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Short communication

Cannibalism and food availability in the talitrid amphipod *Orchestoidea tuberculata*

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ABSTRACT

The availability of limiting resources can potentially influence the intensity of intra- and interspecific interactions. Stranded macroalgae exported from adjacent coastal ecosystems supports abundant intertidal consumers on oceanic sandy beaches, including talitrid amphipods, which can be one of the numerically dominant invertebrates of the upper shore. The allochthonous nature of this donor-controlled food subsidy and its unpredictable delivery by waves and currents, results in highly variable and potentially limiting resource availability for these consumers. In Chile, adults of the talitrid amphipod, *Orchestoidea tuberculata* Nicolet, can influence the survival of juvenile conspecifics through cannibalism, a type of intraspecific interaction we hypothesized could be affected by the availability of macroalgal resources. We experimentally investigated the potential influence of food availability on cannibalism between age classes in *O. tuberculata* in laboratory mesocosms. Juvenile mortality in presence of conspecific adults was significantly higher when juveniles and adults were maintained without food. However, adult mortality was neither density dependent or food dependent. Further, juveniles did not influence adult mortality, either with or without food. The strong effect of food limitation on juvenile mortality from cannibalism by adults of *O. tuberculata* found here, supports our hypothesis that food resource availability on beaches can affect this intraspecific interactions. In addition these results provide evidence of the potential importance of biological interaction in the population dynamics of intertidal consumers on oceanic sandy beaches.

1. Introduction

For rocky shore intertidal habitats, intra and interspecific biological interactions, can significantly affect the regulation of population and community structure (e.g. Dayton, 1975; Paine, 1980; Connell, 1983; Moreno and Jaramillo, 1983; Menge, 1992; Arim and Marquet, 2004; Amarasekare, 2008). The supply of food resources, including trophic subsidies, such as macroalgal wrack, has been shown to influence the intensity of these interactions (Bustamante et al., 1995; Bustamante and Branch, 1996; Rodríguez, 2000). However, the role of biological interactions in macrofaunal communities of oceanic sandy beaches, one of the most physically rigorous coastal habitats, is far less understood (see Dugan et al., 2004).

Due to the continuous shifting of beach sands, no attached intertidal plants persist on sandy beaches and these habitats are characterized by an almost total absence of *in situ* primary production (McLachlan et al., 1981; Inglis, 1989). Thus a large component of the intertidal macrofaunal community of sandy beaches depends almost exclusively on organic subsidies exported from adjacent coastal habitats, like rocky shores and reefs (e.g. Mann and Lazier, 1991; Polis et al., 1997; Dugan et al., 2003). In many temperate regions, this subsidy primarily consists of stranded macroalgae, which comprises the most important food resource for upper beach consumers, such as talitrid amphipods, tylid isopods, and tenebronid and staphylinid insects (Koop and Field, 1980; Griffiths and Stenton-Dozey, 1981; Griffiths et al., 1983; Inglis, 1989; Brown and McLachlan, 1990; Dugan et al., 2003). Since the availability of this allochthonous food resource may widely vary throughout the year (e.g. Stenton-Dozey and Griffiths, 1983; Duarte, 2007), these resources may be potentially limiting during long periods of time. Consequently, we hypothesized that the availability of these subsidies may influence competition (interspecific or intraspecific) and other forms of biological interactions in the consumers guild of the upper zones of sandy beaches.

Talitrid amphipods are one of the most abundant invertebrates of the upper shore levels of temperate sandy beaches throughout the world (Dahl, 1952; Brown and McLachlan, 1990; McLachlan and Jaramillo, 1995). These amphipods are an ecologically important group which play a key role in the biological processing of macroalgal inputs and facilitating the transfer of nutrients from the ocean to the coastline (Griffiths and Stenton-Dozey, 1981; Lastra et al., 2008). These animals orient and actively migrate on diel, tidal and seasonal scales to avoid both dessication and submersion in salt water, as well as to locate stranded macroalgae or wrack food resources (Scapini, 2006; Scapini and Dugan, 2008).

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Differences in space and time partitioning of locomotor activity over the beach surface, have been reported for juveniles and adults of several species of these brooding crustaceans (Craig, 1973; Scapini et al., 1992; Fallaci et al., 1999; Jaramillo et al., 2003). For example, Fallaci et al. (1999) recorded that while juveniles of the amphipod *Talitrus saltator* (Montagu) had their highest locomotor activity towards the upper levels of the beach, adults peaked towards lower beach levels for the French coast. While studying locomotor activities and intraspecific interactions, Kennedy et al. (2000) recorded that, mortality of juveniles of *Orchestoidea tuberculata* Nicolet from southern Chile was significantly higher in the presence of adult conspecifics, than in the absence of adults. That mortality was attributed to intense cannibalism by adults. Based on these observations, Kennedy et al. (2000) concluded that differences in space and time partitioning of locomotor activity over the beach surface, could be a mechanism that reduces contact between adults and juveniles allowing them to avoid negative interactions.

Cannibalism or conspecific predation is a common phenomenon among crustaceans (e.g. Marshall et al., 2005; Moller et al., 2008) and has shown to be an very important population regulating mechanism (e.g. Moksnes and Heck, 2006; Amaral et al., 2009). Recently, Amarasekare (2008) suggested that cannibalism could be an important mechanism in maintaining diversity in communities with intraguild predation. Food shortage has been considered one of the main factors promoting conspecific predation or cannibalism (Jormalainen and Shuster, 1997; Amaral et al., 2009). Further, Ebenman (1988) proposed that intraspecific interaction among different age classes will be higher in those species whose ontogenic groups have similarities in their food resources. Populations of *O. tuberculata* inhabiting sandy beaches of southern Chile experience both of these factors: i) they live in an environment where food availability may be limiting during long periods of time (Duarte, 2007) and ii) the different ontogenic stages use similar food resources (Duarte et al., 2008). Thus, we evaluated the hypothesis that the interaction between food availability and density of adult amphipods, could influence mortality of juveniles of *O. tuberculata* in laboratory conditions. From our results, we discuss the implications of food availability on the general pattern of segregation of locomotor activity between adults and juveniles and on the population dynamics of talitrid amphipods of oceanic sandy beaches.

2. Materials and methods

2.1. Collection of amphipods

Juveniles and adults of *O. tuberculata* were collected by hand from their burial zone at Calfuco beach in southern Chile (ca. 39º S). After collection, amphipods were maintained for 24 h before experimental trials in plastic cages filled with moist sand. Juvenile amphipods were classified as individuals with cephalo-thoracic length <7.0 mm, while adults had a cephalo-thoracic length >14.0 mm. (cf. Jaramillo et al., 1980).

2.2. Coexistence experiments

The experimental design proposed by Underwood (1986) to detect intra and interspecific competition, was used to investigate interactions between adults and juveniles of *O. tuberculata*. This design contrasts interactions between adults and juveniles, as well as interactions within each ontogenic group. The amphipods were placed in 20×20×8 cm high square plastic trays, covered by perforated plastic lids to allow air exchange. Moist sand to a depth of 3 cm collected from the burial zone of *O. tuberculata* was placed in each tray. The experimental design consisted of 18 treatments, each one with three replicates, randomly located on a laboratory bench (Table 1). Four types of interactions (sub-units) were evaluated: i) effects of adults on juveniles; ii) effects of adults on adults; iii) effects of juveniles on adults, and iv) effects of juveniles on juveniles. The low-density treatments were 10 juveniles or 10 adults (250 ind. m^{-2}, Table 1). Juvenils or adults were added in number of 10 or 20 (Table 1); thus, total densities of 10, 20 or 30 amphipods were reached (250, 500 and 750 ind. m^{-2}, respectively), which correspond to those naturally found in sandy beaches from southern Chile (Duarte, 2007). Amphipods were exposed to two experimental conditions: with and without food supply. In the first condition, blade pieces of the macroalgae *Durvillaea antarctica* (Chamisso) Hariot, were provided *ad libitum* throughout the experiments. Experiments were conducted at laboratory temperatures close to 15–17 °C and with a light/dark cycle closely following the natural conditions. Experimental trials lasted 5 days and were conducted from 10–15 October 2004, with the number of dead animals counted at the end of the experiment.

2.3. Data analysis

Percentage mortality (arcsine transformed, Sokal and Rohlf, 1995) in each sub-unit were evaluated with two-way ANOVA to determine the effect of density and food availability and the interaction between these factors. When the analysis showed significant interactions, a one-way ANOVA was carried out for each factor separately in each level from the other factor, followed by Tukey's *a posteriori* HSD test. When the analysis did not show significant interactions, multiple comparisons were carried out using Tukey's *a posteriori* HSD test on each factor that showed significant differences (Underwood, 1997). That statistical analyses were carried out with the Statgraphic 2.0.

3. Results

The mean mortality of juveniles was affected by the presence of conspecific adults in the experimental condition without food (two-way ANOVA, density: $F_{2,\ 12}=24.38$, $p<0.05$; food condition: $F_{1,\ 12}=5.86$, $p<0.05$; density x food condition: $F_{2,\ 12}=27.59$, $p<0.05$; one-way ANOVA, $F_{2,\ 6}=38.70$, $p<0.01$, Fig. 1a). This effect was not density-dependent, that is, the mean mortality of juveniles did not vary significantly between the two abundances of the adults tested (*a posteriori* HSD Tukey test). For the experimental condition with food, mean mortality of juveniles was not significantly influenced by adults (one-way ANOVA: $F_{2,\ 6}=0.56$, $p>0.05$, Fig. 1a). Although mean mortality of juveniles did not vary with increasing juvenile density under the two experimental food conditions, a significantly higher

Table 1
Experimental design to test intraspecific interactions among and between adults and juveniles of .*O. tuberculata*, with and without food (macroalgae). Each treatment had three replicates.

Treatment	Adult density	Juvenile density	Experimental trophic condition
1	0	10	With food
2	0	10	Without food
3	10	0	With food
4	10	0	Without food
5	0	20	With food
6	0	20	Without food
7	20	0	With food
8	20	0	Without food
9	0	30	With food
10	0	30	Without food
11	30	0	With food
12	30	0	Without food
13	10	10	With food
14	10	10	Without food
15	10	20	With food
16	10	20	Without food
17	20	10	With food
18	20	10	Without food

mortality of juveniles was observed in the treatment with food (two-way ANOVA, density: $F_{2, 12} = 0.67$, $p > 0.05$; food condition: $F_{1, 12} = 37.60$, $p < 0.05$; density × food condition: $F_{2, 12} = 1.86$, $p > 0.05$, Fig. 1b).

The mean mortality of adults was much lower than that of juveniles (*cf.* Figs. 1 and 2). That mortality was not affected by the presence of conspecific juveniles under both experimental food conditions (i.e. with and without food; two-way ANOVA, density: $F_{2, 12} = 1.08$, $p > 0.05$; food condition: $F_{1, 12} = 0.80$, $p > 0.05$; density × food condition: $F_{2, 12} = 1.09$, $p > 0.05$, Fig. 2a). No significant differences in adult mortality were found, among either the different adult densities or food conditions and there was no significant interaction between those treatments (two-way ANOVA, density: $F_{2, 12} = 0.59$, $p > 0.05$; food condition: $F_{1, 12} = 0.00$, $p > 0.05$; density × food condition: $F_{2, 12} = 1.50$, $p > 0.05$, Fig. 2b).

4. Discussion

Our results indicating that adults of the talitrid amphipod *O. tuberculata* can increase the mortality of conspecific juveniles through cannibalism, agree with earlier studies which suggested or demonstrated experimentally, that this form of intraspecific predation occurs in these peracarid crustaceans (Dahl, 1952; Jaramillo et al., 1980; Kennedy et al., 2000; Jaramillo et al., 2003). The effect of limiting food resources on these intraspecific interactions as demonstrated here has not been reported for these animals before. In food-limited conditions, juvenile survival was negatively affected by the presence of conspecific adults. This negative interaction among ontogenetic stages was not observed when food was provided in the experimental trials. In the treatments with only juveniles, we also observed higher mortality in the presence of added food resource, which might indicate some exploitative and/or interference competition within this age class. These results are similar to that registered by Wenngren and Ólafsson (2002) for the deposit-feeding amphipod *Monoporeia affinis* (Lindström), although unlike that study, this interaction was not density dependent in *O. tuberculata*.

In many coastal habitats, the intensity of biological interactions has been shown to be modified by the food supply of macroalgae or other nutrients exported from adjacent systems (i.e. subsidies), thus influencing local ecological patterns (e.g. Kim, 1992; Bustamante et al., 1995; Bustamante and Branch, 1996; Polis and Hurd, 1996; Rodríguez, 2000; Menge et al., 2003; Nielsen and Navarrete, 2004). For example, Bustamante and Branch (1996) reported that the subsidy of kelp is crucial for the maintenance of high density of two dominant limpets, which in turn, exert significant top down effects, indirectly favouring crustose corallines and inhibiting invasion of primary substrate space by filter feeder invertebrates. Surprisingly, in sandy beaches where macroalgal subsidies are especially important (Brown and McLachlan, 1990; Colombini et al., 2000; Jaramillo et al., 2006; Duarte, 2007), relatively little attention has been paid to the role of this resource in regulating biotic interactions of the intertidal macrofauna. To date, the information supporting a possible influence

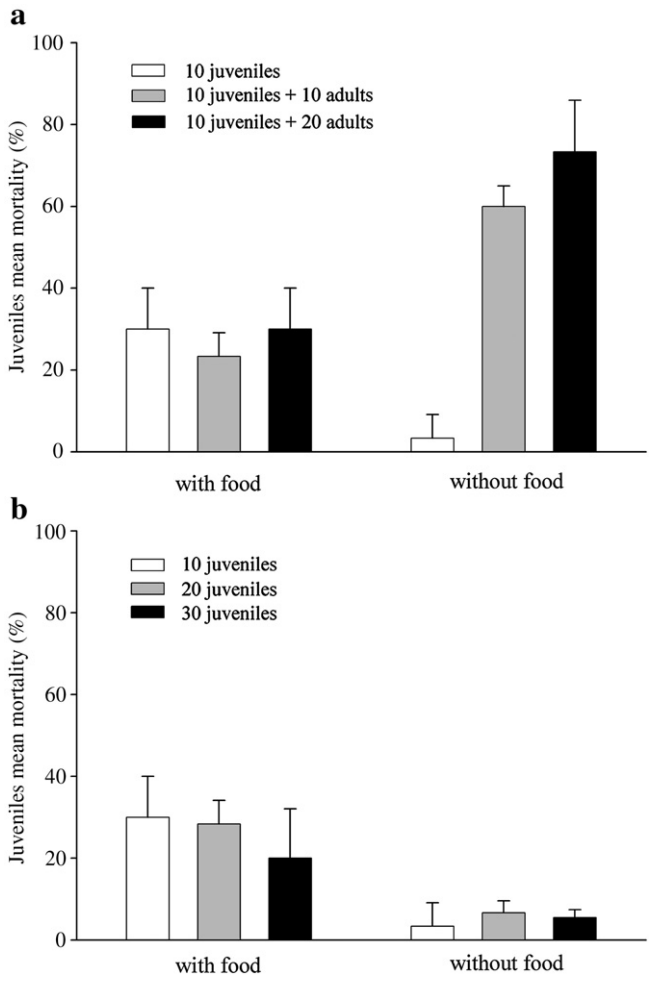

Fig. 1. a) Mean mortality (+1 SD) of juveniles of *Orchestoidea tuberculata* when maintained in a single culture ($n = 10$) and in two adult densities (10 and 20), with and without food (macroalgae). b) Mean mortality (+1 SD) of juveniles of *O. tuberculata* at three juvenile densities (10, 20 and 30), with and without food (macroalgae).

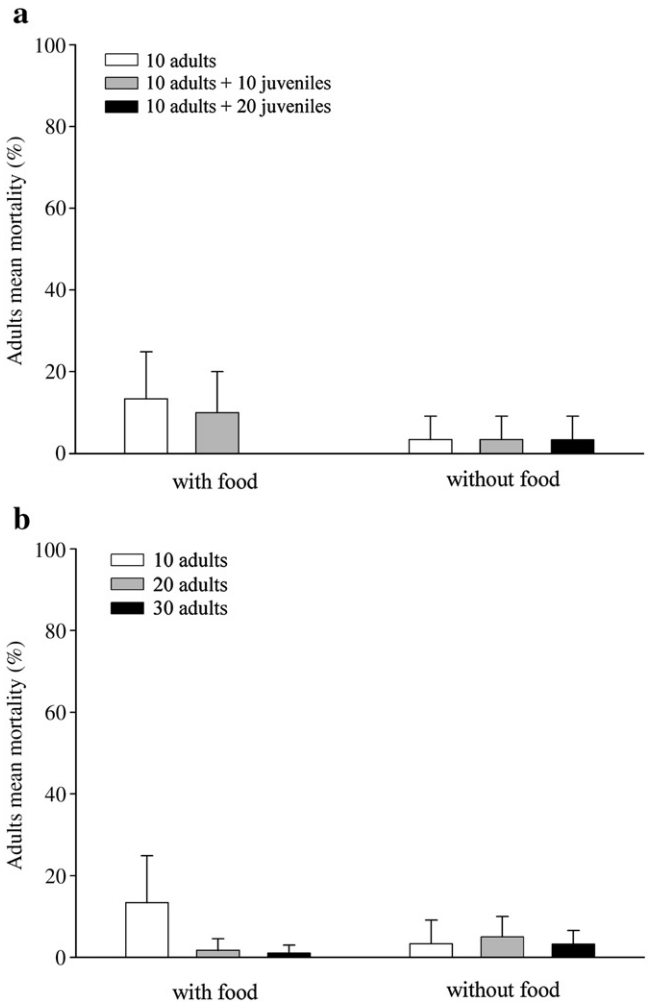

Fig. 2. a) Mean mortality (+1 SD) of adults of *Orchestoidea tuberculata* when maintained in a single culture ($n = 10$) and in two juvenile densities (10 and 20), with and without food (macroalgae). b) Mean mortality (+1 SD) of adults of *O. tuberculata* at three adult densities (10, 20 and 30), with and without food (macroalgae).

of macroalgal availability, has been primarily indirect and unsupported by experimental studies (e.g. Jaramillo et al., 2003, 2006; Duarte et al., 2008). The results of this study provide evidence that macroalgal subsidies can influence the intensity of biological interactions in sandy beaches, and thus could have important effects on the population dynamics and community structure of the intertidal macrofaunal community.

Cannibalism has been shown to be an important regulating factor, influencing population dynamics in both terrestrial and marine systems (Fox, 1975; Polis, 1981; Sparrevik and Leonardsson, 1995; Jormalainen and Shuster, 1997; Persson et al., 2000; Luppi et al., 2001; Wise, 2006; Moller et al., 2008). In crustaceans, this biological interaction may be a primary cause of juvenile mortality (Luppi et al., 2001; Zmora et al., 2005; Christie and Kraufvelin, 2003), and it has been shown to generate spatial segregation between adults and juveniles in several species, as a consequence of active juvenile avoidance of cannibalistic adults (e.g. Wilson, 1989; Jormalainen and Shuster, 1997; Amaral et al., 2009). For example, Amaral et al. (2009) demonstrated that intersize class cannibalism in *Cancer pagurus* (L) was important for juvenile mortality and suggested that this interaction could explain the strong spatial segregation of juvenile and adult individuals in the intertidal zone. In addition, these authors found that the intensity of cannibalism was significantly reduced with increased availability of food. Similarly, Jormalainen and Shuster (1997) suggested that the intersize cannibalism observed in the isopod *Thermosphaeroma thermophilum* (Cole and Bane) was responsible for intraspecific microhabitat segregation between mancas and adults. As mentioned earlier, for Chilean oceanic sandy beaches, avoiding negative interactions, such as cannibalism, has been invoked to explain differences in locomotor activity patterns (i.e. activity segregation) exhibited by different ontogenic groups of talitrid amphipods on the beach face (Kennedy et al., 2000; Jaramillo et al., 2003). Jaramillo et al. (2003) hypothesized that this interaction may be a result of limited macroalgae availability; a hypothesis supported by the results of this study. Further, Duarte (2007) showed that the mean zonation of burrows of adult and juvenile *O. tuberculata* in southern Chile was more similar in beaches with greater amounts of stranded macroalgal wrack, a finding that suggests that the pattern recorded in this study (laboratory conditions) may also occur under natural conditions.

The macroalgae stranded on the beach may increase habitat complexity; thus, apart from food, they may also provide refuge for juveniles of *O. tuberculta*, which would result in decrease of cannibalism from their conespecific adults (*c.f.* Armsby and Tisch, 2006; Amaral et al., 2009). For example, the studies of Amaral et al. (2009) showed that in mesocosmos experiments, juveniles of *C. pagurus* hided within the fronds of the alga *Fucus serratus*, a fact that may restrain movements of larger crabs and visual predation by them, avoiding in this way cannibalism of adults. Consequently, the refuge condition of stranded macroalgae cannot be forgotten in juvenile-adult interactions of talitrid amphipods. Notwithstanding, we did not examined that sort of effect in this study, since only pieces of *D. antarctica* were used and not the whole plants; thus, habitat complexity provided by stranded macroalgae was not recreated in our study.

In addition to cannibalism, other biological interactions such as interspeific predation and competition (e.g. Craig, 1970; Jaramillo et al., 2003; Dugan et al., 2004), could also act as important regulating factors for *O. tuberculata* populations. However, predators or competitors of this amphipod have not been reported for the study area (CD: personal observations). Therefore, cannibalism is likely one of the most important biological interactions regulating population abundance in this species, such as it has been reported in others crustaceans (e.g. Jormalainen and Shuster, 1997; Christie and Kraufvelin, 2003). Consequently, to determine the magnitude of the effect of cannibalism, and the factors that influence this intraspecific interaction on the populations of *O. tuberculata* along the coastline, could be crucial to understand the population dynamics of this abundant and ecologically important intertidal consumer of Chilean sandy beaches.

5. Conclusion

Our study shows that under laboratory conditions, the availability of a key food resource (macroalgal subsidies), can significantly influence intraspecific interactions between juveniles and adults of the talitrid amphipod *O. tuberculata*. Moreover, our results provide new evidence to support the fact that biological interactions are important factors influencing the population dynamics of the intertidal macroinfauna of oceanic sandy beaches (see Dugan et al., 2004), coastal habitats where physical processes have long been considered to exert the primary control of population and community structure of the intertidal macrofauna.

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