

Local feeding behavioural responses to food availability of the amphipod *Orchestoidea tuberculata*

Respuestas locales de comportamiento a la disponibilidad de comida del anfípodo *Orchestoidea tuberculata*

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Abstract. The main food sources in sandy beaches are stranded animals and seaweeds. In species with low dispersal potential or reduced mobility, it is expected that local adaptations or plastic responses arise to confront these environments and maximize fitness. *Orchestoidea tuberculata* is a common semi-terrestrial talitrid amphipod in Chilean sandy beaches and shows a very limited dispersal, with direct developmental mode and reduced mobility at the adult stage. *O. tuberculata* feeds on stranded seaweeds and organic material from animal origin during low tides. The effects of different diets on food preference, growth rate and survival of *O. tuberculata* individuals from two sandy beaches with different types of food availability were evaluated: Punta Hualpén with high abundances of stranded seaweed and animals, and Lenga showing low levels of stranded seaweeds, and high levels of food of animal origin. To evaluate potential local responses in feeding behavior, individuals of *O. tuberculata* from both localities were fed with algae (*Durvillaea incrvata*) and animal carcasses (*Emerita analoga*) disposed in separate and mixed diets (*D. incrvata* + *E. analoga*). Results showed that food preference in *O. tuberculata* varies between individuals from the two sites. Individuals tended to show the highest performances with the diet composed of the most common dietary item available in their site of origin (algal or animal). These results may indicate the existence of potential local adaptations or feeding behavior plasticity in *O. tuberculata* as responses to the spatial variability of food availability observed in sandy beach ecosystems.

Key words: Talitrid amphipod, sandy beach, food preference, stranded algae, Pacific Ocean

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INTRODUCTION

Food availability strongly drives ecological and evolutionary responses at different levels, from individuals to ecosystems. This is more accentuated in habitats with high variability in food provision, and where food is mainly imported from other sites (Claudino *et al.* 2015, Armengol *et al.* 2019). In particular, sandy beaches show low *in situ* primary productivity, and stranded organic material of algal and animal origin constitutes the main food source sustaining local biodiversity (Duarte *et al.* 2008, 2010a, b; Schlacher & Hartwig 2013, Schlacher *et al.* 2017).

Limitation and unpredictability of food availability in sandy beach ecosystems, imposes important selective pressure on species inhabiting these habitats. Consumers must confront different types of preys or items differing for example in abundance, energy content, nutritional value or handling time. These local characteristics of habitats have a direct impact on resident populations (Dufey 2007, Duarte *et al.* 2009, 2010b). Dufey (2007) showed that populations of the amphipod *Orchestoidea tuberculata* Nicolet, 1849 in sites with reduced availability of stranded algae have lower body sizes, fecundity and abundances



compared to sites where the amount of available organic matter is constantly higher. Under this scenario, feeding and food choice behavior play an important role for species inhabiting sandy beaches, in order to optimize energy profit and maximize growth, fecundity and survival (Cruz-Rivera & Hay 2000b, Incera *et al.* 2006, Dufey 2007, Bergamino *et al.* 2011, Duarte *et al.* 2011).

The relationship between food availability and food choice in species inhabiting sandy beaches has been scarcely studied (Pearson & Rosenberg 1987). Veloso *et al.* (2012) observed that the diet of the amphipod *Atlantorchoestoidea brasiliensis* (Dana, 1853) includes macroalgae and animals, although food selection seems to be based on its nutritional quality. In addition, spatial variability of food provision may trigger local adaptations in terms of feeding behavior and food choice. Bell & Sotka (2012) found that the food preference in the isopod *Idotea balthica* (Pallas, 1772) varies among localities (northern *vs.* southern populations). While northern populations preferred the macroalgae *Fucus vesiculosus* Linnaeus, southern populations had a higher preference for the macroalgae *Ulva linza* Linnaeus, suggesting local behavioral responses in the food preference of this species. Under this spatial variability of amount and type of food availability, it is expected that different responses arise in the feeding behavior of organisms inhabiting sandy beaches.

Talitrid amphipods are among the most abundant invertebrates on the upper levels of sandy beaches around the world (Dugan *et al.* 2003, Pérez-Schultheiss 2010). They are considered the main consumers and responsible for the organic matter recycling in these systems, since they are pioneers in the colonization of stranded macroalgae and animals, feeding on them with a high consumption rate (Duarte *et al.* 2010a, b; Veloso *et al.* 2012). Some studies have examined intraspecific differences in diet selection within talitrids (Duarte *et al.* 2014 and references therein). Duarte *et al.* (2008) found that *O. tuberculata* differs in food preferences among different algal items (*Durvillaea incurvata*, *Lessonia spicata* and *Macrocystis pyrifera*), and between ontogenetic stages (juveniles and adults). Interestingly, talitrid amphipods not only consume stranded algae, but also carcasses of stranded animals, and few studies have compared the feeding behavior and food choice when both algal and animal items are present.

Orchestoidea tuberculata is one of the dominant scavenger species in the upper intertidal of exposed sandy Chilean beaches (Baessolo *et al.* 2010, Pérez-Schultheiss 2010). Montecinos *et al.* (2021) found evidence of outbreeding depression in *O. tuberculata*, suggesting that its poor dispersion capacity and spatial variability of sandy beaches, impose strong local selective pressures on organisms that trigger local adaptive responses. This species has the ability to use different feeding strategies that allow the exploitation of different types of food, which can be advantageous in sandy beach habitats

where food availability can be limited for long periods of time (Hermosilla 2007, Duarte *et al.* 2008, Duarte *et al.* 2011). Although *O. tuberculata* commonly feed on stranded seaweeds, individuals also use organic remains from marine invertebrates and stranded fishes (pers. obs.). Thus, *O. tuberculata* could be considered as a scavenger species with a wide diet range. Despite that, most of the previous research have used seaweeds as the main dietary item to evaluate the feeding behavior of this species, and no studies have been carried out using different food types (*i.e.*, from algal and animal origin).

In the present work, responses in food choice behavior were evaluated in individuals from beaches that differ in food type availability: Punta Hualpén has high levels of algae food availability (stranded seaweed), and Lenga showing high levels of food from animal origin and low levels of food from algal origin (Dufey 2007). It is hypothesized that food choice behavior and responses on fitness traits of *O. tuberculata* differ between individuals from the two sampling localities according to the type of food available at each site. Thus, it is expected that individuals from Punta Hualpén prefer algae and those from Lenga prefer animal flesh.

MATERIALS AND METHODS

Individuals of *Orchestoidea tuberculata* were collected in April 2015, in two sandy beaches located in Biobío region, Chile: Punta Hualpén (36°48'30"S; 73°10'18"W), a place with high availability of stranded algae, and Lenga (36°46'01"S; 73°10'17"W) that has high levels of food from animal origin (fish, crustaceans and mollusk carcasses) and low availability of stranded algae (Dufey 2007). Specimens were collected directly by hand from the two beaches and transferred into perforated plastic boxes with wet sand to Estación Costera Abate Juan Ignacio Molina, Universidad Católica de la Santísima Concepción. Simultaneously, recent stranded fronds (*i.e.*, with no appearance of decaying stage), of the macroalgae *D. incurvata* (Suhr) Macaya and dead individuals of the decapod *Emerita analoga* (Stimpson, 1857) were collected from Punta Hualpén beach. In the laboratory, individuals of *O. tuberculata*, between 7-14 mm of body size, were selected and kept in plastic boxes (50 x 50 cm in size), with a layer of wet sand of *ca.* 4 cm, which was moistened with seawater twice a day, using a manual sprinkler. Specimens were acclimated for two days before experiments, with constant temperature and *ad libitum* food. Individuals of different localities were fed according to the type of food available in the locality where they came from (*D. incurvata* for Punta Hualpén and *E. analoga* for Lenga individuals). To avoid the interference of epifauna on the experiments, we conducted a visual inspection of the algae used as food source, and then rinsed the algae with filtered seawater to reduce the presence of epibionts. Individuals of *O. tuberculata* were haphazardly arranged in the different experimental treatments to avoid body size biases.

FOOD CONSUMPTION

Food preference of *O. tuberculata* exposed to different dietary treatments was evaluated in individuals collected from the two localities (Punta Hualpén and Lenga). Diets were offered as either single-species (monodiets) or mixed diets, and consumption rate, growth rate and survival were recorded. Five individuals were maintained in plastic containers (50 x 50 cm) and assigned to one of the following dietary treatments: (1) monodiet of *D. incurvata* (2 g wet weight, ww), (2) monodiet of *E. analoga* (2 g ww), and (3) mixed diet consisting of *D. incurvata* + *E. analoga* (1 g ww each). All boxes were provided with 4 cm of wet sand as natural substrata. A control treatment considering only the dietary items without the presence of the experimental animals was added to estimate losses of food weight by desiccation or degradation during experimental time. Ten replicates per treatments were run, and the position of the plastic boxes was changed randomly every two days to avoid any confounding factor.

Food consumption was calculated using the following formula:

$$(\text{IFW with consumers} - \text{FFW with consumers}) - (\text{IFW without consumers} - \text{FFW without consumers})$$

Where, IFW: Initial food weight; FFW: Final food weight.

Every two days the experimental containers were examined, the consumption of *O. tuberculata* was estimated for each plastic box, and the dietary treatments were replaced according to the initial conditions. This experiment lasted three weeks.

GROWTH RATE AND SURVIVAL ACCORDING TO DIET TYPE AND LOCALITY

To evaluate growth rate and survival of *O. tuberculata* from the two localities (Lenga and Punta Hualpén), individuals were exposed to the three treatments described above. One individual of *O. tuberculata* was placed in a distinct plastic box provided with 4 cm of wet sand as natural substrata and cultivated using the treatments for six weeks. The food was replaced every two days and the position of the plastic boxes changed randomly to avoid any confounding factor. At the beginning and the end of the experiments, individuals were weighted using an analytical balance (0.1 mg sensitivity), and the growth rate was estimated ($\text{mg ind}^{-1} \text{ day}^{-1}$). Survival of *O. tuberculata* was checked and recorded daily (number of days of survival). Ten replicates per treatments were run for six weeks.

DATA ANALYSIS

Responses of *O. tuberculata* to different treatments were compared using two-way ANOVAs, considering two experimental factors: (1) Locality, with two treatments (Punta Hualpén y Lenga); and (2) Diet, with three

treatments (*D. incurvata* monodiet, *E. analoga* monodiet and mixed diet of *D. incurvata* + *E. analoga*). Food preference, growth rate and survival were analysed separately. The assumption of normality and homogeneity of variance was evaluated using Shapiro-Wilk and Cochran tests, respectively. Tukey's post hoc tests were performed when significant differences were detected in the ANOVAs.

RESULTS AND DISCUSSION

FOOD CONSUMPTION

Consumption rate of *O. tuberculata* differed among treatments (Fig. 1A), with a significant interaction between locality and diet factors (ANOVA: Locality x Diet: $F_{2,54} = 18.2$; $P = 0.001$). Tukey *a posteriori* test showed that the significant lowest rates were observed in individuals from Lenga fed with *D. incurvata* (11.07 mg day $^{-1}$ ind $^{-1}$; $P = 0.05$) and the highest in specimens from Punta Hualpén fed with a monodiet of *D. incurvata* and the mixed diet (66.2 mg day $^{-1}$ ind $^{-1}$; $P = 0.001$); no significant differences were detected between both diets ($P = 0.05$). Broadly, individuals from Punta Hualpén showed the highest consumption rates in diets with the presence of *E. analoga*, whilst individuals from Lenga showed the highest values in diets containing *D. incurvata* (Fig. 1A).

GROWTH RATE AND SURVIVORSHIP

Locality of origin and diet significantly affected growth rate of *O. tuberculata* (ANOVA: Locality x Diet: $F_{2,54} = 12.5$; $P = 0.001$; Fig. 1B). Individuals from Lenga fed with *D. incurvata* showed the lowest mean growth, while the highest was observed in individuals from Punta Hualpén fed with the mixed diet (Tukey post hoc test: $P = 0.001$). As general trend, individuals from Punta Hualpén grew rapidly when fed with *D. incurvata* incorporated as monodiet or in a mixed diet (Fig. 1B). In contrast, individuals from Lenga showed the faster growth rates with *E. analoga* diet (Fig. 1B).

Mean survival time varied between 17.6 and 41.7 days with a significant interaction between locality and diet factors (ANOVA: Locality x Diet: $F_{2,54} = 3.6$; $P = 0.03$; Fig. 1C). Similar to the general pattern observed for growth rate, individuals from Lenga showed the highest long-term survival when fed with *E. analoga* as mono or mixed diet. Individuals from Punta Hualpén showed the highest survival when they were fed with *D. incurvata* as mono or mixed diet (Fig. 1C).

The findings of the present study showed that *O. tuberculata* can respond to local conditions of food availability. Thus, food consumption, growth rate and survival were related to the most abundant type of food (algal or animal source) found in their localities of origin.

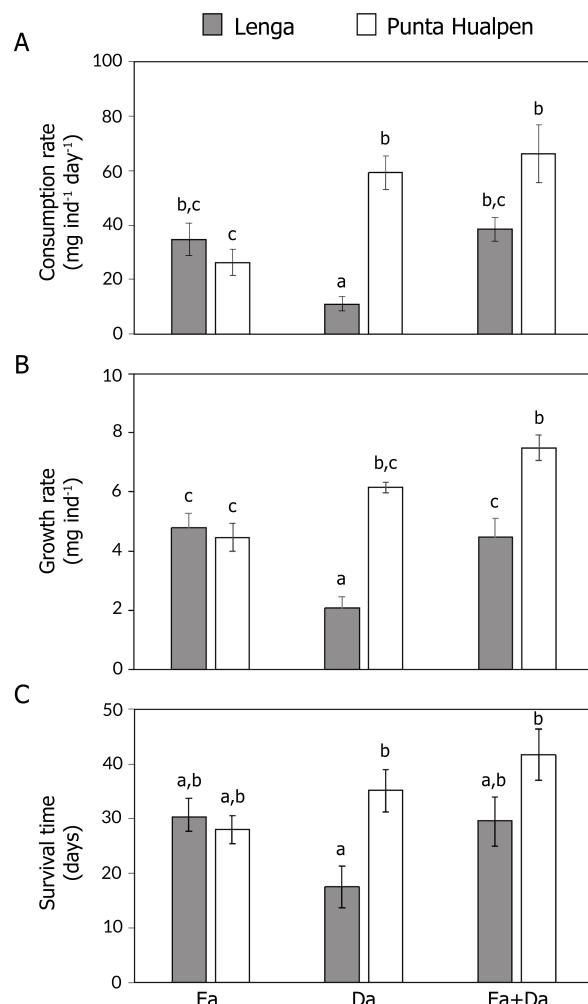


Figure 1. Consumption rate (A), growth rate (B) and survival (C) of *Orchestoidea tuberculata* individuals from Punta Hualpén and Lenga exposed to three different dietary treatments: monodiet of *Emerita analoga* (Ea), monodiet of *Durvillaea incurvata* (Da) and mixed diet of Ea+Da. Vertical lines on bars correspond to ± 1 SE / Tasa de consumo (A), tasa de crecimiento (B) y supervivencia (C) de individuos de *Orchestoidea tuberculata* de Punta Hualpén y Lenga bajo tres tratamientos de dietas: monodieta de *Emerita analoga* (Ea), monodieta de *Durvillaea incurvata* (Da) y dieta mixta de Ea+Da. Las barras verticales indican ± 1 EE

In addition, individuals fed with a mixed diet (seaweed + animal) showed no significant differences in growth and survival relative to those fed by the monodiet with the highest performance. The low potential dispersal of *O. tuberculata* and high spatial variability of food amount and type observed in their natural habitats, would promote local adaptive responses in the feeding behavior and consequently on the fitness of this species.

Amphipods have a wide range of food habits (Buza-Jacobucci *et al.* 2014, Cruz-Rivera & Hay 2000b), varying throughout the ontogeny (Ocampo 2014, Cruz-Rivera & Hay 2000a), between sexes and habitats (Navarro-Barranco *et al.* 2013). According to several studies, feeding behavior in this group is not necessarily related to nutritional food quality. For many amphipods stranded algae are used as shelter, providing protection against predators and desiccation; thus, food choice could respond not only to algal nutritional characteristics but also to the security that stranded algae provide as refuge (Rezende *et al.* 2013, Duarte *et al.* 2014). In addition, Duarte *et al.*

(2014) found that *O. tuberculata* prefers to consume certain algae regardless of their nutritional value, which could be explained by differences in physical characteristics of the algae that may facilitate or complicate its consumption, and the fact that some algal species are more suited to be used as shelter. Although several factors may affect feeding behavior, we hypothesise that the differences in food consumption of *O. tuberculata* observed between localities in our study, and the effects on trait fitness, could be explained by the higher abundance of stranded seaweed in Punta Hualpén in comparison to Lenga, which would also be used as refuge in Punta Hualpén (pers. obs.). Thus, different selective pressures could be operating on both populations: the benefits for survival that offer stranded algae as refuge in Punta Hualpén, which are also used as food, and the higher abundance of animal carcasses in comparison to the scarce presence of stranded algae in Lenga. Additional laboratory and field experiments are needed to test this hypothesis.

It is well-known that animal matter is more easily assimilated than vegetal/algal matter, and in particular, aquatic plants and seaweeds as food impose important challenges for herbivorous species (Mann 1998). In this context, marine herbivorous invertebrates have developed behavioral and physiological strategies to meet their nutritional requirements when feeding on low protein diets such as seaweeds (e.g., Stachowicz & Hay 1996, Cruz-Rivera & Hay 2001, Benítez *et al.* 2016). Experimental works have shown that *O. tuberculata* may compensate for the low nutritional quality and absorption rate of some algal items by increasing the amount of food eaten (Duarte *et al.* 2014). In addition, at a molecular scale, it has been demonstrated that herbivorous marine invertebrates may degrade seaweed polysaccharides to obtain carbohydrates using gastrointestinal enzymes or through fermentation by intestinal bacteria (Erasmus *et al.* 1997, Sawabe *et al.* 2003). Thus, it could be hypothesized that the differences observed in food consumption of *O. tuberculata* from the two localities, could be associated to ecological (*i.e.*, refuge) and physiological compensations (*i.e.*, differences in the nutritional values) that need more investigation.

The effect of the diet on fitness traits has been evaluated in some amphipods inhabiting sandy beaches. Cruz-Rivera & Hay (2000a) evaluated the fitness response of amphipod species with different mobility capacities and fed with different diet types. Results showed that the amphipod *Gammarus mucronatus* Say, 1818 survived and grew similarly in mixed and algae-based diets. In contrast, the amphipod *Cymadusa compta* (S.I. Smith, 1873) showed negative effects on growth and survival when only animal-based diet was provided. According to the authors, mixed diets may benefit vagile species, which have a higher capacity to get different food sources. In contrast, mixed diets seem to be less important for sedentary species that depend on available food around their home range (Cruz-Rivera & Hay 2000b). *O. tuberculata* has direct development (it lacks a larval stage), in which females brood their offspring until they reach the juvenile stage. This life cycle determines a low dispersal potential, resulting in populations being poorly connected and highly genetically structured (Montecinos *et al.* 2021). The particular reproductive mode of *O. tuberculata*, which inherently reduces population-level genetic exchange, coupled with contrasting local conditions in food availability, could facilitate the development of local adaptive behaviors. These factors could help explain the spatial differences observed in feeding behavior and the corresponding fitness-related responses documented in this study.

Amphipods are characterized by showing a high trophic diversity, that includes predators, scavengers, filter feeders and symbionts, among others. This appear to be a pivotal factor to explain their worldwide distribution (Legeyńska *et al.* 2012). Also, they are key organisms for marine ecosystem dynamics, underpinning nutrient recycling, with important implications in energy transfer

among trophic levels (López *et al.* 2010, Rezende *et al.* 2013, Guerra-García *et al.* 2014). Our findings suggest that *O. tuberculata* could play an important role in sandy beach ecosystems by adjusting its feeding behavior in response to local environmental characteristics. These types of adaptations would positively impact on the energy flux within the food web, providing a flexible way for energy injection to ecosystems with low local primary productivity, such as sandy beach ecosystems.

STATEMENTS

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AUTHOR CONTRIBUTIONS

DI, Data analysis, resources, running experiments, writing of first draft; RR, Supervision and writing revised version; AB, Supervision, statistical analysis, revision of last version.

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DATA AVAILABILITY STATEMENT

Data are available upon request from the last author (AB).

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICAL APPROVAL

Not applicable.

USE OF AI

AI was used only to improve the English language of the manuscript.

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