

# Trophic Relationships between Two Gastropods and Seaweeds in Subtropical Rocky Reefs Based on Stable Isotope Analyses

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## TROPHIC RELATIONSHIPS BETWEEN TWO GASTROPODS AND SEAWEEDS IN SUBTROPICAL ROCKY REEFS BASED ON STABLE ISOTOPE ANALYSES

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**ABSTRACT** The wavy turban snail *Megastraea undosa* and keyhole limpet *Megathura crenulata*, two gastropods with commercial importance, five macroalgae, and one seagrass were collected at Bahía Tortugas, Baja California Sur, Mexico, for analysis of stable isotope ratios. The  $\delta^{13}$ C and  $\delta^{15}$ N isotope signatures obtained from gastropod muscle tissue were different between the two gastropods. Isotope signatures of *M. crenulata* had more enriched  $\delta^{13}$ C (-14.35‰ ± 1.66‰) and  $\delta^{15}$ N (15.48‰ ± 0.67‰) than *M. undosa* isotope signatures for  $\delta^{13}$ C (-17.59‰ ± 2.43‰) and  $\delta^{15}$ N (12.42‰ ± 0.61‰). Seaweed isotope signals varied from -21.8‰ to -11.4‰ for  $\delta^{13}$ C and 9.3‰ to 10.9‰ for  $\delta^{15}$ N. The  $\delta^{13}$ C of detritus was -7.93 and of tunicates was -9.3‰ and the  $\delta^{15}$ N of detritus was 12.4 and of tunicates was 8.1‰. Mixing models showed that the greatest contribution to the diet of *M. undosa* was from *Prionitis cornea* and *Gelidium robustum*. For *M. crenulata*, it was from detritus and *Macrocystis pyrifera*. A higher trophic position (3.1) was observed for *M. crenulata* is an omnivore.

KEY WORDS: Megastraea undosa, Megathura crenulata, gastropods, natural diet, macroalgae, stable isotopes

#### INTRODUCTION

Food webs and the factors controlling their structures are among the more intensively studied areas in ecology (Post 2002, Byrnes et al. 2011). Kelp forests are one of the most productive, highly dynamic (Mann 2000), ecosystems in the ocean, and they support high diversity of species and complex food webs subject to changes induced by natural and anthropogenic drivers (Page et al. 2013). Stable isotope analyses have been increasingly used to identify food sources and understand energy flow in food webs. Animals in the same system that show similar carbon and nitrogen stable isotope ratios are assumed to have similar food sources. Carbon stable isotope ratios can indicate feeding and carbon flow pathways because there is little fractionation from prey to predator (fractionation value of 1‰; Peterson & Fry 1987). Nitrogen isotope ratios become enriched at successive trophic levels, thereby allowing estimates of the consumer's trophic position. A fractionation value of 3.4% has been common between trophic levels (Minagawa & Wada 1984), although some variations in the fractionation value have been observed, depending on the tissue (McCutchan et al. 2003). Thus, comparisons of  $\delta^{13}$ C and  $\delta^{15}$ N levels among coexisting plants and animals have improved the understanding of food webs and energy flows in aquatic ecosystems (Post 2002, Behringer & Butler 2006, Guest et al. 2010, Schaal et al. 2010, Won et al. 2013).

In general, along the Pacific Coast of Mexico, particularly off the Baja California Peninsula, few studies have approached trophic status of marine organisms using stable isotope analysis. The few papers include the mako shark *Isurus oxyrinchus* (Velasco-Tarelo 2005) and the green turtle *Chelonia mydas* (Santos-Baca 2008). Recently, a study on the diet of abalone species of the Pacific Coast, using stable isotope analysis, showed that the abalone fed on whatever resources were available (Vega-García et al. 2015). The wavy turban snail Megastraea undosa (Wood, 1828) and the keyhole limpet Megathura crenulata (Sowerby, 1825) are the two common and important gastropods of the rocky reefs along the western side of the Baja California Peninsula. Rocky reefs are characterized by dense forests of macroalgae, such as giant kelp Macrocystis pyrifera (Linnaeus) C. Agardh, as well as dense populations of arame/southern sea palm Eisenia arborea J. E. Areschoug and algae of the genus Rhodymenia Greville, Gelidium J. V. Lamouroux, Gigartina Stackhouse, and Plocamium J. V. Lamouroux, as well as articulated coralline algae of the genus Corallina Linnaeus (Dawson et al. 1960, Guzmán del Próo et al. 1991). The radula of these two gastropods is the rhipidoglossan type (Hickman 1981), which is used to scrape rocky bottoms in search of food, allowing consumption of macroalgae and associated organisms (Aguilar-Rosas et al. 1990, Mazariegos-Villarreal et al. 2013).

The wavy turban snail Megastraea undosa is found from Punta Conception, Santa Barbara, CA, to Punta Abreojos along the Baja California Peninsula (Morris et al. 1980) and is an important fishery (Singh-Cabanillas 1996). Commonly associated with the subtidal kelp, adults and juveniles occur in subtidal and intertidal habitats with little or no kelp biomass (Alfaro & Carpenter 1999). By means of stomach contents analysis and food preferences experiments, this species was considered to be predominantly a macroherbivore with a preference for kelp species (Leighton 1966, Cox & Murray 2006), whereas other studies found that it consumed a variety of macrophytes (Aguilar-Rosas et al. 1990). For example, in the Punta Banda region, M. undosa (as Astraea undosa Wood 1828) was described as opportunistic herbivore. Adults were found to feed on Sphacelaria furcigera Kützing, Cladophora columbiana F. S. Collins, Gelidium pusillum (Stackhouse) L. Jolis, and the coralline algae Jania sp., Corallina sp., and Lithothrix aspergillum J. E. Gray (Aguilar-Rosas et al. 1990).

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The keyhole limpet *Megathura crenulata* is found from Mendocino County, CA, to Isla Asunción along the Baja California Peninsula (Morris et al. 1980). It is a valuable resource because it is the only source of hemocyanin (keyhole limpet hemocyanin), an immune-stimulating protein used in vaccine treatment and immunodiagnostics for treatment of cancer and immune disorders (Harris & Markl 2000, Oakes et al. 2004, Lebrec et al. 2014). From 1950 to the present, its commercial exploitation is well established in Europe and the United States, particularly in California (Harris & Markl 2000), but not in the Baja California Sur Peninsula. It is an omnivore, feeding mainly on invertebrates and macroalgae (Mazariegos-Villarreal et al. 2013).

During early development, both species' feeding preferences change from microalgae to macroalgae, similar to the behavior of abalones of the genus *Haliotis* (Leighton & Boolootian 1963). The aim of the present study was to determine the isotope signature of *Megastraea undosa* and *Megathura crenulata* and six abundant seaweed species to identify each species' ecological role in the area of rocky reefs.

#### MATERIALS AND METHODS

#### Study Site

Bahía Tortugas (27° 40′ N, 114° 52′ W) is in the central portion of the West Coast of the Baja California Peninsula, between Punta Eugenia to the north and Bahía Asunción to the south (Fig. 1). The bay has an approximate extension of  $20.5 \text{ km}^2$  and is about 11 m deep in the center to about 19 m at the mouth. At the mouth, there is a pair of rocky points, one of which extends to the southeast as a series of rocky islets that absorb the force of the waves and currents from the northwest, which is also the direction of the dominant winds (Guzmán del Próo et al. 1991).

#### Sampling

The gastropods were collected at two adjacent rocky reefs outside the bay at 8–12 m deep. Specimens of each species were collected over a span of a few days at Rincón de Méndez during July and November 2009 and at Piedra de Trini in November 2009 for a total of 24 adult *Megastraea undosa* (basal diameter of 10.6 cm  $\pm$  1.3 SD) and 24 *Megathura crenulata* (body length and weight of 11.5 cm  $\pm$  1.4 and 158.6 g  $\pm$  48.1, respectively). They were collected by scuba divers during early morning hours and transported on ice to the laboratory for further analysis. The gastropods were dissected and a sample of muscle tissue of each gastropod was extracted for isotope analysis.

On each collection day, samples of the most abundant seaweed species on the rocky reefs, which had been previously reported as food sources for either gastropod, were collected (Leighton 1966, Aguilar-Rosas et al. 1990, Mazariegos-Villarreal et al. 2013). These included blades from *Macrocystis pyrifera*, *Eisenia arborea*, and the seagrass *Phyllospadix torreyi* S. Watson, and thalli from *Gelidium robustum* (N. L. Gardner) Hollenberg & I. A. Abbott, *Prionitis cornea* (Okamura) E. Y. Dawson, and coralline algae turfs [*Jania rosea* (Lamark) Decaisne, *Corallina officinalis* var. *chilensis* (Decaisne) Kützing, *Corallina pinnatifolia* (Manza) Dawson and *Bossiella orbigniana* (Decaisne) P. C. Silva]. To remove epiphytes from the seaweed,



Figure 1. Location of Bahía Tortugas, Baja California Sur, Mexico.

the samples were scraped and rinsed with distilled water. In addition, three samples of a tunicate were collected at the rocky reefs (November 2010). Because tunicates had been reported as a source of food for *Megathura crenulata*, samples of these organisms were looked for collection, however, no other tunicate samples could be collected at the time of the sampling period partly because diving conditions were unfavorable for collection with low visibility and strong surge and partly because of their availability. Five samples of sediment were collected from the bottom of the rocky reef and were considered as detritus (November 2010) and were then prepared for analysis. All samples were collected within same days at each collection site.

Samples of muscle tissue (Yokoyama et al. 2005) from 24 specimens of each gastropod species, nine blades or thalli of each macroalgae and seagrass species, and three tunicates were oven-dried for 24 h at 60°C, and then grounded to fine powder separately.

Samples from coralline algae and sediments were exposed to HCl vapor for 4 h at room temperature to remove carbonates (Harris et al. 2001). Samples were weighed, packed into  $5 \times$ 9-mm tin cups, and placed in closed containers for further analysis. Samples were analyzed at the Stable Isotope Facility at the University of California Davis. Isotope ratios were obtained in a European Scientific ANCA-NT 20–20 Stable Isotope Analyzer with ANCA-NT Solid–Liquid Preparation Module (PDZ Europa, Crewz, United Kingdom). Stable isotope ratios are given in the conventional delta notation ( $\delta^{13}$ C;  $\delta^{15}$ N) per mil (‰) according to the formula:

$$\delta X(\%_{oo}) = \left[\frac{R \text{ sample}}{R \text{ standard}} - 1\right] \times 1,000$$

where  $X = {}^{13}C$  or  ${}^{15}N$  and  $R = {}^{13}C/{}^{12}C$  or  ${}^{15}N/{}^{14}N$ . Standards for C and N were Pee Dee Belemnite and atmospheric nitrogen, respectively. The standard deviation was  $0.2^{\circ}_{00}$  for  ${}^{13}C$  and  $0.3^{\circ}_{00}$  for  ${}^{15}N$ .

#### Statistical Analyses

Differences in stable isotope ratios among gastropods were tested using the *t*-test for independent samples. An analysis of variance statistical analysis was used to test for differences in isotope values of seaweed species. Significance was set at P < 0.05. Normality and homoscedasticity of the data were assessed. Statistical analyses used Statistica 7.0.

To assess the proportional contributions of the known carbon sources to consumers, a Bayesian mixing model was used (SIAR package; Stable Isotope Analysis in R). For this purpose, the mean  $\delta^{13}$ C and  $\delta^{15}$ N values of the macroalgae, seagrass, and tunicates as the base source and mean  $\delta^{13}$ C and  $\delta^{15}$ N values for the two consumers were used. Enrichment of 2.3 ± 0.18 was assumed for  $\delta^{15}$ N for animals with algal or invertebrate diets because no significant differences have been reported between species, and an enrichment of 1.3 ± 0.3 was assumed for  $\delta^{13}$ C for the muscle tissue (McCutchan et al. 2003).

Isotope signatures of the gastropods were compared with the values of their food sources, using a dual isotope plot of  $\delta^{13}C$  versus  $\delta^{15}N$  to determine trophic position.

Once the major contribution was calculated, the relative trophic position of each gastropod species was determined by means of the stable isotope signature (Post 2002):

$$TP = \lambda + \frac{\delta^{15} N_{secondary \, consumer} - \delta^{15} N_{base}}{\Delta_n}$$

where  $\lambda$  is the known trophic position of the specimen used as the base (such as  $\lambda = 1$  for primary producers), whereas the  $\delta^{15}N_{\text{base}}$  and  $\delta^{15}N_{\text{secondary consumer}}$  are obtained by direct measurement and  $\Delta_n$  is the enrichment in  $\delta^{15}N$  for each trophic level.

#### RESULTS

Differences between *Megastraea undosa* and *Megathura crenulata* isotope signatures were found. The  $\delta^{13}$ C and the  $\delta^{15}$ N signatures of *M. undosa* (t = 5.3, P < 0.05) were significantly depleted, compared with *M. crenulata* (t = -16.5, P < 0.05; Table 1).

The  $\delta^{13}$ C signatures of the macroalgae and seagrass were significantly different, depending on the species ( $F_{42,5} = 70$ , P < 0.05). For example, *Prionitis cornea, Gelidium robustum*, and *Eisenia arborea* had depleted means for  $\delta^{13}$ C ( $-21.8\%_{o} \pm 0.1\%_{o}$ ,  $-21.7\%_{o} \pm 1.4\%_{o}$ , and  $-20.3\%_{o} \pm 2\%_{o}$ , respectively), compared with *Phyllospadix torreyi* and *Macrocystis pyrifera* ( $-17.8\%_{o} \pm 1.8\%_{o} \pm 1.8\%_{o} \pm 0.9\%_{o}$ , respectively). The coralline articulated algae were enriched ( $-11.4\%_{o} \pm 1.3\%_{o}$ ; Table 1).

The  $\delta^{15}$ N signature of the seaweeds varied between species; *Macrocystis pyrifera* had enriched  $\delta^{15}$ N values (10.9‰ ± 2.9‰), followed by the coralline articulated algae (10.1‰ ± 0.8‰), whereas *Prionitis cornea*, *Gelidium robustum*, *Eisenia arborea*, and the seagrass *Phyllospadix torreyi* had very similar values; however, no significant differences were found ( $F_{42,5} = 1.6, P =$ 0.1; Table 1).

The  $\delta^{13}$ C signature for the detritus was  $-7.9\%_{00} \pm 0.3\%_{00}$ ; for the tunicates, it was  $-9.3\%_{00} \pm 0.5\%_{00}$ . The  $\delta^{15}$ N signature was  $12.4\%_{00} \pm 0.2\%_{00}$  for detritus and  $8.1\%_{00} \pm 1.1\%_{00}$  for tunicates.

According to the mixing model, the macroalgae species that contributed the most to the diet of *Megastraea undosa* were *Prionitis cornea* (mean 24; range 0%-44%) and *Gelidium robustum* (mean 21; range 0%-41%; Fig. 2A). The major contribution to the diet of *Megathura crenulata* was detritus (mean 22; range 0%-36%) and *Macrocystis pyrifera* (mean 18; range 0%-35%; Fig. 2B).

The trophic position of *Megathura crenulata* was 3.1 and *Megastraea undosa* was 2.3. In the dual isotope plot, three trophic levels were evident between the gastropods and the seaweed (trophic level one considered for primary producers as the base of the food chain; Fig. 3).

#### DISCUSSION

Measuring the isotope signature of *Megastraea undosa* and *Megathura crenulata* and the common seaweed species is important because they advance the understanding of benthic community interactions and the role of these two species in kelp forests. It is useful in assessing food sources for aquaculture studies or conservation programs. The  $\delta^{13}$ C and  $\delta^{15}$ N signatures show differences in feeding habits, as was previously shown for *M. undosa* as an herbivore and *M. crenulata* as an

#### TABLE 1.

Mean (minimum; maximum)  $\delta^{13}$ C and  $\delta^{15}$ N isotope values, size range, and number of sampled (*N*) gastropods, macroalgae, and seagrass at Bahía Tortugas, Baja California Sur, Mexico.

	δ <sup>13</sup> C	$\delta^{15}N$	Size range (cm/g)	N
Gastropods				
Megastraea undosa	-17.6 (-22.9; -13.9)	12.4 (11.6; 13.8)	8.0-13.1 (basal-diameter); 90.9-600.0 (weight)	24
Megathura crenulata	-14.3 (-16.9; -11.9)	15.5 (14.6; 16.9)	8.0-13.6 (length); 56.5-265.0 (weight)	24
Macroalgae				
Eisenia arborea	-20.3 (-23.2; -17.6)	9.3 (8.5; 9.9)	_	9
Macrocystis pyrifera	-15.2 (-16.1; -13.8)	10.9 (6.9; 13.4)	_	9
Gelidium robustum	-21.7 (-23.7; -19.9)	9.5 (7.7; 11.3)	_	9
Prionitis cornea	-21.8 (-21.9; -21.7)	9.6 (9.4; 9.7)	_	9
Articulated coralline algae	-11.4 (-13.0; -9.6)	10.1 (9.25; 11.7)	_	9
Seagrass				
Phyllospadix torreyi	-17.8 (-20.5; -16.2)	9.4 (8.8; 9.9)	-	9
Tunicates	-9.3 (-9.8; 8.9)	8.1 (8.9; 7.4)	_	3
Detritus	-7.9 (-8.3; 7.7)	12.4 (12.0; 12.6)	_	5



Figure 2. Distribution of feasible contributions to the diet of (A) Megastraea undosa and (B) Megathura crenulata (SIAR 4.1). Ea = Eisenia arborea; Mp = Macrocystis pyrifera; Gr = Gelidium robustum; Pc = Prionitis cornea; ACA = articulated coralline algae; Pt = Phyllospadix torreyi; Det = detritus, and Tun = tunicates. Number above the box plot indicates mean value.

omnivore. Values fall within the range of gastropod species with similar feeding habits (Grall et al. 2006) in the Bay of Brest (Table 2). The  $\delta^{13}$ C content in *M. undosa* and *M. crenulata* suggests that their carbon sources were also different; therefore, they have different feeding habit. This is consistent with studies that found that *M. undosa* feed mainly on macroalgae, whereas *M. crenulata* have a mixed diet of tunicates and red algae (Aguilar-Rosas et al. 1990, Mazariegos-Villarreal et al. 2013). The  $\delta^{15}$ N mean values were similar to that in the reports of other gastropods (Table 2). The differences in signatures of gastropods suggest that they belong to different trophic levels, as was found in the coast of the Bay of Brest (Grall et al. 2006).

A variation of approximately 10% in the  $\delta^{13}$ C values of macroalgae species was found. Variations between red and brown algae are expected, because in general, isotope values of carbon for brown algae are typically lighter than that in red algae (Table 2). The differences in  $\delta^{13}$ C result from different photosynthesis pathways of CO<sub>2</sub> and/or active uptake of HCO<sub>3</sub> (Farquhar et al. 1989, Raven et al. 2002, Guest et al. 2008). Particularly in the case of articulated coralline algae *Corallina officinalis*, values close to -10%, as determined in this study, suggest the presence of a CO<sub>2</sub> concentrating mechanism (Marconi et al. 2011).

The  $\delta^{15}$ N isotope values of macroalgae and seagrass showed little variation between species, reflecting the local source (Guest et al. 2008) in the Bahía Tortugas. The enriched  $\delta^{15}$ N values that were observed compared with other studies (5‰-6.4‰; Table 2) could be based on upwelling currents that provide a  $\delta^{15}$ N value greater than or equal to 8‰ (Foley & Koch 2010).

The mixing model suggests that *Prionitis cornea* and *Gelidium robustum* were the most important contributors to the diet of *Megastraea undosa*. These two species are among the most important components of the rocky reefs. Nevertheless, content analysis of snails from the region showed that the most important components were *Macrocystis pyrifera* or *Eisenia arborea* (depending on the site) and the coralline algae *Corallina* sp., whereas several red algae are of secondary importance (Fierro-Jáuregui, unpublished data). Aguilar-Rosas et al. (1990) described that adult *M. undosa* at another site fed on a large variety of macroalgae (*Sphacelaria furcigera, Cladophora columbiana*, and *Gelidium pusillum*) and coralline alga



Figure 3.  $\delta^{13}$ C versus  $\delta^{15}$ N biplot for gastropods ( $\blacklozenge =$  mean Megathura crenulata ( $\pm$ SD);  $\diamondsuit =$  M. crenulata;  $\blacktriangle =$  mean Megastraea undosa ( $\pm$ SD);  $\bigtriangleup =$  M. undosa); macroalgae and seagrass ( $\blacksquare =$  Eisenia arborea;  $\square =$  Macrocystis pyrifera;  $\forall =$  Gelidium robustum;  $\blacksquare =$  Prionitis cornea;  $\blacksquare =$  articulated coralline algae;  $\blacksquare =$  Phyllospadix torreyi);  $\bigcirc =$  detritus; and \* = tunicates. Horizontal lines denote the trophic level. 1 = primary producers, 2 = herbivores, 3 = omnivores, with an enrichment of 2.2‰ per level.

(Jania sp., Corallina sp., and Lithothrix aspergillum). In a laboratory experiment, M. undosa (as Lithopoma undosum) had preferred M. pyrifera and E. arborea, but assimilated carbon, nitrogen, and total organic matter with higher efficiency from red macroalgae, rather than from its preferred macrophyte food (Cox & Murray 2006). These results are of importance because preferences observed in laboratory appear to be variable in nature. Laboratory preferences could be considered irrelevant because benthic invertebrate herbivores are in a natural setting with strong predation pressures where preferred seaweeds could be scarce or mixed among other potential macrophyte foods (Cox & Murray 2006). Results indicate that red algae are more important to the diet of M. undosa than previously considered, and this may result from the high assimilation rate of red algae, rather than preferential consumption in the wild.

For Megathura crenulata, the mixing model suggests that detritus was the most important contributor to its diet, followed by Macrocystis pyrifera. Results were unexpected because tunicates were an abundant item in the stomach contents and M. pyrifera was incidental. Despite their abundance, the importance of tunicates seems questionable because it is known that their protein content is usually less than 1%; they contain a high proportion of refractory material and low digestibility (Mazariegos-Villarreal et al. 2013). Therefore, tunicates should be considered a food incidental and a supplement as observed in other herbivores. Many herbivorous fish actively seek out animal-derived proteinaceous material to supplement their diet (Robertson 1982). Here, isotope analysis indicates that tunicates are not fully assimilated. Detritus proved to be the most important contributor to the diet of M. crenulata, as it has been shown that it represents a potentially valuable food source for gastropods (Fredriksen 2003, Schaal et al. 2009). In sites where there is a biomass dominance of a kelp species, detritus was found to display the same isotopic signature than fresh kelp (Fredriksen 2003, Guest et al. 2008, Schaal et al. 2009). Gastropods must be consuming detritus derived from other organisms and *Macrocystis* fronds.

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7 species of seagras12.6 and 8.8Grice et al.Sparine alerrifore and Sparine derrines17.4 $\pm$ 2 and 5.8Fantle et al.Sparine alerrifore and Sparine derrines1Bruish Columbia-7.4 $\pm$ 2 and 5.8Fantle et al.Sparine alerrifore and Sparine1Bruish Columbia-7.4 $\pm$ 2 and 5.8Fantle et al.Sparine alerrifolia1Erimoy, Norway-11.67-Romanuk:Coralline officialis1Catalina Island, CA-7.45-Rowen et aCoralline officialis1Bay of Brest-11.167-Rowen et aCoralline officiand-Norway-11.167Rowen et aCoralline officiand-Norway-11.67Rowen et aCoralline officiand-Norway-11.167Rowen et aMacrosystis prifera1Bay of Brest-2.24 ± 1.55.0MacroalgaeMacroalgaeMacroalgaeMacroalgaeMacroalgaeMacroalgaeMacroalgae <td>species of seagrass</td> <td>1</td> <td>Ι</td> <td>-3.0 to -23.8</td> <td>Ι</td> <td>McMillan et al. (1980)</td>	species of seagrass	1	Ι	-3.0 to -23.8	Ι	McMillan et al. (1980)				
Sparting alternifion and Sparting deritus1 $ 7.4 \pm 2$ and 5.8Fantle et alSparting alternifion and Sparting deritus1 $ 7.4 \pm 2$ and 5.8Fantle et alPlango lancoalgae1British Columbia $-16.9$ $6.4$ Romanuk:Plango lancoalgae1British Columbia $-16.9$ $6.4$ Romanuk:Coradina officiadis1Erimoy, Norway $-11.67$ $ -$ Raven et aCoradina officiadis1Erimoy, Norway $-11.67$ $ -$ Raven et aCoradina officiadis1Raven et al $-7.45$ $-$ Raven et aCoradina officiadis1Raven et al $-7.45$ $-$ Raven et aCoradina officiadis1Raven et al $-7.45$ $-$ Raven et alMacrosysis pyrifera1Bay of Brest $-7.45$ $ -$ Macrostagae1Bay of Brest $-2.24 \pm 1.5$ $4.7 \pm 1.7$ Grall et al.Macrostagae1 $    -$ Macrostagae1 $    -$ Macrostagae2.66 (filter feeder) $    -$ Macrostagae $      -$ Macrostagae $       -$ Macrostagae $          -$ <td< td=""><td>pecies of seagrass</td><td>1</td><td>Ι</td><td>I</td><td>2.6 and 8.8</td><td>Grice et al. (1996)</td></td<>	pecies of seagrass	1	Ι	I	2.6 and 8.8	Grice et al. (1996)				
Benthic macroalgae1 $-17,6$ $-$ Benthic macroalgae1British Columbia $-16,9$ $6,4$ RomanukPlanage lanceolata1Finnoy, Norway $-11,67$ $-$ Reven et aCoralling principlia1Ergen Stork Kalovy, Norway $-11,67$ $-$ Reven et aCoralling principlia1Bergen Stork Kalovy, Norway $-15,86$ $ -$ Reven et aCoralling principlia1Bergen Stork Kalovy, Norway $-15,86$ $ -$ Reven et aMacrosystis pyrifera1Bay of Brest $-22,4\pm1.5$ $4,7\pm1.7$ Grall et al.Macrosystis pyrifera1Bay of Brest $-22,4\pm1.5$ $4,7\pm1.7$ Grall et al.Macrosystis pyrifera1Bay of Brest $-22,4\pm1.5$ $4,7\pm1.7$ Grall et al.Macrosystis pyrifera1 $-22,4\pm1.5$ $4,7\pm1.7$ $-22,4\pm1.5$ $5,0$ Macrosystis pyrifera1 $-22,4\pm1.5$ $4,1.7\pm1.7$ $-22,4\pm1.5$ $5,0$ Macrosystis pyrifera $-16,0,0,0$ $-16,0,0,0$ $0,0,0,0,0$ $-16,0,0,0$ $0,0,0,0,0,0$ Macrosystis pyrifera $-16,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0$	artina alterniflora and Spartina detritus	1	Ι	I	$7.4 \pm 2$ and $5.8$	Fantle et al. (1999)				
Plantago lancedata1British Columbia $-16.9$ $6.4$ RomanukCorallina officialis $1$ $Finnoy, Norway-16.96.4RomanukCorallina officialis1Finnoy, Norway-11.67-Raven et a.Corallina officialis1Finnoy, Norway-11.67-Raven et a.Corallina pinatjolia1Bergen Store Kalsoy, Norway-17.45-Raven et a.Macrocysis pyrifera1Bergen Store Kalsoy, Norway-17.45 -Raven et a.Macrocysis pyrifera1Bay of Brest-22.4\pm1.54.7\pm1.7Grall et al.Macroalgae1Bay of Brest-22.4\pm1.54.7\pm1.7Grall et al.Macroalgae1-22.4\pm1.54.7\pm1.7Grall et al.Macroalgae-11.1-20.75.0-Macroalgae-11.60.6.410.26.0.60.3\pm0.2Macroalgae-11.6-22.4\pm1.54.7\pm1.7Grall et al.Macroalgae-11.490.2.6* (filter feeder) -14.912.0Macroalgae-14.912.0-14.912.0-14.912.8Macroalgae-14.9-14.912.0-14.912.80.8Macroalgae-14.9-14.912.0-14.912.8Energind formacus, 1758)3.4^* (carrivore) -14.912.0Diadora gracea (Linnaeus, 1758)3.4^* ($	nthic macroalgae	1	Ι	-17.6	Ι	I				
Coralina officialis1Finnoy, Norway $-11.67$ $-$ Raven et alCoralina pinatifolia1Erinoy, Norway $-7.45$ $-$ Raven et alGorgonema latifolium1Bergen Store Kalsoy, Norway $-11.67$ $-$ Raven et alMacrocystis pyrifera1Bay of Brest $-7.45$ $ -7.45$ $-$ Macrocystis pyrifera1Bay of Brest $-15.86$ $ -7.45$ $ -7.45$ Macrocystis pyrifera11Bay of Brest $-2.2.4 \pm 1.5$ $4.7 \pm 1.7$ Grall et al.Macrolgae11 $-2.24 \pm 1.5$ $4.7 \pm 1.7$ $-2.24 \pm 1.5$ $5.0$ Macrolgae11 $-2.2.4 \pm 1.5$ $4.7 \pm 1.7$ $-2.2.4 \pm 1.5$ $5.0$ Macrolgae11 $-2.24 \pm 1.5$ $4.7 \pm 1.7$ $-2.2.4 \pm 1.5$ $5.0$ Macrolgae11 $-2.24 \pm 1.5$ $4.7 \pm 1.7$ $-2.2.4 \pm 1.5$ $5.0$ Macrolgae1 $-2.24 \pm 1.5$ $4.7 \pm 1.7$ $-2.2.4 \pm 1.5$ $5.0$ $-2.6 + (filter feeder)$ Macrolgae1 $-2.24 \pm 1.5$ $5.0$ $-2.24 \pm 1.5$ $5.0$ $-2.6 + (filter feeder)$ Gastropods2.8* (filter feeder)2.8* (filter feeder) $-2.24 \pm 1.5$ $4.7 \pm 1.7$ $-2.0$ Endoting acrea (Linnaeus, 1758) $3.4* (carnivore)$ $-2.24 \pm 1.5$ $3.2.8 + (carnivore)$ $-1.49$ $10.8$ Enorging acrea (Linnaeus, 1758) $3.5* (carnivore)$ $-2.8* (carnivore)$ $-1.49$ $10.8$ $-1.69$ $10.2$ <td>mtago lanceolata</td> <td>1</td> <td>British Columbia</td> <td>-16.9</td> <td>6.4</td> <td>Romanuk and Levings (2005)</td>	mtago lanceolata	1	British Columbia	-16.9	6.4	Romanuk and Levings (2005)				
$ \begin{array}{c ccc} Coralina pinatifolia \\ Coralina pinatifolia \\ Gongromena latifolium \\ Macrosystis pyrifera \\ Macrosystis pyrifera \\ Phytoplankton \\ Macrosystis pyrifera \\ Phytoplankton \\ Macrosystis pyrifera \\ Phytoplankton \\ Macroslae \\ Cepidua formicat (Linnaeus, 1758) \\ Macroslae \\ Crepidua formicata (Linnaeus, 1758) \\ Diodora gracea (Linnaeus, $	vallina officinalis	1	Finnoy, Norway	-11.67	Ι	Raven et al. (2002)				
Gongromena latifolium1Bergen Store Kalsoy, Norway $-15.86$ $-15.86$ Macrocystis pyriferaWide geographical range $-11.1$ to $-20.7$ $-2$ Phytoplankton1Bay of Brest $-22.4 \pm 1.5$ $4.7 \pm 1.7$ Grall et al.Macrostystis pyriferaWide geographical range $-11.1$ to $-20.7$ $-5.0$ Macrostystis pyrifera29.7 $5.0$ $-22.4 \pm 1.5$ $4.7 \pm 1.7$ Macrostyste29.7 $5.0$ $-22.4 \pm 1.5$ $4.7 \pm 1.7$ Macrostyste $-29.7$ $5.0$ $-22.4 \pm 1.5$ Macrostyste $-29.7$ $5.0$ Gastropods $-16.0 \pm 0.6$ $10.3 \pm 0.2$ Crepidula formacus. 1758) $3.2*$ (filter fieder)- $-14.9$ $12.0$ Environe distropods $-16.0 \pm 0.6$ $10.3 \pm 0.2$ Diodora gracea (Linnaeus. 1758) $3.4*$ (carnivore)- $-16.3 \pm 12.8$ $12.0$ Nassarius reticulatus (Linnaeus. 1758) $3.5*$ (carnivore)- $-15.1 \pm 0.3$ $13.2 \pm 0.3$ Buccimm undatum (Linnaeus. 1758) $3.6*$ (carnivore)- $-15.3 \pm 0.3$ $13.5 \pm 0.3$ Buccimm nudatum (Linnaeus. 1758) $3.6*$ (carnivore)- $-15.3 \pm 0.3$ $13.5 \pm 0.3$ Buccimm nudatum (Linnaeus. 1758) $3.6*$ (carnivore)- $-15.3 \pm 0.3$ $13.5 \pm 0.3$ Buccimm nudatum (Linnaeus. 1758) $3.6*$ (carnivore)- $-15.3 \pm 0.3$ $5.5 \pm 0$	vallina pinatifolia	1	Catalina Island, CA	-7.45	Ι	. 1				
Macrocystis pyrifera-Wide geographical range-11.1 to $-20.7$ -Phytoplankton1Bay of Brest $-22.4 \pm 1.5$ $4.7 \pm 1.7$ Grall et al.Phytoplankton1Bay of Brest $-22.4 \pm 1.5$ $4.7 \pm 1.7$ Grall et al.Macroalgae $-29.7$ $5.0$ $-29.7$ $5.0$ Macroalgae $-16.0 \pm 0.6$ $10.3 \pm 0.2$ $-14.9$ Macroalgae $-16.0 \pm 0.6$ $10.3 \pm 0.2$ Gastropods $-16.0 \pm 0.6$ $10.3 \pm 0.2$ <i>Crepidula fornicata</i> (Linnaeus, 1758) $3.2*$ (micrograzer)- $-14.9$ $12.0$ <i>Emarginula fissura</i> (Linnaeus, 1758) $3.4*$ (carnivore)- $-16.3$ $12.0$ <i>Diodora gracea</i> (Linnaeus, 1758) $3.5*$ (carnivore)- $-15.1 \pm 0.3$ $13.2 \pm 0.3$ <i>Naswrius reticulatus</i> (Linnaeus, 1758) $3.6*$ (carnivore)- $-15.1 \pm 0.3$ $13.2 \pm 0.3$ <i>Buccimm undatum</i> (Linnaeus, 1758) $3.6*$ (carnivore)- $-15.1 \pm 0.3$ $13.2 \pm 0.3$ <i>Buccimm undatum</i> (Linnaeus, 1758) $3.6*$ (carnivore)- $-15.1 \pm 0.3$ $13.2 \pm 0.3$ <i>Buccimm undatum</i> (Linnaeus, 1758) $3.6*$ (carnivore)- $-16.9$ $6.6$ $9.9$ <i>Buccimm undatum</i> (Linnaeus, 1758) $1.758$ $-15.3$ $13.2 \pm 0.3$ $13.5 \pm 0.3$ <i>Buccimm undatum</i> (Linnaeus, 1758) $-16.9$ $6.6$ $6.6$ $6.6$ $6.6$ <i>Buccimm undatum</i> (Linnaeus, 1758) $-16.6$ $6.6$ $6.6$	ngronema latifolium		Bergen Store Kalsoy, Norway	-15.86	I	1				
Phytoplankton1Bay of Brest $-224\pm1.5$ $4.7\pm1.7$ Grall et al.Macroalgae1 $-29.7$ 5.0 $-29.7$ 5.0Macroalgae $-29.7$ $5.0$ $-29.7$ $5.0$ Gastropods $-29.7$ $5.0$ $-29.7$ $5.0$ Gastropods $-16.0\pm0.6$ $10.3\pm0.2$ $-16.0\pm0.6$ $10.3\pm0.2$ <i>Crepidula fornicata</i> (Linnaeus, 1758) $3.2*$ (micrograzer) $-14.9$ $12.0$ <i>Emarginula fissura</i> (Linnaeus, 1758) $3.4*$ (carnivore) $-16.3$ $12.0$ <i>Emarginula fissura</i> (Linnaeus, 1758) $3.4*$ (carnivore) $-16.3$ $12.0$ <i>Diodor a graeca</i> (Linnaeus, 1758) $3.5*$ (carnivore) $-15.3$ $13.2 \pm 0.3$ <i>Nasarius reticulatus</i> (Linnaeus, 1758) $3.5*$ (carnivore) $-15.3$ $13.2 \pm 0.3$ <i>Buccimum undatum</i> (Linnaeus, 1758) $3.6*$ (carnivore) $-15.1\pm0.3$ $13.2 \pm 0.3$ <i>Buccimum undatum</i> (Linnaeus, 1758) $3.5*$ (carnivore) $-15.3$ $13.2 \pm 0.3$ <i>Buccimum undatum</i> (Linnaeus, 1758) $3.6*$ (carnivore) $-15.3$ $13.2 \pm 0.3$ <i>Buccimum undatum</i> (Linnaeus, 1758) $-15.1\pm0.3$ $13.2 \pm 0.3$ $-15.3$ <i>Buccimum undatum</i> (Linnaeus, 1758) $-15.3$ $13.2 \pm 0.3$ $-15.4\pm0.3$ <i>Buccimum undatum</i> (Linnaeus, 1758) $-15.3$ $-15.3$ $5.6.9.9$ <i>Gastropod species</i> $-10.3$ $-10.5$ $5.6.9.9$ Won et al. <i>Gastropod species</i> $-10.5$ $5.6.9.9$ $-10.5$ $-10.5$ $-10.5$ <i>Gastropod species</i> $-10.5$ $-10.5$	acrocystis pyrifera	I	Wide geographical range	-11.1 to $-20.7$	I	1				
Macroalgae1 $ -29.7$ $5.0$ Macroalgae $  -29.7$ $5.0$ Gastropods $  -29.7$ $5.0$ Gastropods $  -16.0 \pm 0.6$ $10.3 \pm 0.2$ Gastropods $-14.9$ $12.0$ $-14.9$ $12.0$ Emarginula fissura (Linnaeus, 1758) $3.2*$ (micrograzer) $ -14.9$ $12.0$ Emarginula fissura (Linnaeus, 1758) $3.4*$ (carnivore) $ -16.3$ $12.0$ Diodora graeca (Linnaeus, 1758) $3.5*$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Nasarius reticulatus (Linnaeus, 1758) $3.5*$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.5*$ (carnivore) $  -15.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.5*$ (carnivore) $  -15.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.5*$ (carnivore) $  -15.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.5*$ (carnivore) $  -15.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.5*$ (carnivore) $  -15.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $5.5*$ (or 99) $ -15.3$ $-15.3$ $-15.9$ Gastropod species on coralline crustos algaeDifferent trophic levels $  -13.3$ $0.16.7$ $5.5*$ (or 99)Condot species on coralline crustos algaeDifferent trophic levels<	ytoplankton	1	Bay of Brest	$-22.4\pm1.5$	$4.7 \pm 1.7$	Grall et al. (2006)				
Gastropods $-16.0 \pm 0.6$ $10.3 \pm 0.2$ Gastropods $-16.0 \pm 0.6$ $10.3 \pm 0.2$ $Crepidula fornicata (Linnaeus, 1758)3.2^* (micrograzer)-14.912.0Emarginula fissura (Linnaeus, 1758)3.2^* (carnivore)-14.912.0Emarginula fissura (Linnaeus, 1758)3.4^* (carnivore)-16.312.8Diodora graeca (Linnaeus, 1758)3.4^* (carnivore)-15.1 \pm 0.313.2 \pm 0.3Nasarius reticulatus (Linnaeus, 1758)3.5^* (carnivore)-15.1 \pm 0.313.2 \pm 0.3Buccimum undatum (Linnaeus, 1758)3.5^* (carnivore)-15.1 \pm 0.313.2 \pm 0.3Buccimum undatum (Linnaeus, 1758)3.5^* (carnivore)-15.1 \pm 0.313.5 \pm 0.3Buccimum undatum (Linnaeus, 1758)3.5^* (carnivore)-15.1 \pm 0.313.5 \pm 0.3Buccimum undatum (Linnaeus, 1758)3.5^* (carnivore)-15.313.5 \pm 0.3Buccimum undatum (Linnaeus, 1758)-15.313.2 \pm 0.34.6Buccimum undatum (Linnaeus, 1758)-15.3-15.313.5 \pm 0.3Buccimum undatum (Linnaeus, 1758)-15.3-15.313.5 \pm 0.3Buccimum undatum (Linnaeus, 1758)-15.3-15.3-15.3Buccimum undatum (Linnaeus, 1758)-15.3-15.3-15.3Buccimum undatum (Linnaeus, 1758)-15.3-15.3-15.3Buccimum undatum (Linnaeus, 1758)-15.3-15.3-15.3Buccimum elegans-17-15.3-15.9-15.9$	acroalgae	1	Ι	-29.7	5.0	Ι				
Crepidula fornicata (Linnaeus, 1758) $2.6^{*}$ (filter feeder) $ -16.0 \pm 0.6$ $10.3 \pm 0.2$ <i>Gibbula magus</i> (Linnaeus, 1758) $3.2^{*}$ (micrograzer) $ -14.9$ $12.0$ <i>Emarginula fissura</i> (Linnaeus, 1758) $3.2^{*}$ (micrograzer) $ -14.9$ $12.0$ <i>Emarginula fissura</i> (Linnaeus, 1758) $3.4^{*}$ (carnivore) $ -16.3$ $12.0$ <i>Emarginula fissura</i> (Linnaeus, 1758) $3.4^{*}$ (carnivore) $ -16.3$ $12.0$ <i>Nassarius reticulatus</i> (Linnaeus, 1758) $3.5^{*}$ (carnivore) $ -16.3$ $12.8$ <i>Nassarius reticulatus</i> (Linnaeus, 1758) $3.5^{*}$ (carnivore) $ -16.3$ $12.8$ <i>Nassarius reticulatus</i> (Linnaeus, 1758) $3.5^{*}$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ <i>Nassarius reticulatus</i> (Linnaeus, 1758) $3.6^{*}$ (carnivore) $ -15.3$ $13.2 \pm 0.3$ <i>Nassarius reticulatus</i> (Linnaeus, 1758) $3.6^{*}$ (carnivore) $ -15.3$ $13.2 \pm 0.3$ <i>Nassarius reticulatus</i> (Linnaeus, 1758) $3.6^{*}$ (carnivore) $ -15.3$ $13.2 \pm 0.3$ <i>Nassarius reticulatus</i> (Linnaeus, 1758) $3.6^{*}$ (carnivore) $ -15.3$ $13.2 \pm 0.3$ <i>Buccimum udatum</i> (Linnaeus, 1758) $1$ $10.9$ $-16.9$ $4.6$ Won et al. <i>Gelsenium elegans</i> $  -13.3$ $5.5.0.9.9$ Won et al. <i>Gastropod species on coralline crustose algae</i> $0.16.7$ $5.5.0.9.9$ $0.9.9$ $0.0.10.9$	istropods	I	Ι	I	I	I				
Gibbula magus (Linnaeus, 178) $3.2*$ (micrograzer) $ -14.9$ $12.0$ Emarginula fissura (Linnaeus, 178) $3.2*$ (micrograzer) $ -14.9$ $12.0$ Emarginula fissura (Linnaeus, 178) $3.4*$ (carnivore) $ -18.5$ $10.8$ Diodora graeca (Linnaeus, 178) $3.4*$ (carnivore) $ -16.3$ $12.0$ Nassarius reticulatus (Linnaeus, 178) $3.5*$ (carnivore) $ -16.3$ $13.2\pm0.3$ Nassarius reticulatus (Linnaeus, 178) $3.5*$ (carnivore) $ -15.1\pm0.3$ $13.2\pm0.3$ Buccimum undatum (Linnaeus, 178) $3.6*$ (carnivore) $ -15.1\pm0.3$ $13.2\pm0.3$ Buccimum undatum (Linnaeus, 178) $3.6*$ (carnivore) $ -15.1\pm0.3$ $13.2\pm0.3$ Buccimum undatum (Linnaeus, 178) $3.6*$ (carnivore) $ -15.1\pm0.3$ $13.2\pm0.3$ Buccimum undatum (Linnaeus, 178) $1$ Japan $-16.9$ $4.6$ Won et al.Galsemium elegans $-17$ $5.1$ $-17$ $5.1$ $5.09.9$ Won et al.Control aspecies on coralline crustose algaeDifferent trophic levels $ -13.3$ $5.60.99$ Won et al.	epidula fornicata (Linnaeus, 1758) 2.6	5* (filter feeder)	Ι	$-16.0\pm0.6$	$10.3 \pm 0.2$	I				
Emarginula fissura (Linnaeus, 1758) $2.8*$ (carnivore) $ -18.5$ $10.8$ Diodora graeca (Linnaeus, 1758) $3.4*$ (carnivore) $ -16.3$ $12.8$ Nassarius reticulatus (Linnaeus, 1758) $3.5*$ (carnivore) $ -16.3$ $13.2 \pm 0.3$ Nassarius reticulatus (Linnaeus, 1758) $3.5*$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.6*$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.6*$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.6*$ (carnivore) $ -15.1 \pm 0.3$ $13.5$ Buccimum undatum (Linnaeus, 1758) $1$ $Japan$ $-16.9$ $4.6$ Won et al.Gastropol species on corralline crustose algaeDifferent trophic levels $ -13.3$ to $-16.7$ $5.5$ to $9.9$ Won et al.Constropol species on trophic levels $  -13.3$ to $-16.7$ $5.5$ to $9.9$ Won et al.	<i>bbula magus</i> (Linnaeus, 1758) 3.2	2* (micrograzer)	Ι	-14.9	12.0	1				
Diodora graeca (Linnaeus, 1758) $3.4^{*}$ (carnivore) $ -16.3$ $12.8$ Nassarius reticulatus (Linnaeus, 1758) $3.5^{*}$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Nassarius reticulatus (Linnaeus, 1758) $3.5^{*}$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Buccinum undatum (Linnaeus, 1758) $3.6^{*}$ (carnivore) $ -15.3$ $13.2 \pm 0.3$ Buccinum undatum (Linnaeus, 1758) $3.6^{*}$ (carnivore) $ -15.3$ $13.5$ Buccinum undatum (Linnaeus, 1758) $1$ $Japan$ $-16.9$ $4.6$ Won et al. $-17.3$ $-16.9$ $5.1$ $-17.5$ Gelsemium elegans $-17.5$ $5.10.9.9$ Won et al.Gastropol aspecies on coralline crustose algaeDifferent trophic levels $ -13.3 to -16.7$ $5.5 to 9.9$ Control aspecies on the hold $ -13.3 to -16.7$ $5.5 to 9.9$ Won et al.	narginula fissura (Linnaeus, 1758) 2.8	3* (carnivore)	Ι	-18.5	10.8	1				
Nassarius reticulatus (Linnaeus, 1758) $3.5*$ (carnivore) $ -15.1 \pm 0.3$ $13.2 \pm 0.3$ Buccimum undatum (Linnaeus, 1758) $3.6*$ (carnivore) $ -15.3$ $13.5$ $13.5$ Buccimum undatum (Linnaeus, 1758) $3.6*$ (carnivore) $ -15.3$ $13.5$ $13.5$ Buccimum undatum (Linnaeus, 1758) $3.6*$ (carnivore) $ -16.9$ $4.6$ Won et al.Buccimum elegans $ -16.9$ $5.1$ $-17$ $5.1$ $5.1$ $-13.3$ to $-16.7$ $5.5$ to $9.9$ Won et al.Concord aspects on the holdsDifferent trophic levels $ -13.3$ to $-16.7$ $5.5$ to $9.9$ Won et al.	odora graeca (Linnaeus, 1758) 3.4	<pre>l* (carnivore)</pre>	Ι	-16.3	12.8	1				
Buccimum undatum (Linnaeus, 1758) $3.6^*$ (carnivore) $ -15.3$ $13.5$ Eisenia bicyclis1 $Japan$ $ -16.9$ $4.6$ Won et al.Eisenia bicyclis $  -17$ $5.1$ $5.1$ Gelsemium elegans $  -17$ $5.1$ $5.1$ Gastropol species on coralline crustose algaeDifferent trophic levels $ -13.3$ to $-16.7$ $5.5$ to $9.9$ Won et al.	ssarius reticulatus (Linnaeus, 1758) 3.5	5* (carnivore)	Ι	$-15.1\pm0.3$	$13.2\pm0.3$	I				
Eisenia bicyclis  1  Japan  -16.9  4.6  Won et al.    Gelsemium elegans  -  -  -17  5.1    Gastropod species on coralline crustose algae  Different trophic levels  -  -13.3 to -16.7  5.5 to 9.9	ccinum undatum (Linnaeus, 1758) 3.6	5* (carnivore)	Ι	-15.3	13.5	I				
Gelsemium elegans  -  -17  5.1    Gastropod species on coralline crustose algae  Different trophic levels  -  -13.3 to -16.7  5.5 to 9.9    Contracted approximation of the hole  -  -  -13.3 to -16.7  5.5 to 9.9	senia bicyclis	1	Japan	-16.9	4.6	Won et al. (2008)				
Gastropod species on coralline crustose algae Different trophic levels – – –13.3 to –16.7 5.5 to 9.9 Won et al.	lsemium elegans	Ι	Ι	-17	5.1	Ι				
1) 1 to 16 0 5 0 to 17 3	istropod species on coralline crustose algae Di	fferent trophic levels	I	-13.3 to -16.7	5.5 to 9.9	Won et al. (2013)				
	istropod species on kelp beds	I	I	-12.1 to -16.0	5.9 to 12.2	I				

## STABLE ISOTOPES IN GASTROPODS AND SEAWEEDS

Feeding activities based on isotope discrimination indicate whether gastropods are more herbivorous than carnivorous and influence fractionation (Vander Zanden & Rasmussen 2001, Won et al. 2008). Metabolic fractionation is expected to be the dominant process for carnivores because animal-derived nitrogen is biochemically more homogeneous and dominated by proteins. For herbivores, both assimilative and metabolic factors affect fractionation; therefore, a higher signature indicates omnivorous behavior because higher signals are expected for carnivores (Riera et al. 2009). Trophic enrichment of  $\delta^{15}N$  is generally attributed to fractionation during amino acid deamination and transamination (Vander Zanden & Rasmussen 2001), whereby the <sup>14</sup>N amine groups are preferentially removed to produce isotopically light metabolites, leaving the remaining nitrogen pool enriched in <sup>15</sup>N ("metabolic fractionation") and a more enriched signal for carnivores (Gannes et al. 1997, Mill et al. 2007). Therefore, even when tunicates or other invertebrates were not important contributors to the diet of Megathura crenulata, its enriched signal shows that pathways other than those for herbivores are taking place during feeding by M. crenulata.

Differences between diets in reports based on stomach contents and isotope studies highlight the importance of using complementary approaches. Together, they provide a more robust understanding of diets (Condini et al. 2015), because studies of stomach contents focus on ingested rather than assimilated food. Results can be biased toward less digestible material (Wangensteen et al. 2011, Page et al. 2013). The stable isotope signatures of carbon and nitrogen of an animal depend on the isotope signature of their food sources and fractionation during assimilation of food. Studies that involve food sources are needed to understand ecological implications of the food chain and food consumption of gastropods and other benthic marine species that are ecologically or economically valuable; therefore, isotope studies are important sources of information about diet.

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