Journal of Sea Research 87 (2014) 1–7

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

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

Cristian Duarte [a,*], Karin Acuña [b], Jorge M. Navarro [b], Iván Gómez [b], Eduardo Jaramillo [c], Pedro Quijón [d]

[a] *Departamento de Ecología y Biodiversidad, Facultad de Ecología y Recursos Naturales, Universidad Andres Bello, Santiago, Chile*
[b] *Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile*
[c] *Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile*
[d] *Department of Biology, University of Prince Edward Island, 550 University Avenue, Charlottetown, Prince Edward Island, C1A 4P3, Canada*

ARTICLE INFO

Article history:
Received 10 June 2013
Received in revised form 22 November 2013
Accepted 2 December 2013
Available online 12 December 2013

Keyword:
Food preference
Macroalgae
Food quality
Orchestoidea tuberculata
Sandy beaches

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

---

[*] Corresponding author.
E-mail address: cristian.duarte@unab.cl (C. Duarte).

1385-1101/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.seares.2013.12.003

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 × 30 × 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 × 15 × 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