Research article

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Exploring the role of macroalgal traits on the feeding behaviour of a generalist herbivore in Malaysian waters

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Abstract: With the potential adverse effects of climate change, it is essential to enhance the understanding of marine ecosystem dynamics, which can be driven by the co-evolutionary interaction between autotrophs and herbivores. This study looked into the autotroph-herbivore interactions in Malaysian waters, mainly to determine if autotroph nutritional quality significantly influences herbivore consumption rates. We documented the relative consumption rate of a generalist herbivore (*Chanos chanos* Forsskal) obtained from the Straits of Malacca through multiple feeding trials using 12 macroalgal species collected from different coastal areas of the Straits of Malacca, the Straits of Johor, and the South China Sea. The herbivore fed selectively on the tested macroalgal species, with the most and least consumed species having the lowest and highest total nitrogen content, respectively. Besides total nitrogen content, the least consumed species also had the highest total phenolic content. Interestingly, we observed that the herbivore generally preferred to consume filamentous macroalgae, especially those collected from the South China Sea. Overall, our findings demonstrated that the feeding behaviour of a generalist herbivore could be influenced by the nutritional quality of the autotrophs, which may depend directly or indirectly on other factors such as autotroph morphology and geography.

1 Introduction

The marine biome covers approximately three-fourths of the biosphere, providing essential ecosystem services such as habitats for species and carbon sequestration (Townsend et al. 2018). Being the largest biome, it accounts for nearly 90% of the world's water supply and plays a significant role in preserving millions of existing marine species (Moosdorf and Oehler 2017). Anthropogenic activity has been one of the main drivers of global warming, influencing both temperatures and rainfall distribution globally (Abram et al. 2014; Abram et al., 2014; Asmida et al., 2017; Bagarinao, 1991). The shift in weather patterns due to climate change can also lead to significant ecosystem changes, which are mostly negative. Ocean warming, for instance, has been reported to cause a shift to dominance by invasive species and facilitate their invasions, and consequently affecting the structure and function of ecosystems worldwide (Lafoley and Baxter 2016), including coastal and marine ecosystems in Malaysia (Bishop et al. 2017).

Species interactions take place in nature regularly, and one of the most dominant interactions is between autotrophs and herbivores. The autotroph-herbivore interactions in both terrestrial and aquatic biomes have thus far displayed a dynamic evolutionary history, whereby the autotrophs have evolved intricate defence mechanisms to reduce the impact of herbivory. Likewise, the herbivores have evolved countermeasures to outwit these mechanisms (Burkepile and Parker 2017; de Vries et al. 2017; Poore et al. 2012). In the case of marine ecosystems, several studies demonstrated that autotroph characteristics largely influence the consumption patterns of herbivorous fish (Mantyka and Bellwood 2007; Schwartz et al. 2016; Van Alstyne et al. 2009). According to Elger and Lemoine (2005), autotroph palatability depends primarily on

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autotroph characteristics and their interactions. Nutritional quality of autotrophs such as their levels of nitrogen was found to correlate with the consumption rates of generalist herbivores in native communities (Chan et al. 2012; Elger and Lemoine 2005; Van Alstyne et al. 2009).

To date, the value of autotroph nutritional quality and geography (especially in terms of novelty) in predicting herbivore consumption have not been widely explored, especially for aquatic communities (Clements et al. 2009; Grutters et al. 2017). Several studies on aquatic ecosystems showed that the dynamic interactions between autotroph-herbivore could prevent or reduce the detrimental effects of the presence of invasive autotroph species (Grutters et al. 2017; Parker et al. 2006). Nonetheless, the consumption rate of generalist herbivores whether to consume native or non-native autotrophs has been inferred to lie beyond the evolutionary novelty theory which consists of two dominant hypotheses: (1) enemy release hypothesis which posits that herbivores are maladapted to consume non-native autotrophs; and (2) biotic resistance hypothesis which posits that non-native autotrophs are maladapted to fend off herbivores (Grutters et al. 2017; Maron and Vila 2001; Parker et al. 2006).

Although the autotroph-herbivore synergies have been previously discussed for both terrestrial and aquatic environments in different parts of the world, many studies have reported contradictory findings and conclusions on the effects of nutritional quality and novelty of autotrophs and herbivore feeding patterns (Cronin et al. 2002; Grutters et al. 2017; Raubenheimer et al. 2009; Wong et al. 2010). To the best of our knowledge, the critical characteristics in marine autotrophs such as their nutritional qualities (Behmer and Joern 2008) and geography (Lamarre et al. 2012) that attract or deter herbivores have not been well-addressed in Malaysia. Hence, the current study delved into the value of major nutritional qualities of macroalgae, and their relationships with geography and other possible factors in determining the feeding behaviours of a generalist herbivore. Macroalgae were used as autotrophs in this study because they represent a distinguished group of photosynthetic organisms in the marine biome and are known to have strong interaction with marine herbivores. The overall outcome of this study can help manage the local coastal and marine biodiversity in a changing climate.

2 Materials and methods

2.1 Study organisms

Generalist herbivory is considered the dominant form of autotroph consumption (Dudgeon et al. 2006; Gregory 1983; Vilà et al. 2009). Milkfish (*Chanos chanos* Forsskål), which is relatively abundant in the tropical waters of the Indian Ocean, was used as an herbivore in this

study due mainly to its generalist tendencies (Bagarinao 1991, 1999). Nevertheless, milkfish have yet to be found in some tropical estuaries such as Ponggol (Singapore) and Kretam (North Borneo) (Bagarinao 1991). In the present study, milkfish fingerlings were used instead of adults because they have a higher metabolic rate, which allows them better access to quality feeding patches (Gotceitas and Godin 1992; Millidine et al. 2009). The fingerlings were collected from the northern part of the West Coast of Peninsular Malaysia (06°09'20"N, 100°34'11"E). They were then transferred and placed in specialized design fibreglass tanks (i.e. artificial seawater systems) in a glasshouse in Rimba Ilmu, University of Malaya (Supplementary Figure S1). These tanks were equipped with a mechanical filtration system with appropriate water quality levels of >5 mg l⁻¹ dissolved oxygen, 30 salinity, 7–8 pH, and 19–20 °C temperature (Sumagaysay-Chavoso and San Diego-McGlone 2003). All these water parameters were monitored at least twice a week using a YSI-Pro Plus multiprobe (YSI Incorporated, Ohio, USA) and a salinity refractometer (Spartan Refractometers, Japan) (Sumagaysay-Chavoso 1998). Protein skimmer was added in the tanks daily to remove the excess organic nutrients and wastes from water. During an acclimation period of 14 days, the fingerlings were only fed with Malaysian sea lettuce (*Ulva reticulata* Forsskål) once a day and fish food pellets once a week.

The 12 marine macroalgal species used in this study consist of those commonly found near Malaysian waters, collected along the coastal areas of the Straits of Malacca, the Straits of Johor, and the South China Sea (Table 1; Figure 1). The geographical origin of all tested macroalgal species was documented based on previous literature (Asmida et al., 2017; Lee et al. 2014; Muta Harah et al. 2014; Phang et al. 2010; Abram et al., 2014; Asmida et al., 2017; Lee et al., 2014; Muta Harah et al., 2014; Phang et al., 2010). We worked with multiple macroalgal species from six different sampling locations to help ensure that our results would be general. Samples were collected in intertidal and subtidal zones at low tide between September 2017 and April 2019. Only healthy-looking samples with minimal epiphytes were collected from the sampling sites. The samples were cleaned and kept in fibreglass tanks in Rimba Ilmu until the feeding trials were conducted.

Marine macroalgae occur in a variety of size, shape, toughness, and degree of calcification, and classified into different functional form groups based on their specific morphology, growth form and ecological characteristics (Diaz-Pulido and McCook 2003; Hanley et al. 2007; Padilla and Allen 2000). The macroalgal species evaluated in this study were categorized into several functional groups based on previous literature (Table 1). Based on Morrison and Hay (2011), some autotroph-herbivore pairs in the present study may be classified as evolutionary novel to each other because they occurred on three territorial waters (i.e. the Straits of Malacca, the Straits of Johor, and the South China Sea) (Figure 1). This can be applied to the pairings of milkfish with macroalgal species collected from coastal areas of the Straits of Johor and the South China Sea, given that milkfish were obtained from the Straits of Malacca and have not been found in some tropical estuaries as mentioned in the previous section (Bagarinao 1991).

2.2 Feeding trials

We employed the no-choice feeding trial because this approach provides the flexibility to determine compensatory feeding in herbivores (Duarte et al. 2010; Elger and Barrat-Segretain 2002; Grutters et al. 2017). Based on established protocols, 48 h no-choice feeding trials were conducted for all macroalgal species in triplicate (Burlakova et al. 2009; Elger et al. 2002). All the juvenile milkfish were starved for 48 h prior to the feeding trials. Three fishes with almost the same body

Table 1: Sampling areas and coordinates and morpho-functional groups of tested macroalgae.

Macroalgal species	Coastal area	Coordinate of sampling site	Morpho-functional group
<i>Dictyota ciliolata</i> Kützting	SOM	02°30'60"N, 101°47'60"E	Corticated foliose ^a
<i>Gracilaria firma</i> Chang et Xia	SOM	02°48'49"N, 101°30'06"E	Corticated terete ^b
<i>Gracilaria salicornia</i> (C. Agardh) Dawson	SOM	02°48'49"N, 101°30'06"E	Corticated terete ^c
<i>Padina gymnospora</i> (Kützting) Sonder	SOJ	01°18'60"N, 103°36'60"E	Corticated foliose ^d
<i>Ulva reticulata</i> Forsskål	SOJ	01°18'60"N, 103°36'60"E	Foliose ^e
<i>Amphiroa fragilissima</i> (Linnaeus) Lamouroux	SOJ	01°18'60"N, 103°36'60"E	Non-calcified ^f
<i>Ceratodictyon spongiosum</i> Zanardini	SOJ	01°18'60"N, 103°36'60"E	Filamentous ^g
<i>Cladophora sericea</i> (Hudson) Kützting	SOJ	01°18'60"N, 103°36'60"E	Filamentous ^a
<i>Acanthophora muscoides</i> (Linnaeus) Bory de Saint-Vincent	SCS	05°48'00"N, 102°37'10"E	Corticated ^h
<i>Chaetomorpha antennina</i> (Bory de Saint-Vincent) Kützting	SCS	05°48'00"N, 102°37'10"E	Filamentous ^g
<i>Cladophora prolifera</i> (Roth) Kützting	SCS	04°24'60"N, 103°26'6"E	Filamentous ^g
<i>Valoniopsis pachynema</i> (G. Martens) Børgesen	SCS	04°24'60"N, 103°26'60"E	Filamentous ^e

SOM: Straits of Malacca, SOJ: Straits of Johor, SCS: South China Sea.

^aBenvenuto et al. 2003.

^bBeach et al. 2006.

^cSousa-Dias and Melo 2008.

^dCladeira et al. 2017.

^eSidik et al. 2001.

^fWilliams et al. 2008.

^gBalata et al. 2011.

^hPadilla and Allen 2000.

Figure 1: Distribution and collection site of juvenile milkfish and sampling sites of macroalgae in Malaysia.

weight (1.4 ± 0.5 g) were grouped and placed into each fibreglass tank. Then, each group of fish was randomly fed a standardized amount of fresh fragments of each macroalgal species ($FW_{\text{algae:initial}}$) that had been blotted dry. After 48 h, the three fishes from each treatment were dried to obtain their body dry mass, which was used to express the consumption standardized for fish mass (DW_{fish}). The remaining macroalgal fragments from each treatment were then dried in an oven at 60 °C for at least 72 h before reweighing ($DW_{\text{algae:final}}$).

To calculate the relative consumption rate (RCR), the mean of initial fresh-to-final dry mass ratio of the controls were used to calculate the $DW_{\text{algae:initial}}$ from $FW_{\text{algae:initial}}$. The linear relationship was assessed for each macroalgal species separately using six controls. Following Elger and Barrat-Segretain (2004), the RCR ($\text{mg g}^{-1} \text{ day}^{-1}$) was calculated as follows: $\text{RCR} = (DW_{\text{algae:initial}} - DW_{\text{algae:final}}) / DW_{\text{fish}} / \text{time}_{\text{day}}$

2.3 Autotroph nutrient analysis

Previous studies reported the correlation between autotrophs characteristics such as nitrogen and phosphorus content to herbivore consumption rates (Cronin et al. 2002; Dorenbosch and Bakker 2011). Hence, five critical nutritional components of macroalgae, including total dry matter, nitrogen, phosphorus, carbon and phenolic contents, were evaluated in this study. Fresh fragments ($n = 5$) of each macroalgal species were weighed and dried at 60 °C for at least 48 h or until constant weight to obtain their total dry matter content (Elger and Willby 2003). The dried material samples were finely ground and was used to determine the total nitrogen, phosphorus, carbon, and phenolic content. Each analysis was performed in triplicate, with the average value used as the datum for each variable.

2.4 Estimation of nitrogen, phosphorus and carbon contents

A modified Nessler's reagent spectrophotometry method was used to analyse the total nitrogen content (Makino and Osmond 1991). Ammonium sulphate ($(\text{NH}_4)_2\text{SO}_4$) was used as the standard compound. The Nessler's reagent was prepared by mixing 10 g of Mercury (II) iodine with 7 g of potassium iodine (KI) and 50.0 ml of 20% sodium hydroxide (NaOH). Concentrated sulphuric acid (H_2SO_4) and saturated potassium were used to digest 0.1 g of sample. After digestion, 0.5 ml aliquot of the digested solution was poured into a 10.0 ml test tube and added with 7.0 ml of Nessler's reagent, 0.1 ml of 50% concentrated H_2SO_4 , 0.1 ml of saturated potassium persulphate and 2.3 ml of distilled water. Using the UV Mini-1240 spectrophotometer (Shimadzu, Kyoto, Japan), the absorbance of the samples along with a reagent blank was measured at 480 nm. A calibration curve of $(\text{NH}_4)_2\text{SO}_4$ was plotted and used to determine the nitrogen content.

The total phosphorus content was determined using the vanadomolybdate method with minor modifications (Legiret et al. 2013). Digestion was performed with diacid mixture (3 nitric acid:1 perchloric acid) using 0.5 g of dried sample. The volume was made up to 50.0 ml with distilled water. Then, 10.0 ml of digested solution were mixed with 10.0 ml of ammonium molybdate solution. Distilled water was added to the mixed solution until a total volume of 50.0 ml was obtained. The change in colour due to different level of acidity was measured at 420 nm on a UV Mini-1240 spectrophotometer (Shimadzu, Kyoto, Japan) against a phosphorus solution calibration curve. To determine the total carbon content, dry combustion analysis was performed using the CHN628 Series Elemental Determinator according

to the manufacturer's protocol (LECO, Michigan, USA). The instrument automatically determines carbon, hydrogen, and nitrogen by oxidizing the samples and the combustion products (i.e. combination of gases) were then separated and determined via a thermal conductivity detector. In the combustion chamber, oxidation process was carried out in the presence of catalyst at the nominal temperature of 950 °C in a stream of pure oxygen (99.99%).

2.5 Estimation of total phenolic content

The modified Folin-Ciocalteu method was used to determine the total phenolic content, with gallic acid as the standard compound (Blainski et al. 2013). A 0.25 ml aliquot of sample extract (1.0 mg ml^{-1} of ethanol) was mixed with 1.25 ml of Folin-Ciocalteu reagent. After 5 min of incubation at room temperature, 1.00 ml of 7.5% sodium carbonate solution was added and the mixture was mixed thoroughly. Sample was incubated at room temperature for 2 h before obtaining the absorbance value at 760 nm using the UV Mini-1240 spectrophotometer (Shimadzu, Kyoto, Japan). The concentration of total phenolic, which expressed as $\mu\text{g g}^{-1}$ gallic acid equivalents of the sample dry weight, was obtained from gallic acid calibration curve.

2.6 Statistical analysis

All data sets obtained were subject to descriptive statistics. The normality of the distributions was tested using Shapiro-Wilk Test. One-way analysis of variance (ANOVA) was carried out to compare means between two or more variables, followed by the Tukey's honestly significant difference (HSD) post hoc test (Poore and Steinberg 1999). Linear regression was performed to evaluate the relationships among studied variables. All possible two-way interactions (macroalgal nutrient, morphology, and novelty) were analysed using a linear mixed-effects model, with macroalgae as the random intercept. All analyses were performed using SPSS Statistics Software Version 25 (SPSS Inc., Chicago, USA) and the significance level for the P -value was set at 0.05.

3 Results

3.1 Herbivore consumption rates

The present study looked into the effects of critical autotroph nutritional quality and its relationships with other factors (biogeographical and morphological) on the consumption rates of a generalist herbivore. The results from our no-choice feeding trials showed that the herbivore preferred to feed on certain species of macroalgae (Table 2; Figure 2). *Valoniopsis pachynema* and *Cladophora prolifera* were the two most preferred species, having significantly higher RCR ($P < 0.05$) than other species. Both the species were collected from the coastal areas of the South China Sea (Figure 2). The least consumed species was *Padina gymnospora*, with a significantly lower RCR than all tested species (Table 2). This species was collected from Tanjung Balau Beach near the Straits of Johor, which is situated north of Singapore (Figure 1).

Based on the results of RCR, all the filamentous macroalgae were consumed in higher amounts than other functional form groups of macroalgae. Two of the filamentous species (*V. pachynema* and *C. prolifera*) were among the most consumed species by the generalist herbivore (Tables 1 and 2). On the other hand, the most heavily calcified macroalga (*Amphiroa fragilissima*), which expected to have the least RCR due to calcification in their thalli, was consumed within the intermediate range by herbivore in this study (Tables 1 and 2).

3.2 Compositional analysis

Table 2 also shows the mean values of five autotroph nutritional characteristics evaluated in this study. The total dry matter content in *A. fragilissima* (59.21%) was higher ($P < 0.05$) than all other species. The highest total nitrogen content was found in the least consumed species *P. gymnospora* (7.55%), whereas the most consumed species *V. pachynema* recorded the lowest mean (0.69%). *V. pachynema* also recorded the lowest total phosphorus (0.04%) and carbon content (5.90%). Similar to *V. pachynema*, *Acanthophora muscoides* recorded significantly lower total phosphorus content (0.04%) than other tested species. Besides total nitrogen content, the least consumed species *P. gymnospora* also recorded the highest total phenolic content (1261.80 $\mu\text{g g}^{-1}$). The total phenolic content for six species were not detected in the present study (Table 2), indicating that these species had total phenolic content lower than 5 $\mu\text{g g}^{-1}$ and this is not uncommon in phycological research (Figueroa et al. 2014; Jerez-Martel et al. 2017; Machu et al. 2015).

A linear mixed-effects model with macroalgae as the random intercept was constructed to identify the parameters (macroalgal nutrient, morphology, and novelty) that best explained the RCR of the generalist herbivore (Table 3). Among these parameters, the macroalgal morphology recorded the highest *F*-value ($F = 20.7$) (Table 3), indicating that this factor could play the most significant role in influencing the herbivore consumption rates in our study. Among the five tested nutritional characteristics, the total phenolic content showed the strongest correlation with the RCR of the generalist herbivore ($F = 13.1$), followed by total carbon ($F = 5.0$) and nitrogen ($F = 3.3$) contents (Table 3). In our regression analysis, the total nitrogen demonstrated the strongest relationship with the RCR of the generalist herbivore, showing a negative correlation with RCR ($R^2 = 0.414$) (Supplementary Figure S2). This was observed when the least consumed macroalgae (*P. gymnospora*) in this study recorded the highest total nitrogen content (Table 2).

Table 2: Relative consumption rate (RCR) and important nutritional components of macroalgae.

Macroalgal species	Relative consumption rate ($\text{mg g}^{-1} \text{ day}$)	Total dry matter (%)	Total nitrogen content (%)	Total phosphorus content (%)	Total carbon content (%)	Total phenolic content ($\mu\text{g g}^{-1}$)
<i>Acanthophora muscoides</i>	37.34 ± 2.76^{bc}	29.74 ± 0.48^e	0.86 ± 0.10^g	0.04 ± 0.00^g	6.29 ± 0.00^j	ND
<i>Amphiroa fragilissima</i>	29.32 ± 3.14^{bc}	59.21 ± 0.81^a	2.36 ± 0.04^e	0.12 ± 0.00^d	14.30 ± 0.00^i	ND
<i>Ceratodictyon spongiosum</i>	39.80 ± 0.65^{bc}	7.82 ± 0.07^j	6.66 ± 0.04^b	0.06 ± 0.00^f	11.20 ± 0.00^b	691.80 ± 0.85^b
<i>Chaetomorpha antennina</i>	46.85 ± 4.39^{bc}	19.33 ± 0.90^g	1.91 ± 0.05^d	0.18 ± 0.00^c	19.25 ± 0.00^c	231.90 ± 0.99^c
<i>Cladophora prolifera</i>	78.20 ± 7.31^a	47.89 ± 1.87^b	2.44 ± 0.19^{de}	0.10 ± 0.01^e	12.40 ± 0.01^g	ND
<i>Cladophora sericea</i>	50.02 ± 8.72^b	16.25 ± 0.58^{gh}	1.63 ± 0.03^f	0.19 ± 0.00^{bc}	17.10 ± 0.00^e	191.60 ± 1.13^d
<i>Dictyota ciliolata</i>	27.49 ± 2.11^c	21.92 ± 0.79^j	4.62 ± 0.22^c	0.09 ± 0.00^a	26.05 ± 0.00^a	9.70 ± 0.14^f
<i>Gracilaria firma</i>	34.67 ± 3.48^{bc}	16.91 ± 0.03^g	2.99 ± 0.05^d	0.23 ± 0.00^a	25.31 ± 0.00^b	ND
<i>Gracilaria salicornia</i>	39.13 ± 0.05^{bc}	12.53 ± 0.11^h	2.94 ± 0.11^d	0.19 ± 0.00^b	19.22 ± 0.00^d	ND
<i>Padina gymnospora</i>	1.74 ± 0.81^d	31.53 ± 0.55^{de}	7.55 ± 0.09^a	0.13 ± 0.00^d	9.40 ± 0.00^f	1261.80 ± 0.06^a
<i>Ulva reticulata</i>	29.37 ± 3.61^{bc}	40.98 ± 0.06^c	6.60 ± 0.12^b	0.13 ± 0.00^d	25.30 ± 0.00^b	ND
<i>Valoniopsis pachynema</i>	94.04 ± 6.04^a	34.62 ± 0.76^d	0.69 ± 0.04^g	0.04 ± 0.00^g	5.90 ± 0.00^k	17.40 ± 0.05^e

Means ($\pm$ SD) followed by the same letter within columns do not differ significantly between treatments ($P > 0.05$, Tukey HSD test). ND, not detected ($< 5 \mu\text{g g}^{-1}$).

Figure 2: Relative consumption rate (RCR; $\text{mg g}^{-1} \text{day}^{-1}$) of juvenile milkfish (*Chanos chanos* Forsskål) on tested macroalgae collected from three territorial waters of Malaysia. Error bars represent standard deviation.

4 Discussion

The interactions between autotroph and herbivore have been previously discussed for both terrestrial and aquatic environments; however, many studies have reported conflicting findings and conclusions on the effects of autotroph nutritional quality and geography on herbivore feeding patterns (Cronin et al. 2002; Grutters et al. 2017; Raubenheimer et al. 2009; Wong et al. 2010). With the potential adverse effects of climate change, coupled with the increasing human impacts on marine environments, it is essential to enhance the understanding of the marine ecosystem dynamics, which can be driven by the co-evolutionary interaction between autotrophs and herbivores. In Malaysia, anthropogenic activities near

the coastal areas such as fishing and trade have been reported as one of the major threats to marine ecosystems (Islam and Jorgensen 2018). It is evident that the coastal ecosystems are getting more vulnerable to both point source and non-point source pollution, which may lead to environmental degradation (Bakke et al. 2013; Islam and Jorgensen 2018). Hence, the current study was carried out to predict the consumption rates of a generalist herbivore based mainly on the nutritional characteristics of macroalgae found along the coastal areas in Malaysia, and to deduce if other factors such as macroalgal morphology and novelty also play a role in determining the herbivore feeding behaviours.

The characteristics of the tested macroalgae in this study, especially their total nitrogen content, were found to influence the RCR of the generalist herbivore (Table 2). The highest and lowest total nitrogen content was found in the least (*P. gymnospora*) and most (*V. pachynema*) consumed macroalgal species, respectively. This is further supported by our regression analysis, which revealed a strong negative correlation between the RCR and the total nitrogen content of macroalgae (Supplementary Figure S2). Interestingly, *V. pachynema* also recorded the lowest total phosphorus and carbon contents. These results may be explained by compensatory feeding, which is regarded as an adaptive strategy that allows herbivores to enhance nutrient intake from low quality autotrophs (Cruz-Rivera and Hay 2001). This strategy has been reported in several studies, where herbivores were observed to graze more on autotrophs with lower nutritional quality to maintain their growth and development (Cruz-Rivera and Hay 2001; Duarte et al. 2014). It is important to note that compensatory feeding is necessary for generalist herbivores to maintain their populations during seasonal changes or periods when high-quality foods are unavailable,

Table 3: Results of mixed-effect linear model fit by reduced maximum likelihood for testing nutritional factors best related to herbivore consumption rates, with species as random intercept.

Fixed effects	F	Numerator d.f.	Denominator d.f.	P-value
Intercept	14.5	1	12.70	0.002
Total dry matter content	0.03	1	12.32	0.872
Total carbon content	5.0	1	15.75	0.040
Total nitrogen content	3.3	1	18.54	0.086
Total phosphorus content	1.3	1	17.44	0.278
Total phenolic content	13.1	1	16.10	0.002
Morphology	20.7	1	12.16	0.001
Evolutionary novelty	1.9	1	12.97	0.195

Bold values indicate statistical significance ($P < 0.05$).

especially when generalists are less constrained than specialist in their selection of foods that have noticeable nutritional disparity (Cruz-Rivera and Hay 2000).

Based on our linear mixed-effects model, the RCR of the herbivore was also found to be influenced largely by the total phenolic content of macroalgae (Table 3), indicating that the generalist herbivore preferred to consume macroalgae with low phenolic compounds. Previous studies have demonstrated that the presence of substantial amounts of phenolic compounds in autotrophs may play a role in anti-herbivore defence (Qiu and Kwong 2009; Vergés et al. 2007). In general, marine autotrophs have a lower total phenolic content than most terrestrial autotrophs, although it is considered an important characteristic that may involve in defending aquatic autotrophs against pathogens and herbivores (Smolders et al. 2000). This can be supported by several observations conducted previously on some generalist herbivores, including freshwater fish *Scardinus erythrophthalmus* (Linnaeus) and *Ctenopharyngodon idella* (Cuvier and Valenciennes) (Dorenbosch and Bakker 2011) and snail species *Pomacea canaliculate* (Lamarck) and *Lymnaea stagnalis* (Linnaeus) (Grutters et al. 2017; Qiu and Kwong 2009). On the contrary, the total dry matter, carbon, and phosphorus contents did not exhibit a significant correlation with RCR in the present study. Similar results were obtained in some earlier studies, which highlighted that nutritional characteristics of autotrophs alone could merely provide an accurate prediction on herbivore feeding behaviour (Paz et al. 2019; Pillans et al. 2004; Tomas et al. 2011).

It is worth noting that the linear model also showed that the macroalgal morphology may play a role in determining the herbivore feeding behaviour. The two most consumed species (*V. pachynema* and *C. prolifera*) are both filamentous macroalgae, and each of the other three tested filamentous macroalgae (*Ceratodictyon spongiosum*, *C. antennia*, and *Cladophora sericea*) recorded an RCR of at least $43 \text{ mg g}^{-1} \text{ day}^{-1}$ (Table 2). This may be because filamentous macroalgae have low thallus toughness and are easy to ingest. Thallus toughness has been reported as one of the primary morphological properties that could affect the feeding rates of herbivores marine invertebrate grazing herbivores, such as abalone, sea snails and amphipods (Goecker and Káll 2003; McShane et al., 1994; Pennings et al., 2000). Nevertheless, the articulated calcareous species *A. fragilissima* with tough thallus was not the least consumed macroalgae in this study. This result is in line with several previous studies where some marine herbivorous fish species were relatively insensitive to autotrophs toughness (Mantyka and Bellwood, 2007).

In terms of geography, it was observed that the generalist herbivore in this study generally consumed higher amount of macroalgae collected from the South China Sea, including the

two most consumed species, *V. pachynema* and *C. prolifera* (Figures 1 and 2). The herbivore was collected from the Straits of Malacca, which is one of the busiest straits in the world (Islam and Jorgensen 2018). On the other hand, the least consumed species *P. gymnospora* was collected from the Straits of Johor, which is located close to Ponggol estuary in Singapore where juvenile milkfish was reported not to be found (Bagarinao, 1999). Although milkfish has a wide geographical distribution, it has not been observed in several tropical estuaries in Singapore and North Borneo, which are close to the Straits of Johor and the South China Sea, respectively (Bagarinao, 1991, 1994). Presuming that macroalgae collected from the Straits of Malacca were native to the herbivore and those collected from the Straits of Johor and the South China Sea were non-native, our results are in line with some earlier reports, whereby certain herbivores preferentially consumed invasive autotrophs although both native and invasive autotrophs contained similar nutritional values (Parker and Hay 2005; Parker et al. 2012; Strong et al. 2009). However, it is important to mention that the macroalgal novelty recorded a low *F*-value ($F = 1.9$) (Table 3) in the present study, indicating that this factor had the least influence on herbivore consumption rates.

Based on the results of this study, we infer that the feeding behaviour of the generalist herbivore are largely determined by the nutritional characteristics and morphology of macroalgae, and possibly their novelty (Tables 2 and 3). Our results are consistent with a recent study conducted by Grutters et al. (2017), which utilized freshwater species as the study system. We believe that our findings lead to further insights into the dynamics that occur between marine autotrophs and herbivores based on important autotroph characteristics, including total nitrogen and phosphorus contents. Intensive research should be carried out to test the major hypotheses in invasion biology such as biotic resistance and enemy release hypotheses to ensure that the current ecosystems continue to have the ability to resist disturbances to their dynamics. We suggest future research to include appropriate autogenic controls to achieve more meaningful results. Additionally, we recommend the incorporation of geographic variation in future studies that aim to develop theories of ecology.

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