and potential food sources with the assumed trophic enrichment factors showed that the likely food sources of bivalves at S1 are POM, SP captured by sediment traps, fish feeds, and/or SOM (Figs. 4a–d, 5). Bivalves can assimilate fish feeds and feces (mainly preferring fish feeds to feces) derived from aquaculture (Yokoyama et al. 2002; Gao et al. 2006). *Septifer virgatus*, with the lowest $\delta^{13}\text{C}_{\text{bivalve}}$, appears to have relied more on ^{13}C -depleted riverine POM ($\delta^{13}\text{C}_{\text{POC}}: -27.2\text{‰}$) and/or fish feeds, and the other bivalves relied more on ^{13}C -enriched SP and/or SOM. Conversely, $\delta^{13}\text{C}_{\text{bivalve}}$ at S2, located at the margin of seagrass beds in the eastern embayment inlet, was higher than at S1. It is possible that bivalves depended on a mixture of a ^{13}C -enriched source such as seagrass and a ^{13}C -depleted source such as POM. However, assuming the low availability of seagrass for bivalves, the most likely food source appears to be SP and/or SOM, but not POM. At the outer seagrass-bed sites, $\delta^{13}\text{C}_{\text{bivalve}}$ had consistently high values (-11.3‰ to -13.1‰), and did not show a clear gradient with distance from the embayment inlet, as previously reported for the fish *Parupeneus barberinus* (approximately -12 to -15‰) and *Acreichthys tomentosus* (-8 to -13‰) at this site (Watai et al. 2015). The most likely food source also appears to be SP and/or SOM. The bivalve species sampled in the present study belong to subclasses Pteriomorphia and Heterodonta (but not superfamily Tellinoidea, such as *Macoma*), thus most of them would be suspension-feeders (Ward and Shumway 2004).

The large variation observed in $\delta^{15}\text{N}_{\text{bivalve}}$ in the outer seagrass beds might be attributed to the difference of trophic enrichment factor between species. In addition, detrital organic matter is usually enriched in ^{15}N during decomposition, presumably due to microbial transformations of nitrogen (Wada 1980; Owens and Law 1989). Thus, $\delta^{15}\text{N}_{\text{bivalve}}$ might have increased with an increasing fraction of detritus in the food source.

Therefore, bivalves appear to have shifted their dominant food source from riverine POM, fish feeds, SP, and/or SOM at S1 to SP and/or SOM at seagrass-bed sites (S2 and the outer seagrass-bed sites). This presumably reflects the ready availability of these food sources. Compared to the seagrass-bed sites, particles including phytoplankton for bivalve food sources at S1 appeared to be more abundant. At the seagrass-bed sites, at least, POC and $\delta^{13}\text{C}_{\text{POM}}$ at S2 were almost equal to those at S1. However, different food sources appeared to have been utilized between S2 and S1. The distinct difference between $\delta^{13}\text{C}_{\text{SP}}$ and surface $\delta^{13}\text{C}_{\text{POM}}$ (-20.2 and $-24.4\text{\textperthousand}$, respectively, at S2, -14.0 and $-19.9\text{\textperthousand}$, respectively, in the outer seagrass beds) suggests that the SP around the sea bottom was different from surface-suspended POM, which implies that SP was dominated by resuspended particles, but not freshly sinking particles from the surface. Thus, resuspended (represented as SP) and/or settled (SOM) particles around the sea bottom were likely to be the dominant food source in seagrass beds. The $\delta^{13}\text{C}_{\text{bivalve}}$ values were sometimes lower than $\delta^{13}\text{C}_{\text{SOM}}$ values (Fig. 4a, b). Considering the $\delta^{13}\text{C}$ order of food sources mentioned above, this suggests that a mixture of resuspended/settled microalgae (microphytobenthos and epiphytes), and detritus of the microalgae and/or unanalyzed macroalgae having lower $\delta^{13}\text{C}$ is likely the predominant food source. Kennedy et al. (2004) reported from a survey conducted during the dry season that the seagrass was not the dominant SOM source at their study site. This predominance of benthic algal food source was ascribed to enhanced algal growth. One of the possible factors would be high nutrient input from the river and mariculture activities, which is similar to the site of Lebreton et al. (2011) as discussed above.

Coral mucus from reef areas might also be an additional organic carbon source for SP and SOM (Wild et al. 2004) via trapping of materials and forming aggregates inside the seagrass beds. The low $\delta^{15}\text{N}_{\text{SP}}$ and $\delta^{15}\text{N}_{\text{SOM}}$ values might relate to nitrogen fixation in corals by endosymbiotic cyanobacteria (e.g. Lesser et al. 2004) and in seagrass beds (e.g., McGlathery 2008). Further studies in tropical and subtropical seagrass beds would help clarify the effect of coral reefs on seagrass-bed food webs. Fatty acid analysis could also help identify individual food sources using characteristic markers (Kharlamenko et al. 2001; Lebreton et al. 2011).

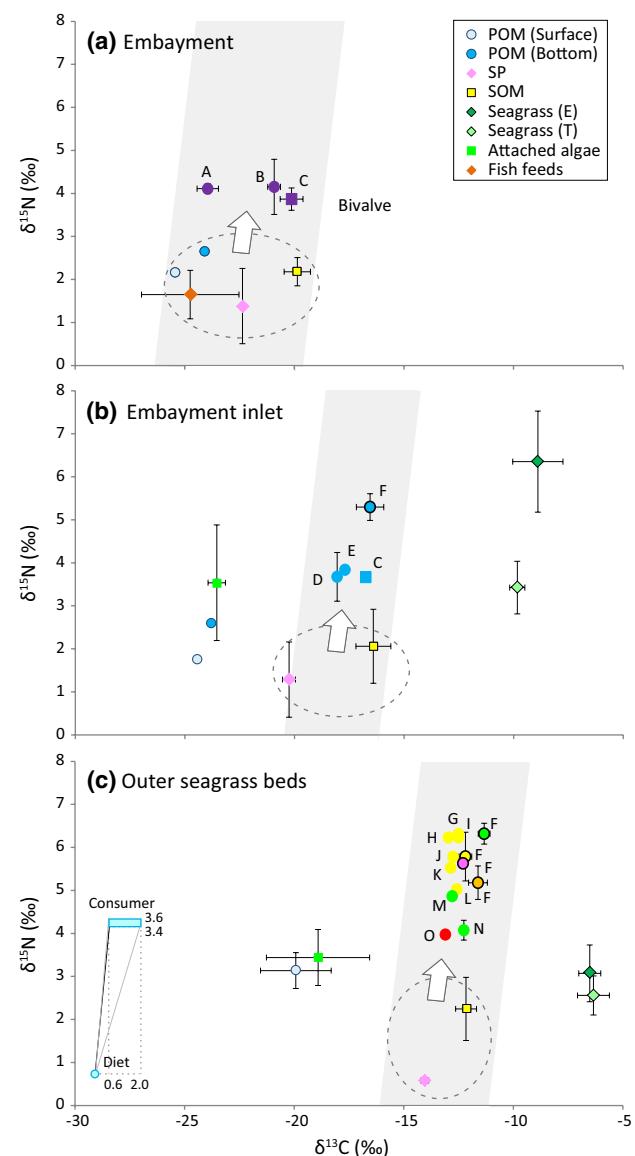


Fig. 5 Estimates of bivalve food sources from the comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bivalves, and potential food sources in **a** embayment (S1), **b** embayment inlet (S2), and **c** outer seagrass beds (T1, S3, T0, S4). Bars indicate $\pm \text{SD}$. Different capital letters indicate bivalve species (see Fig. 2). The figure in the bottom left corner of **c** indicate assumed trophic fractionation between consumer and its diet in the present study

For C/N, the ratios of all potential food sources were higher than those of bivalves were (Fig. 4e, f). Generally, $\text{C/N}_{\text{bivalve}}$ ratios increase under high food availability, because bivalves store surplus carbon by synthesizing lipids (Gabbott 1975; Hawkins et al. 1985). Increased and high $\text{C/N}_{\text{bivalve}}$ ratios by the embayment water during the transplantation experiment and field samples, respectively, are attributed to river discharge and mariculture activities, which provide abundant food for bivalves. High $\text{C/N}_{\text{bivalve}}$

ratios might also be ascribed to localization of more C-rich species in the embayment and its inlets.

Tight trophic linkage between bivalves and algae/seagrass in seagrass beds

In the outer seagrass beds of Bolinao, bivalves showed consistently high $\delta^{13}\text{C}_{\text{bivalve}}$ values (-11.8 to $-13.9\text{\textperthousand}$). However, appreciably lower $\delta^{13}\text{C}_{\text{bivalve}}$ values (-16.2 to $-19.5\text{\textperthousand}$) have been reported in several seagrass beds exposed to the open ocean along the Corsica and Mississippi coasts (Lepoint et al. 2000; Moncreiff and Sullivan 2001; Table 2). This suggests that high dependence on ^{13}C -enriched food sources such as detritus of microalgae might not be common even in exposed seagrass beds where low food availability from the overlying water column is estimated. According to previous studies, seagrass beds have mutualistic interactions with bivalves. Bivalves promote seagrass growth via increasing pore water nutrients by releasing regenerated nutrients (Bertness 1984; Reusch et al. 1994), and reducing epiphytic load on seagrass leaves (Peterson and Heck 2001). Seagrass beds increase bivalve survivorship (Peterson and Heck 2001) by providing food and habitat. Seagrass beds also promote the retention of particles by trapping materials within the canopy (Ward et al. 1984; Gacia and Duarte 2001), and enhance the growth of epiphytes through the release of dissolved organic carbon (DOC) from the blade (Allen 1969, 1971; Harlin 1973). Nutrient excretion by bivalves also appears to promote micro/macroalgal growth. External nutrient inputs from rivers, mariculture activities, and possible additional food sources such as the coral mucus in our study site are also beneficial for the growth of both seagrass and these algae, which results in supporting and enhancing these mutualistic interactions. Broad and shallow landform of seagrass beds might also have helped with material retention by reducing the flow velocity and offering protection from the outflow of materials. Therefore, due to these characteristics of seagrass beds and the local environment, it might be more likely that increased availability of micro/macroalgae for bivalve food sources caused the priority in feeding to shift from planktonic sources to benthic sources. This could have led to a tight trophic linkage between bivalves and benthic algae, resulting in a semi-closed material cycle within the vicinity of the sea bottom via the bivalves. Thus, the benthic-pelagic coupling becomes relatively insignificant, which implies a decline in water-purification function in the water column through bivalve biofiltering. Once this tight linkage is organized, it might be difficult to return, even when water quality improves, like a kind of alternative stable

state (regime shift; Scheffer et al. 2001). Therefore, these cycles will need to be taken into account when estimating the biogeochemical cycles in eutrophicated coastal ecosystems.

Macrobenthos species composition, dominated by mollusks in the outer seagrass beds as observed by Leopardas et al. (2016), might be explained by this trophic system. The higher species diversity and abundance of bivalves at the transitional site of pollution (near S2 in our study) than at the outer seagrass-bed sites suggests that a moderate level of pollution is advantageous for bivalves. In addition, in our transplantation experiment, the efflux of eutrophic embayment water positively affected the growth of bivalves transplanted to the moderately eutrophic site T1. However, all the bivalves transplanted to the highly polluted embayment site C1 died during the dry season, probably due to hypoxia. Therefore, the water quality degradation caused by river- and mariculture-derived nutrient inputs can pose both negative and positive impacts on the survivorship of bivalves, depending on the degree of eutrophication. Negative impacts have already been reported for benthos and fish communities, even in the outer seagrass beds, along the pollution gradient (e.g., Tanaka et al. 2014; Watai et al. 2015). However, as of now, each bivalve species has its own favorable/tolerable habitat, and even the presence of serious pollution might be supporting their feeding requirements. The present study suggests that bivalves employ various feeding strategies depending on species and eutrophication level, and the role of bivalves can substantially vary along the eutrophication gradient in biogeochemical carbon and nitrogen cycles.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

- Allen HL (1969) Chemo-organotrophic utilization of dissolved organic compounds by planktonic algae and bacteria in a pond. *Int Rev Ges Hydrobiol* 54:1–33
- Allen HL (1971) Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecol Monogr* 41:97–127
- Asmus RM, Asmus H (1991) Mussel beds: limiting or promoting phytoplankton? *J Exp Mar Biol Ecol* 148:215–232
- Azanza RV, Fukuyo Y, Yap LG, Takayama H (2005) *Prochlorococcus minimum* bloom and its possible link to a massive fish kill in Bolinao, Pangasinan, Northern Philippines. *Harmful Algae* 4:519–524
- Bayne BL, Hawkins AJS (1992) Ecological and physiological aspects of herbivory in benthic suspension-feeding molluscs. In: John DM, Hawkins SJ, Price JH (eds) *Plant-animal interactions in the marine benthos*. Clarendon Press, Oxford, pp 265–288
- Bayne BL, Newell RC (1983) Physiological energetics of marine molluscs. In: Saleuddin ASM, Wilburg KM (eds) *The Mollusca*, vol 4. Academic Press, New York, pp 407–515
- Bertness MD (1984) Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology* 65:1794–1807
- Cebrián J (1999) Patterns in the fate of production in plant communities. *Am Nat* 154:449–468
- Cifuentes LA, Sharp JH, Fogel ML (1988) Stable carbon and nitrogen isotope biogeochemistry in the Delaware estuary. *Limnol Oceanogr* 33(5):1102–1115
- Dame RF (2011) *Ecology of marine bivalves: an ecosystem approach*. CRC Press, Florida
- David LT, Pastor-Rengel D, Talaue-McManus L, Magdaong E, Salalila-Aruelo R, Bangi HG, San Diego-McGlone ML, Villanoy C, Cordero-Bailey K (2014) The saga of community learning: Mariculture and the Bolinao experience. *Aquat Ecosyst Health Manag* 17(2):196–204
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- Dreier A, Loh W, Blumenberg M, Thiel V, Hause-Reitner D, Hopfert M (2014) The isotopic biosignatures of photo- vs. thiotrophic bivalves: are they preserved in fossil shells? *Geobiology* 12:406–423
- Duarte CM, Chiscano CL (1999) Seagrass biomass and production: a reassessment. *Aquat Bot* 65:159–174
- Dubois S, Blin JL, Bouchaud B, Lefebvre S (2007) Isotope trophic-step fractionation of suspension-feeding species: implications for food partitioning in coastal ecosystems. *J Exp Mar Biol Ecol* 351:121–128
- Eklöf JS, de la Torre-Castro M, Gullstrom M, Uku J, Muthiga N, Lyimo T, Bandeira SO (2008) Sea urchin overgrazing of seagrasses: A review of current knowledge on causes, consequences, and management. *Estuar Coast Shelf Sci* 79:569–580
- Ferrera CM, Watanabe A, Miyajima T, San Diego-McGlone ML, Morimoto N, Umezawa Y, Herrera E, Tsuchiya T, Yoshikai M, Nadaoka K (2016) Phosphorus as a driver of nitrogen limitation and sustained eutrophic conditions in Bolinao and Anda, Philippines, a mariculture-impacted tropical coastal area. *Mar Pollut Bull* 105:237–248
- Fortes MD, Go GA, Bolisay K, Nakaoka M, Uy WH, Lopez MR, Leopoldas V, Lerorato J, Pantallano A, Paciencia FJ, Watai M, Honda K, Edralin M (2012) Seagrass response to mariculture-induced physico-chemical gradients in Bolinao, northwestern Philippines. *Proc 12th Int Coral Reef Symp* 9–13
- Franco-Nava MA, Blancheton JP, Deviller G, Le-Gall JY (2004) Particulate matter dynamics and transformations in a recirculating aquaculture system: application of stable isotope tracers in seabass rearing. *Aquac Eng* 31:135–155
- Fry B (1984) $^{13}\text{C}/^{12}\text{C}$ ratios and the trophic importance of algae in Florida *Syringodium filiforme* seagrass meadows. *Mar Biol* 79:11–19
- Gabbott PA (1975) Storage cycles in marine bivalve molluscs: a hypothesis concerning the relationship between glycogen metabolism and gametogenesis. In: Barnes H (ed) *Proc 9th Europ Mar Biol Symp*. Aberdeen Univ Press, Aberdeen, pp 191–211
- Gacia E, Duarte CM (2001) Sediment retention by a Mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension. *Estuar Coast Shelf Sci* 52:505–514
- Gao QF, Shin PKS, Lin GH, Chen SP, Cheung SG (2006) Stable isotope and fatty acid evidence for uptake of organic waste by green-lipped mussels *Perna viridis* in a polyculture fish farm system. *Mar Ecol Prog Ser* 317:273–283
- Gosling E (2015) *Marine Bivalve Molluscs*, 2nd edn. Wiley, UK
- Harlin MM (1973) Transfer of products between epiphytic marine algae and host plants. *J Phycol* 9:243–248
- Harrison PG (1982) Control of microbial growth and of amphipod grazing by water soluble compounds from leaves of *Zostera marina*. *Mar Biol* 67:225–230
- Haven DS, Morales-Alamo R (1966) Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnol Oceanogr* 11:487–498
- Hawkins AJS, Salkeld PN, Bayne BL, Gnaiger E, Lowe DM (1985) Feeding and resource allocation in the mussel *Mytilus edulis*: evidence for time-averaged optimization. *Mar Ecol Prog Ser* 20:273–287
- Hummel H (1985) Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. *Neth J Sea Res* 19:52–76
- Jaschinski S, Brepolh DC, Sommer U (2008) Carbon sources and trophic structure in an eelgrass *Zostera marina* bed, based on stable isotope and fatty acid analyses. *Mar Ecol Prog Ser* 358:103–114
- Kanaya G, Takagi S, Kikuchi E (2008) Spatial dietary variations in *Laternula marinina* (Bivalva) and *Hediste* spp. (Polychaeta) along environmental gradients in two brackish lagoons. *Mar Ecol Prog Ser* 359:133–144
- Kasai A, Horie H, Sakamoto W (2004) Selection of food sources by *Ruditapes philippinarum* and *Mactra veneriformis* (Bivalva: Mollusca) determined from stable isotope analysis. *Fish Sci* 70:11–20
- Kautsky N, Evans S (1987) Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. *Mar Ecol Prog Ser* 38:201–212
- Kennedy H, Gacia E, Kennedy DP, Papadimitriou S, Duarte CM (2004) Organic carbon sources to SE Asian coastal sediments. *Estuar Coast Shelf Sci* 60:59–68
- Kharlamenko VI, Kiyashko SI, Imbs AB, Vyshkvertzev DI (2001) Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. *Mar Ecol Prog Ser* 220:103–117
- Larkum A, Orth RJ, Duarte CM (2006) Seagrasses: biology, ecology and conservation. Springer, The Netherlands
- Lebreton B, Richard P, Gallois R, Radenac G, Pfleger C, Guillou G, Mornet F, Blanchard GF (2011) Trophic importance of diatoms in an intertidal *Zostera noltii* seagrass bed: Evidence from stable isotope and fatty acid analyses. *Estuar Coast Shelf Sci* 92:140–153
- Lefebvre S, Barill L, Clerc M (2000) Pacific oyster (*Crassostrea gigas*) feeding responses to a fish-farm effluent. *Aquaculture* 187:185–198

- Lehmann MF, Bernasconi SM, Barbieri A, McKenzie JA (2002) Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. *Geochim Cosmochim Acta* 66:3573–3584
- Leopardas V, Honda K, Go GA, Bolisay K, Pantallano AD, Uy W, Fortes M, Nakaoka M (2016) Variation in macrofaunal communities of sea grass beds along a pollution gradient in Bolinao, northwestern Philippines. *Mar Pollut Bull* 105:310–318
- Lepoint G, Nyssen F, Gobert S, Dauby P, Bouquegneau JM (2000) Relative impact of a seagrass bed and its adjacent epilithic algal community in consumer diets. *Mar Biol* 136:513–518
- Lesser MP, Mazel CH, Gorbunov MY, Falkowski PG (2004) Discovery of symbiotic nitrogen-fixing cyanobacteria in corals. *Science* 305:997–1000
- MacDonald BA, Robinson SMC, Barrington KA (2011) Feeding activity of mussels (*Mytilus edulis*) held in the field at an integrated multi-trophic aquaculture (IMTA) site (*Salmo salar*) and exposed to fish food in the laboratory. *Aquaculture* 314:244–251
- McClanahan TR, Nugues M, Mwachireya S (1994) Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *J Exp Mar Biol Ecol* 184:237–254
- McGlathery KJ (2008) Seagrass habitats. In: Capone DG, Bronk DA, Mulholland MR, Carpenter EJ (eds) Nitrogen in the marine environment, 2nd edn. Elsevier, Amsterdam, pp 1037–1061
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Miyajima T, Hori M, Hamaguchi M, Shimabukuro H, Adachi H, Yamano H, Nakaoka M (2015) Geographic variability in organic carbon stock and accumulation rate in sediments of East and Southeast Asian seagrass meadows. *Glob Biogeochem Cycle* 29:397–415
- Moncreiff CA, Sullivan MJ (2001) Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Mar Ecol Prog Ser* 215:93–106
- Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J Shellfish Res* 23(1):51–61
- Ólafsson EB (1986) Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *J Anim Ecol* 55:517–526
- Owens NJP, Law CS (1989) Natural variations in ^{15}N content of riverine and estuarine sediments. *Estuar Coast Shelf Sci* 28:407–416
- Parsons TR, Takahashi M, Hargrave B (1984) Biological oceanographic processes, 3rd edn. Pergamon Press, UK
- Peterson BJ, Heck KL Jr (1999) The potential for suspension feeding bivalves to increase seagrass productivity. *J Exp Mar Biol Ecol* 240:37–52
- Peterson BJ, Heck KL Jr (2001) Positive interactions between suspension-feeding bivalves and seagrass – a facultative mutualism. *Mar Ecol Prog Ser* 213:143–155
- Reusch TBH, Chapman ARO, Gröger JP (1994) Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. *Mar Ecol Prog Ser* 108:265–282
- Riera P, Richard P (1997) Temporal variation of $\delta^{13}\text{C}$ in particulate organic matter and oyster *Crassostrea gigas* in Marennes-Oleron Bay (France): effect of freshwater inflow. *Mar Ecol Prog Ser* 147:105–115
- Rossi F, Baeta A, Marques JC (2015) Stable isotopes reveal habitat-related diet shifts in facultative deposit-feeders. *J Sea Res* 95:172–179
- San Diego-McGlone ML, Azanza RV, Villanoy CL, Jacinto GS (2008) Eutrophic waters, algal bloom and fish kill in fish farming areas in Bolinao, Pangasinan, Philippines. *Mar Pollut Bull* 57:295–301
- Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596
- Tamondong AM, Blanco AC, Fortes MD, Nadaoka K (2013) Mapping of seagrass and other benthic habitats in Bolinao, Pangasinan using Worldview-2 satellite image. *Proc IEEE IGARSS*, 1579–1582
- Tanaka Y, Miyajima T, Yamada K, Hori M, Hasegawa N, Umezawa Y, Koike I (2008) Specific growth rate as a determinant of the carbon isotopic composition of a temperate seagrass *Zostera marina*. *Aquat Bot* 89:331–336
- Tanaka Y, Go GA, Watanabe A, Miyajima T, Nakaoka M, Uy WH, Nadaoka K, Watanabe S, Fortes MD (2014) 17-year change in species composition of mixed seagrass beds around Santiago Island, Bolinao, the northwestern Philippines. *Mar Pollut Bull* 88:81–85
- Thayer GW, Parker PL, LaCroix MW, Fry B (1978) The stable carbon isotope ratio of some components of an eelgrass, *Zostera marina*, bed. *Oecologia* 35:1–12
- van der Heide T, Govers LL, de Fouw J, Olff H, van der Geest M, van Katwijk MM, Piersma T, van de Koppel J, Silliman BR, Smolders AJP, van Gils JA (2012) A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science* 336:1432–1434
- Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: Implication for aquatic food web studies. *Limnol Oceanogr* 46(8):2061–2066
- Villanueva RD, Yap HT, Montaño MNE (2006) Intensive fish farming in the Philippines is detrimental to the reef-building coral *Pocillopora damicornis*. *Mar Ecol Prog Ser* 316:165–174
- Wada E (1980) Nitrogen isotope fractionation and its significance in biogeochemical processes occurring in marine environments. In: Goldberg ED, Horibe Y, Saruhashi K (eds) Isotope Marine Chemistry. Uchida Rokkakuho, Tokyo, pp 375–398
- Ward JE, Shumway SE (2004) Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *J Exp Mar Biol Ecol* 300:83–130
- Ward LG, Kemp WM, Boyton WR (1984) The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar Geol* 59:85–103
- Watai M, Nakamura Y, Honda K, Bolisay KO, Miyajima T, Nakaoka M, Fortes MD (2015) Diet, growth, and abundance of two seagrass bed fishes along a pollution gradient caused by milkfish farming in Bolinao, northwestern Philippines. *Fish Sci* 81:43–51
- White PG (2009) EIA and monitoring for clusters of small-scale cage farms in Bolinao Bay: a case study. In FAO Environmental impact assessment and monitoring of aquaculture. FAO Fisheries and Aquaculture Technical Paper, No. 527. FAO, Rome, pp 537–552
- Wild C, Huettel M, Klueter A, Krebs SG, Rasheed MYM, Jørgensen BB (2004) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature* 428:66–70
- WoRMS Editorial Board (2016) World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ. Accessed 21 Jan 2016
- Yokoyama H, Higano J, Adachi K, Ishii Y, Yamada Y, Pichitkul P (2002) Evaluation of shrimp polyculture system in Thailand based on stable carbon and nitrogen isotope ratios. *Fish Sci* 68:745–750
- Yokoyama H, Tamaki A, Harada K, Shimoda K, Koyama K, Ishii Y (2005) Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. *Mar Ecol Prog Ser* 296:115–128
- Yokoyama H, Abo K, Ishii Y (2006) Quantifying aquaculture-derived organic matter in the sediment in and around a coastal fish farm using stable carbon and nitrogen isotope ratios. *Aquaculture* 254:411–425
- Yoshikai M (2016) Analysis of environmental impacts of intensive mariculture activities on hypoxic water formation and seagrass bed degradation in Bolinao and Anda, Philippines. Master thesis, Tokyo Institute of Technology