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Variable feeding behavior in *Orchestoidea tuberculata* (Nicolet 1849): Exploring the relative importance of macroalgal traits

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ABSTRACT

The feeding behavior of algal consumers inhabiting sandy beaches and the consequences of this behavior on their performance are poorly understood. Food quality has been shown to influence the food preference of algal consumers. However, food preference can often be altered or subordinated to habitat choice. This study analyzes the feeding behavior (preference and consumption rate), absorption efficiency and growth rates of the talitrid amphipod *Orchestoidea tuberculata* (Nicolet, 1849) in relation to the nutritional characteristics of two of the most common macroalgae stranded in the Chilean north-central region. Our experiments show that these amphipods prefer *Macrocystis integrifolia* over *Lessonia nigrescens* when presented with fresh fragments of both algae simultaneously. However, this preference did not match the performance of the amphipods when reared on diets of a single algal species: in that growth rates were not different. These results suggest that *M. integrifolia* is not a superior food item compared to *L. nigrescens*. The lower content of proteins and total organic matter found in *M. integrifolia* supports this interpretation. The preference of the amphipods for *L. nigrescens* over *M. integrifolia* when dry powdered algae of each species were provided (artificial food), suggested that some aspect of the physical structure of these two algae determined food preference. When the amphipods were maintained with each of the algal species in no choice experiments, they consumed 2 times more *M. integrifolia*, but showed higher absorption efficiency on *L. nigrescens*. These results suggest that food quantity and not absorption efficiency was used to compensate for the lower nutritional quality of *M. integrifolia*. The feeding behavior documented in this study differs significantly from that observed in populations of the same species inhabiting southern Chile, cautioning against generalizing results obtained even within a single species. Our results suggest that physical features rather than chemical characteristics of the food drive feeding preferences, including the potential (indirect) roles played by the fronds of these seaweeds as refuges against competition and desiccation.

1. Introduction

Although macroalgae do not grow on sandy beach habitats, algal wrack is a prominent trophic subsidy from nearby rocky shores and reefs (e.g. Dugan et al., 2003; Mann and Lazier, 1991; Polis et al., 1997). These subsidies become the most important food source for upper beach consumers, such as talitrid amphipods, tylid isopods, and tenebrionid and staphylinid insects (Brown and McLachlan, 1990; Dugan et al., 2003; Griffiths and Stenton-Dozey, 1981; Griffiths et al., 1983; Inglis, 1989; Jaramillo et al., 2006; Koop and Field, 1980). Few studies on this topic show considerable variation in the way macroalgae wrack (Duarte et al., 2008, 2010, 2011; Lastra et al., 2008; MacMillan and Quijon, 2012; Rodil et al., 2008). For example, Rodil et al. (2008) provide experimental evidence that upper shore amphipods inhabiting sandy beaches of Northern Spain do not use available algal species uniformly. These authors attributed differences primarily to changes in nutrient content and the microclimatic conditions generated by the stranded macroalgae. Similarly, Adin and Riera (2003) showed that in the northern coast of Brittany (France), the amphipod *Talitrus saltator* prefers to consume wrack of the brown alga *Fucus serratus*. Food selectivity has been also demonstrated by Lastra et al. (2008) for the talitrid amphipod *Megalorchestia corniculata* inhabiting sandy beaches along the Californian coast of USA. These authors related fitness of this amphipod to its food preference patterns in that the preferred macroalgae sustained the highest amphipod growth rates.

The nutritional content of macroalgae, including carbohydrates and proteins, has been shown to influence food preference, growth rate and fitness of primary consumers (e.g. Barile et al., 2004; Cruz-Rivera and Hay, 2003; Duarte et al., 2010; Jormalainen et al., 2001a; Mattson, 1980; Wakefield and Murray, 1998; White, 1985). For example, many studies show that herbivores feed selectively on macroalgae or algal

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parts of high nutritional value to fulfill their nutritional requirements. Thus, many researchers accept the close relationship between food preference and fitness of the organisms (Barile et al., 2004; Cruz-Rivera and Hay, 2003; Duarte et al., 2010, 2011; Fairhead et al., 2005; Pansch et al., 2008). In addition to nutritional quality, shape and toughness of macroalgae and the presence of chemical defenses (secondary metabolites) have been also showed to influence herbivores' food choices and fitness (Bolser and Hay, 1996; Jormalainen et al., 2005; Lyons and Scheibling, 2007; Lucas et al., 2000; Pavia and Toth, 2000; Pennings et al., 1998; Vergés et al., 2007).

Macroalgae also provide habitat and/or refuge for many marine invertebrates (Pavia et al., 1999; Rodil et al., 2008; Vandendriessche et al., 2006; Wakefield and Murray, 1998). The complex structure created by algal fronds provides refuge for invertebrates to avoid predation and harsh environmental conditions (e.g. desiccation, wave action) (e.g. Jormalainen et al., 2001a,b; Vandendriessche et al., 2006). To date, several studies have shown that structural complexity of macroalgae (e.g. levels of branching) significantly affects the distribution and abundance of invertebrates seeking refuge on them (e.g. Goecker and Kåll, 2003; Hacker and Steneck, 1990; Rodil et al., 2008). Thus, habitat (or refuge) may indeed be a more important fitness component than nutritional quality for macroalgal grazers (e.g. Jormalainen et al., 2001; Wakefield and Murray, 1998). Optimal feeding may be constrained as those characteristics (refuge) increase in relative relevance (e.g. Duffy and Hay, 1990; Jormalainen et al., 2001a,b, 2005).

The talitrid amphipod *Orchestoidea tuberculata* Nicolet is one of the most abundant species along Chilean sandy beaches (Duarte et al., 2008; Jaramillo et al., 2006; Kennedy et al., 2000). Duarte et al. (2010) showed that in south-central Chile (ca. 39°S), *O. tuberculata* feeds preferentially on stranded *Durvillaea antarctica* (Chamisso), the seaweed species highest in nutritional quality among local algal species; moreover, the highest growth rate of *O. tuberculata* also occurred when feeding on *D. antarctica.* At first glance, other sandy beaches of the Chilean coast might be expected to show a similar pattern for this species; this is, higher consumption rates should occur on macroalga with the highest nutritional value. However, the dominance of other macroalgae and the coexistence of amphipods with competitor in some beaches – such as those of north-central Chile (Jaramillo et al., 2003) – beg the following question: does wrack composition and coexistence of *O. tuberculata* with the tenebrionid beetle *Phalerisida maculata* Kulzer and the oniscid isopod *Tylos spinulosus* Dana (both prominent algal consumers) precludes the generality of earlier findings?

The aim of this study was to analyze growth rates of *O. tuberculata* feeding on two of the most common stranded macroalgae along sandy beaches of north-central Chile (*Macrocystis integrifolia* and *Lessonia nigrescens*; both present in similar amounts). We examined growth rates of this amphipod in relation to food preferences (using fresh and artificial algae) and consumption rates in no-choice experiments. The use of artificial (agar based) food removed the potential influence of characteristic such as morphology and toughness, allowing us to assess food preference based primarily on chemical quality (Hay et al., 1998). Subsequently, we related all these results to the chemical quality of the macroalgae (proteins, carbohydrates, organic content, and content of phlorotannins) and estimations of amphipod absorption rates. Finally, we discuss these results with respect to similar experiments conducted in other geographic areas in Chile and elsewhere.

2. Materials and methods

2.1. Collection of amphipods and macroalgae

Individuals of *O. tuberculata* were manually collected during the summer of 2009 from the intertidal zone of El Apolillado, a sandy beach located on the Coquimbo coast, north-central Chile (ca. 29° S). The amphipods were maintained in damp sand and transported to the laboratory, where they were held in plastic boxes covered with holes punched in the lids (for air exchange) over a layer of damp sand. All individuals were deprived of food for 48 h prior to the start of the experimental trials in order to avoid any influence of past diet on feeding behavior (e.g. Duarte et al., 2010; Pennings et al., 1993) or any influence of prior gut contents on the estimation of absorption efficiency Fresh *L. nigrescens* and *M. integrifolia* macroalgal fragments were collected from the rocky intertidal shore nearby El Apolillado. We used coolers to transport the macroalgae to the laboratory where they were immediately used in food preference experiments.

2.2. Analysis of food preference

2.2.1. Fresh food experiments

One pre-weighed allotment (~4 g) of each species of macroalgae and five experimental adult amphipods (8–10 mm of cephalothorax length) were placed in individual 10-cm diameter Petri dishes with holes punched on the lids (to allow air exchange). Dishes ($n = 5$) were then placed within a larger plastic box ($40 \times 30 \times 20$ cm) set with a moist sand layer of 5 cm, to maintain constant humidity. The experiments run for 24 h in a temperature-controlled environmental chamber at 20 °C (average temperature in the study area, Di Castri and Hajek, 1976 and personal observations) with a natural light/dark cycle. Each of the five Petri dish replicates was associated with a control dish which contained only macroalgae; the variation recorded in these control dishes was used to estimate potential changes in weight unrelated to feeding by amphipods (c.f. Roa, 1992).

After 24 h, the amphipods were carefully removed from the Petri dishes and the fragments of experimental and control macroalgae were separately blotted and reweighed to determine mass changes during the experiment. To remove variation in mass that was not related to feeding, we subtracted the change in control replicates from the change in each experimental macroalga piece (see, Roa, 1992; Silva et al., 2004). Consumption rates were estimated as follow:

$$\text{Consumption rate} = (E_{\text{initial}} - E_{\text{final}}) - (C_{\text{initial}} - C_{\text{final}});$$

where E and C denote Experimental and Control algal weights, respectively. Rates were standardized as algal consumption per day per individual.

2.2.2. Artificial food experiments

Agar pellets with algal tissue were prepared for each macroalgal species following the methodology proposed by Hay et al. (1994). Fresh pieces of each macroalgae were dried with silica to attain a constant weight and then ground with a mortar and pestle into a fine, homogeneous powder. Before the analyses, the silica was carefully removed with a brush. The ground tissue was mixed with the agar solution to produce a final ground algal concentration of 0.15 g for each gram of food. This mix was immediately emptied into a plastic cuvette and subdivided into receptacles measuring $15 \times 15 \times 15$ mm. Fragments averaging 1 g for each species of macroalgae were offered simultaneously to the amphipods following the same protocol described for fresh algae. Rates were standardized to algal consumption per day per individual.

2.3. Food consumption and absorption rates

Consumption rates were evaluated separately for each algal species (i.e. a no-choice experiment). Five replicates and associated controls were used for each experiment following the procedure described above. The results were again standardized as algal consumption per day per individual.

Absorption efficiency was measured following the methods described by Conover (1966), which are based on the relationship between organic and inorganic matter values of ingested food and fecal material. This method assumes that absorption processes affect only the organic fraction of the food. The absorption efficiency was calculated as follows:

$$AE = \left[(F' - E')/(1 - E')\,F'\right] * 100,$$

where: AE = Absorption Efficiency expressed as a percentage value, F′ = Organic matter proportion in food and E′ = Organic matter proportion in feces.

Five amphipods were maintained in Petri dishes with fragments of either *L. nigrescens* or *M. integrifolia* (n = 5) in order to obtain fecal pellets. The experimental dishes were maintained in conditions similar to those described for the consumption experiments. Every 12 h, feces were collected and frozen until analysis, and all fragments of macroalgae were removed and replaced with fresh fragments. The experiment ran for four days. To determine percentage of organic matter, feces were dried at 60 °C for 2 days, incinerated in a muffle furnace at 500 °C for 4 h and then reweighed. A similar methodology was used to determine the percentage of organic matter in each of the two macroalgal species studied.

2.4. Growth rate

Individual amphipods (~200–300 mg wet weight) were separately placed with a fragment of either *L. nigrescens* or *M. integrifolia* in a Petri dish similar to those used in the experiments described above (n = 12). Algal fragments were replaced daily with fresh pieces and the experiments ran for 15 days. At the beginning and at the end of the experiments, each amphipod was gently blotted and then weighed on an analytical balance. Amphipod growth rates were calculated as the difference between final and initial weights. Rates were standardized as amphipod growth rate per day.

2.5. Food and chemical analyses

To estimate differences in nutritional quality we measured the concentration of proteins, carbohydrates and total organic matter in algal tissues. To estimate levels of chemical defenses, we estimated the concentration of phlorotannins. Each of the analyses was replicated (from three independent samples of algal tissue), using dry and finely ground material.

To quantify protein content of the macroalgae we used the bicinchoninic acid method (BCA) from Pierce (BCA Protein Assay Kit) using bovine serum albumin as a standard. Samples were mixed with SDS (0.5%), sonicated for 1.5 min and centrifuged at 5500 rpm for 35 min. The supernatant was incubated with BCA at 45 °C for 30 min. Protein concentration was determined colorimetrically by measuring the absorbance at 562 nm.

Total carbohydrates were determined on weighed samples (~10 mg) of dry algae tissue, using the phenol-sulphuric acid method of Dubois et al. (1956), after extraction by boiling in 5% trichloroacetic acid (TCA) containing 0.1% silver sulfate (Barnes and Heath, 1966). Carbohydrate was estimated by reading absorbance at 490 nm, using glucose as a standard.

To determine the total content of phlorotannins we used the technique from Folin–Ciocalteu (modified by Nurmi et al., 1996) using Phloroglucinol as the standard. We used the term phlorotannins because brown macroalgae are not known to contain other polyphenols (Targett and Arnold, 1998).

2.6. Data analysis

Food preference experiments with fresh and artificial food were separately assessed using paired *t*-test (Zar, 1999). Consumption rates, absorption efficiency and growth of *O. tuberculata* were compared using unpaired *t*-tests (Zar, 1999). An unpaired *t*-test was also used to evaluate the differences in the nutritional characteristics and phlorotannin content of the different algae species (Zar, 1999). The assumptions of normality and homocedasticity of the *t*-test were evaluated with the Kolmogorov–Smirnov and Bartlett tests, respectively. All statistical analyses were performed using the Data Analysis Program System Statistica 7.0.

3. Results

The results of food preference (i.e. choice) experiments conducted with fresh macroalgae showed that *O. tuberculata* consumed ~23.3 times more *M. integrifolia* than *L. nigrescens* (p = 0.01, paired *t*-test, Fig. 1a). In contrast, amphipods consumed ~7.1 times more artificial *L. nigrescens* than *M. integrifolia* (p = 0.01, paired *t*-test, Fig. 1b). In no choice experiments conducted simultaneously, consumption rates were ~2.2 times higher on *M. integrifolia* than on *L. nigrescens* (p = 0.02, unpaired *t*-test, Fig. 1c).

Protein contents were ~1.2 times higher in *L. nigrescens* than in *M. integrifolia* (p = 0.03, unpaired *t*-test, Fig. 2a). No significant differences were observed in the carbohydrate content between both macroalgae (p = 0.07, unpaired *t*-test, Fig. 2b). Organic matter contents were ~1.4 times higher in *L. nigrescens* than in *M. integrifolia*, respectively (p = 0.03, unpaired *t*-test, Fig. 2a,c). Similarly, the phlorotannin

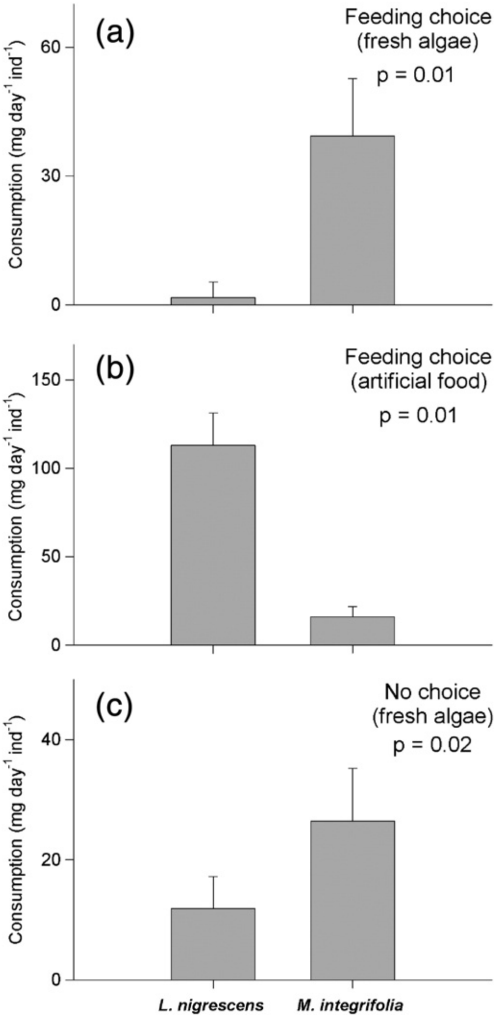

Fig. 1. Feeding preference of *O. tuberculata* between *L. nigrescens* and *M. integrifolia* based on fresh alga (a), or artificial food (b) and consumption rate on each alga individually (no choice) (c). The bars correspond to means (+1 sd). p values from paired *t*-test (a and b) and unpaired *t*-test (c) comparing both species are given.

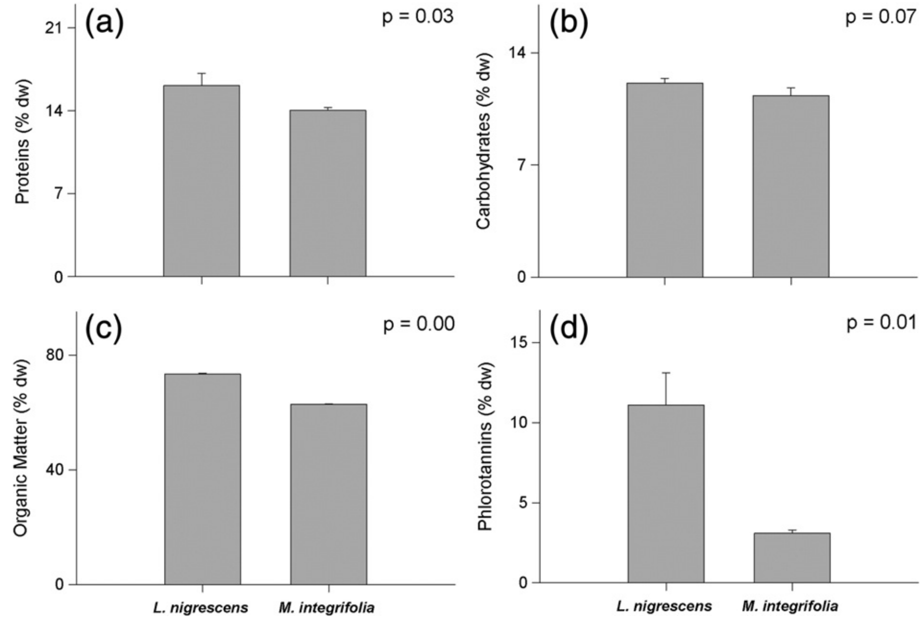

Fig. 2. Content of proteins (a), carbohydrates (b), total organic matter (c) and phlorotannins (d) in *L. nigrescens* and *M. integrifolia*. The bars correspond to means of % dry weight (+1 sd). p values from unpaired *t*-test comparing both species are given.

content estimated in the tissues of *L. nigrescens* was ~3.5 times higher than that found in *M. integrifolia* ($p = 0.01$, unpaired *t*-test, Fig. 2d).

O. tuberculata had an absorption efficiency of 49% while feeding on *L. nigrescens*, ~3.5 times higher than the efficiency observed on *M. integrifolia* ($p = 0.01$, unpaired *t*-test, Fig. 3). The average growth rate of *O. tuberculata* did not differ significantly between the two food items ($p = 0.66$, unpaired *t*-test, Fig. 4).

4. Discussion

Talitrid amphipods are among the most common organisms inhabiting the upper shore levels of exposed sandy beaches (Brown and McLachlan, 1990; McLachlan and Jaramillo, 1995). Because these organisms rely primarily on stranded algal wrack for food and habitat resources (Duarte et al., 2011; Dugan et al., 2004; Olabarria et al., 2007; Rodil et al., 2008) it is reasonable to expect strong responses to the distinctive morphological and chemical features of these seaweeds. Previous studies have shown that the highest growth rates of *O. tuberculata* and others talitrids occur when amphipods feed on their preferred algal species or algal parts (Duarte et al., 2010, 2011; Lastra et al., 2008). These studies suggest that these algae were indeed the food items with the highest nutritional quality for the amphipods (see Duarte et al., 2010). In light of these studies, our findings are clearly unexpected as they show a mismatch between alga quality and feeding preferences. Even when the nutritional quality of *L. nigrescens* was significantly higher than that of *M. integrifolia*, the feeding rates of *O. tuberculata* were consistently higher on *M. integrifolia*, both in choice and no choice experiments.

Protein content is widely regarded as an appropriate proxy of the nutritional quality of plants and macroalgae (e.g. Barile et al., 2004; Cruz-Rivera and Hay, 2003). Several studies conducted with amphipods (Cruz-Rivera and Hay, 2000a; Jimenez et al., 1996), gastropods (Barile et al., 2004; Yates and Peckol, 1993), and echinoderms (González et al., 2008), show that these herbivores feed selectively upon macrophytes with the highest protein content. In contrast, our study suggests that nutritional quality is not the most important factor in determining food preferences in *O. tuberculata*. *M. integrifolia*, the preferred food item, had lower protein and organic matter contents than *L. nigrescens*. Moreover, the amphipod's absorption efficiency of *L. nigrescens* was significantly lower than that observed for *M. integrifolia*. Recalling that the content of carbohydrates which has been also shown to influence food preference (see Duarte et al., 2011; Jormalainen et al., 2001a,b), but did not differ significantly between both algal species. Consequently, this algal feature cannot explain the results of our feeding preference

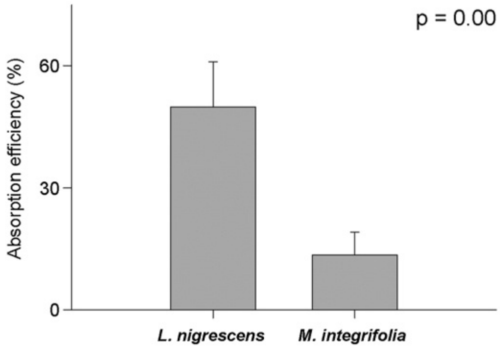

Fig. 3. Absorption efficiency (%) of *O. tuberculata* on *L. nigrescens* and *M. integrifolia*. The bars correspond to means (+1 sd). p value from unpaired *t*-test comparing both species is given.

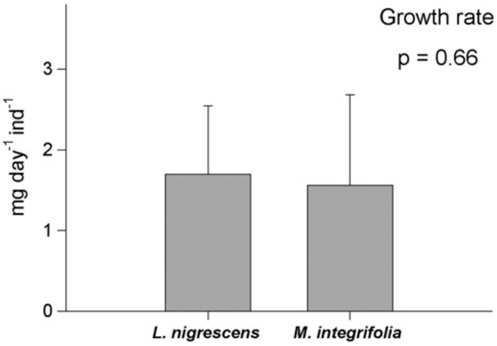

Fig. 4. Growth rate of *O. tuberculata* on *L. nigrescens* and *M. integrifolia*. The bars correspond to means (+1 sd). p value from unpaired *t*-test comparing both species is given.

experiments. Nonetheless, we acknowledge that our study estimated only the content of soluble carbohydrates (and not insoluble carbohydrates), which could influence the feeding preferences of *O. tuberculata* (see Jormalainen et al., 2001a,b).

Although the importance of food quality in the growth and overall fitness of herbivores is undisputable, food preference may in some cases (such as ours) couple from the nutritional value of the macroalgae. Other characteristics of the algae are therefore expected to influence the selectivity of their consumers (e.g. Barile et al., 2004; Cruz-Rivera and Hay, 2003), among them physical features such as shape and toughness of blades and the presence of chemical defenses (Barile et al., 2004; Cronin and Hay, 1996; Cruz-Rivera and Hay, 2003; Littler and Littler, 1980; Pennings et al., 1998, 2000; Van Alstyne et al., 1999). Our results suggest that amphipod feeding preferences were likely influenced by the physical traits of the macroalgae. The strong preference for artificial *L. nigrescens* (in contrast to the low preference for fresh tissues of this macroalgae), suggests that the physical structure of *L. nigrescens* somehow influences amphipod consumption. Seaweed shape and toughness have been shown to be important drivers of herbivore diet choices by influencing their ability to manipulate, remove, or ingest algal tissue (e.g., Fairhead et al., 2005; Pennings et al., 1998; Taylor et al., 2002). For example, Pennings et al. (1998) found that plant toughness was the most important factor in determining preference patterns in the salt marsh crab *Armases cinereum*. Similarly, Kennish (1996) concluded that the food handling capacity was the most important factor in feeding preference by the herbivorous crab *Grapsus albolineatus*. The structure (toughness and shape) of *L. nigrescens* blades likely discourage grazing by herbivores, as reflected in the preferences of *O. tuberculata* in experiments conducted with fresh macroalgae.

The lack of preference for macroalgae of high nutrient quality can be also explained by the existence of chemical deterrents such as phlorotannins in algal tissue. These components have been shown to deter feeding by a broad array of consumers, including amphipods, gastropods, isopods and fishes (Boettcher and Targett, 1993; Hay, 1996; Pavia and Toth, 2000; Poore, 1994; Steinberg and Van Altena, 1992; Targett and Arnold, 1998), although in some cases these compounds do not necessarily inhibit algal consumption (e.g. Macaya and Thiel, 2008; Rothäusler et al., 2005; Van Alstyne et al., 2001). As expected, the concentrations of phlorotannins were higher in *L. nigrescens* tissues, the least preferred algae. However, choice experiments conducted with artificial food (where the chemical characteristics were not altered), showed the opposite outcome. Hence, our results do not support the hypothesis of palatability differences resulting from seaweed chemical defense differences, as previously demonstrated for other seaweed species (Duarte et al., 2010, 2011). Our results instead support a predominant role for physical traits (likely shape and toughness) as the most plausible explanation for the feeding preferences of *O. tuberculata* in sandy beaches of north-central Chile.

As previously shown (see Duarte et al., 2010, 2011), talitrid amphipods feed on detached macroalgae (wrack) that may be fresh or undergoing decomposition for hours or days. The chemical characteristics of these seaweeds (e.g. chemical defenses and nutritional quality) may differ from fresh individual's macroalgae and, therefore, their palatability to herbivores may also differ (Rothäusler et al., 2005, Rothäusler and Thiel 2006). Several authors have suggested that talitrid amphipods prefer fresh over decomposing macroalgal tissues (e.g., Colombini et al., 2000; Griffiths and Stenton-Dozey, 1981; Inglis, 1989; Jaramillo et al., 2006; Macmillan and Quijon, 2012). However, more studies evaluating temporal changes in chemical characteristics of stranded macroalgae and their influence on feeding preferences and performance are necessary to better understand feeding behavior of this species and other talitrid amphipods.

Typically, food quality corresponds to grazer's growth and feeding rates (Cruz-Rivera and Hay, 2000b; Hay, 1996; Jormalainen et al., 2001a). However, some species exhibit "compensatory feeding", defined as an increase in their rate of consumption of less nutritious food in order to achieve optimal growth. This strategy may explain the mismatch between food preference and growth rate (Cruz-Rivera and Hay, 2000a). Our results suggest that palatability differences (likely linked to blade toughness) may drive compensatory feeding to balance the negative effects of the low nutritional quality of *M. integrifolia*. Although some grazers increase ingestion rates to compensate for suboptimal food quality items, this phenomenon does not necessarily operates in the same way among different species, or even among populations of the same species. Duarte et al. (2011) documented feeding compensation in *O. tuberculata* individuals feeding on different tissues of *D. antarctica*. However, the same authors did not find compensation while studying diet choice of the same species feeding on three different species of macroalgae (Duarte et al., 2010). The specific factors behind these behavioral differences are unknown but previous studies have proposed physical and physiological constraints as potential explanations (see Cruz-Rivera and Hay, 2001 for details). Furthermore, compensation for lower quality food has also been shown to be achieved by increasing absorption efficiency (Simpson and Simpson, 1990), but this was not the case in our study.

Herbivore food preferences may become uncoupled with the nutritional value of algae not only due to shape, toughness or chemical defenses. External factors such as predation and competition may often constrain optimal feeding and fitness (e.g. Duffy and Hay, 1990; Jormalainen et al., 2001a,b, 2005). Predation avoidance, for example, has been already suggested as a cause or partial cause for macroalgal preference in other talitrid amphipods (e.g., Olabarria et al., 2007; Rodil et al., 2008). We do not have information on feeding rates of shorebird or other predators on upper shore amphipods from the Chilean coast; however, based on body shape alone, we can hypothesize that *M. integrifolia* offers a much better refuge than *L nigrescens*. A similar argument can be applied to an alternative but related characteristic of stranded seaweeds: the provision of refuge against desiccation (see Colombini et al., 2000; Inglis, 1989; Jędrzejczak, 2002a,b; Olabarria et al., 2007). Due to its morphology, *M. integrifolia* is likely to offer fuller shade and better humidity retention than *L nigrescens*. Protection against desiccation becomes most critical on stranded seaweeds closer to the upper shore levels of a coastal range characterized by a very low and irregular rainfall (Di Castri and Hajek, 1976). Consequently, obvious differences in shape as those observed between *M. integrifolia* and *L. nigrescens* may become more important than the food quality of their tissues (see Jormalainen et al., 2001a,b; Olabarria et al., 2007).

5. Conclusions and further directions

Overall, our study shows that the mismatch between amphipod feeding preferences and the nutritional quality of *M. integrifolia* and *L nigrescens* does not affect the growth rates of populations fed with these common macroalgae. We also provide evidence that compensatory feeding allows this amphipod to fulfill its nutritional requirements in order to maintain growth. We hypothesize that in this case physical features (shape and toughness) of macroalgae are more important than their chemical characteristics. In addition, the feeding behavior documented in this study differs from that observed in other populations of *O. tuberculata*. This calls for caution when conclusions arise from snapshot studies and not from systematic analyses carried out along relatively large geographic regions, such as the one spanned by *O. tuberculata* along the Chilean coast (ca. 28–42°S). These studies should attempt to identify the specific mechanisms (e.g. physiological adaptations) that drive some populations to compensate for the low nutritional quality of various stranded seaweed species. External factors that constrain or alter optimal feeding selection likely play a role as well on the interactions between amphipods and their predators and competitors.

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