

# Ontogenetic habitat shift of an herbivorous crab: a chemically mediated defense mechanism?

Cambio ontogenético de hábitat de una especie de jaiba herbívora:  
¿un mecanismo de defensa mediado químicamente?

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**Resumen.**- La mayoría de los herbívoros se especializan en tipos específicos de huéspedes que les sirven como refugios y alimento. Tales asociaciones, sin embargo, no necesariamente perduran a lo largo de su ontogenia. Por ejemplo, en observaciones de terreno se ha encontrado una fuerte asociación entre la jaiba herbívora *Taliepus dentatus* y las algas pardas. Sin embargo, individuos recién asentados y juveniles se encuentran sólo en parches del alga parda *Glossophora kunthii*, mientras que los individuos adultos de la población se encuentran más frecuentemente asociados al huro submareal *Lessonia trabeculata*. Nuestros experimentos de terreno y laboratorio mostraron que distintas clases de tamaño de esta especie de jaiba podrían seleccionar activamente estas especies de algas siendo estas preferencias más conspicuas en individuos recién asentados. Experimentos de bioensayos mostraron que los peces evitan a *T. dentatus* o *G. kunthii*, lo cual sugiere que el consumo de esta alga por *T. dentatus* podría disminuir sus tasas de mortalidad natural debido a la depredación por peces. Estos resultados se corroboraron además mediante experimentos de amarre en terreno, donde individuos de esta especie exhibieron una alta sobrevivencia independiente del sustrato del enterno donde fueron expuestas. En este estudio se especula que la incorporación de defensas anti-depredatorias de algas podrían aumentar la sobrevivencia de juveniles, disuayendo así a consumidores como peces carnívoros comunes en estos ambientes. Aunque menos amenazados, porque son muy grandes para ser consumidos por peces carnívoros, los individuos adultos también podrían beneficiarse viviendo en el alga *L. trabeculata*, la cual es rica en metabolitos secundarios.

**Palabras clave:** Metabolitos secundarios, *Taliepus dentatus*, *Glossophora kunthii*, *Lessonia trabeculata*

**Abstract.**- Many herbivores specialize on a specific type of host that can serve both as food and shelter. Such associations, however, do not necessarily last throughout the ontogeny of the herbivore. For example, in field surveys a close association between the herbivorous crab *Taliepus dentatus* and brown algae has been found. However, newly settled and juvenile individuals were only found on patches of the brown algae *Glossophora kunthii*, while older individuals of the population were most frequently found living on the common brown kelp *Lessonia trabeculata*. Our field and laboratory experiments showed that different size classes of this crab species may actively select these algal habitats, and that these preferences are even more conspicuous for small newly settled individuals. Bioassay experiments showed that fish specifically avoided either *T. dentatus* or *G. kunthii*, which suggests that consumption of this alga by *T. dentatus* could decrease their natural rates of mortality due to fish predation. These results were further corroborated through field tethering experiments, where individuals of this species exhibited high survivorship regardless of the surrounding substrate on which they were placed. In this study, we speculate that incorporation of anti-predator defenses from algae may then enhance the survivorship of juveniles, thus, deterring consumers like carnivorous fish common in these environments. Although less threatened, because they are too large to be consumed by predatory fish, older individuals might also benefit from living on *L. trabeculata*, which is rich in secondary metabolites.

**Key words:** Secondary metabolites, *Taliepus dentatus*, *Glossophora kunthii*, *Lessonia trabeculata*

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## INTRODUCTION

Many marine organisms with complex life cycles can undergo dramatic size changes from the time they settle on the benthos until they become adults. It is at the time when such small individuals reach the benthos that high mortality rates are common (Gosselin & Qian 1997). If predation is important at this point, survivorship of newly settled individuals will increase if they are effective at avoiding predators. For a variety of species that live in shallow marine environments, newly settled individuals are common prey of either larger conspecifics that already exist on the bottom (*e.g.*, cannibalism in crabs: Hines & Ruiz 1995), or more typically, by predatory fish (Wahle & Steneck 1991, Carr & Hixon 1995, Tupper & Boutilier 1996, Palma & Ojeda 2002). However, as individuals grow larger, it is common to observe a size escape from predation (Jones 1991, McConaugha 1992, Gosselin & Qian 1997, Cruz-Rivera 2001), and therefore maintaining costly anti-predator chemical or behavioral defenses may no longer be necessary.

Most decapods are mobile immediately after reaching the bottom, thus they can actively select a certain habitat both during and after settlement. For these species, habitat selection can be the result of two non-mutually exclusive possibilities: (1) individuals settle indiscriminately and show higher survivorship on a specific type of habitat (*e.g.*, Palma *et al.* 1998) or (2) they actively seek those habitats where mortality is lower (Morgan *et al.* 1996, Palma *et al.* 1999). In either case, the existence of a suitable 'nursery' environment is critical (Lough *et al.* 1989). Predation risk in decapods can also be mediated by the use of camouflage strategies (Palma & Steneck 2001, Hultgren & Stachowicz 2008). In terms of recruitment ('nursery') habitat however, cobble-stone throughout the habitat represents one of the preferred types of substrate where many brachyuran species settle, recruit or use as a juvenile habitat (Pallas *et al.* 2006, Palma *et al.* 2006, Pardo *et al.* 2007).

In shallow marine environments, plants or algae often dominate the benthic substrate and represent a safe habitat for a variety of marine animals by providing shelter and food (Gotceitas 1990, Pohle *et al.* 1991, Moreno 1995, Heck *et al.* 2003). However, it is important to distinguish between the physical and the visual protection provided by such habitats. The former is related to the use of the physical characteristics of the habitat as an effective way of hiding against visual predators (*i.e.*, physical crypsis: Hacker & Steneck 1990) and the latter to the degree in which individuals will 'blend' with their surrounding

background (*i.e.*, visual crypsis: Wilson 1987, Hacker & Madin 1991, Palma & Steneck 2001, Palma *et al.* 2003, Hultgren & Stachowicz 2008, Manriquez *et al.* 2008). In addition to shelter provision, algae or seagrass also represent a source of food for organisms (particularly for mesograzers) that live on them (Edgar 1983, Dean & Connell 1987, Edgar 1990). Just as structural complexity provides refuge by physically excluding some predators, noxious antipredator chemicals often deter a wide range of larger consumers and provide local safe sites for smaller animals. It has been demonstrated that algae can diminish the effects of herbivores by producing noxious chemicals that deter grazers (Hay 1991, Hay & Steinberg 1992, Paul 1992). By living on or near chemically defended plants that are rarely visited by larger omnivores, some small grazers (*e.g.*, insects, crustaceans, polychaetes, sea slugs) are able to reduce their encounter rates with potential predators (Bernays & Graham 1988, Hay 1992). However, some species use chemically defended plants as shelter yet feed on other species. For example, decorator crabs cover their carapace with algae or sessile invertebrates as camouflage from predators-and thus never abandon their shelter-but they need not feed on them (Hines 1982). One species, *Libinia dubia*, practices a form of chemical camouflage (Stachowicz & Hay 1999) in which it decorates itself with the chemically noxious brown alga *Dictyota menstrualis*, rendering itself unpalatable to fishes. The diterpene alcohol produced by the alga to deter herbivores cues decoration behavior in the crab; thus the crabs are, in a sense, behaviorally sequestering seaweed chemical defenses (Stachowicz & Hay 1999). For many marine invertebrates that use these chemically defended algae as both shelter and food, there are cases where consumers incorporate those chemicals into their tissues to further deter carnivores (Hay 1992).

The herbivorous brachyuran crab, *Taliepus dentatus* (Majoidea, Epialtidae) is very common in the shallow subtidal environments of the central coast of Chile (Palma *et al.* 2003). Like other closely related kelp crabs (*e.g.*, *Acanthonix petiveri* or *Pugettia product*, Wilson 1987 and Hultgren & Stachowicz 2010, respectively), large individuals of this species have been described as 'kelp crabs' because of their close association with the subtidal brown kelp *Lessonia trabeculata*, and have a characteristic brownish coloration, which resembles that of the kelp on which they live and consume. However, smaller individuals of *T. dentatus*, are generally rare or absent from *L. trabeculata* but are found almost exclusively on another brown algae, *Glossophora kunthii*,

that forms discrete patches in these same environments (Palma *et al.* 2003). Since this algal species belongs to a group (Dyctiotaales) known for presenting secondary chemical compounds, it is possible that the association observed between small *T. dentatus* crabs inhabiting *G. kunthii*, may be due to the presence of such metabolites that crabs can garner from their algal host. Hence, in this study we describe the pattern of habitat utilization of *T. dentatus* through its ontogeny and examine the hypothesis that the differential use of habitat among different-sized individuals is related to a chemically-mediated antipredatory mechanism. Specifically, we investigate the role that secondary metabolites, present in the host plants and possibly sequestered by *T. dentatus*, may play in mediating this process. Throughout we focused our efforts in experiments (*i.e.*, field tethering and bioassays in the laboratory) that considered using juveniles, which represent the most vulnerable segment of the population after they have settled.

## MATERIALS AND METHODS

### SITE SURVEYS AND FIELD METHODS

Field observations were made on the central Chilean coast at Punta de Tralca (33°35'S, 71°42'W) between May of 1999 and November of 2000. This site was chosen because of its protected nature and location near the flowing seawater facilities of the Marine Laboratory in Las Cruces (ECIM). Estimation of the abundance of individuals was made by means of substrate-specific suction samples using an air-lift device (for more details on method see Palma *et al.* 1998). This method was appropriate for the estimation of the abundance of newly settled and in general small individuals (< 10 mm in carapace width). Larger individuals, however, were quantified through visual surveys of specific substrata. The three main substrata investigated, which represent different-quality habitats for this species (Palma *et al.* 2003), corresponded to two species of brown macroalgae (*Glossophora kunthii* and *Lessonia trabeculata*) and cobble stone habitats. The later was also considered since it represents a prime nursery environment for many decapod crustaceans (Pallas *et al.* 2006). Square 0.25 m<sup>2</sup> frames were haphazardly placed on patches of *G. kunthii* or cobble beds and suction lasted (*ca.* 5 min) as long as all the algae and accompanying organisms (for kelp beds) or all cobble were overturned and the loose material and organisms were collected into a 1 mm mesh-size bag. Because of their large size (> 1 m tall plants) the quantification of

crabs on *L. trabeculata* was made by visually inspecting haphazardly selected plants for at least 5 min and all individuals found were *in situ* measured (carapace width in mm), their sex determined and then released. For an estimation of the abundance of crabs on each plant the size of the basal disc (maximum diameter) of each plant was obtained and used to estimate its biomass using an allometric equation ( $Y = 0.12 X^{3.17}$ ,  $r = 0.93$ , after Villouta & Santelices 1984). Surveys on all types of substrata were made at depths between 7-12 m below MLW, the main distribution range of these algae and crab species (A. Palma pers. obs.). To ensure that we were not missing small newly settled individuals from *L. trabeculata*, 10 complete plants (holdfast and fronds) were collected during the May 1999 field survey and *in situ* placed into individual large plastic bags and all decapods found were then counted and measured in the laboratory.

### BIOASSAY EXPERIMENT

The palatability of *Taliepus dentatus* and *Glossophora kunthii* by common predatory fish was evaluated through a multiple choice feeding experiment. To test this, samples of this crab and algae species (*G. kunthii*) plus another crab species (the palatable brachyuran *Paraxanthus barbiger*, Palma & Ojeda 2002) were homogenized and offered to fish in the form of pellets. Samples of small (newly settled size individuals) crabs and algae were oven dried at 60°C until constant dry weight was reached (3-4 days). Equal amounts of the dried and previously ground up material were then mixed with a paste of mashed mussel flesh (*Mesodesma donacium*) in a 1:1 proportion. This procedure was followed to ensure a better palatability and standardization of the different pellets (4 types). The pellets were prepared by using a 100% mass/volume solution in seawater to which 3 % of agar solution was added. The pellets were allowed to dry for 1 to 2 days prior to their use in the feeding choice experiment. The fourth pellet type contained only mussel flesh.

Two different fish species (the redspotted catshark, *Schroederichthys chilensis*, and surfperch, *Cheilodactylus variegatus*) known to prey on *T. dentatus* (Fariña & Ojeda 1993, Palma & Ojeda 2002) were used for this experiment. One individual of each species was placed into separate 500 L circular tanks with flowing seawater. Fish were acclimated for 45 min prior to the introduction of the 4 different pellets described above. The pellets were weighed before and after they were offered to the fish. All pellets had similar initial weight ( $14.0 \pm 0.1$  g). Trials were run with each individual of the two fish species

utilized: 6 times with *S. chilensis*, and 9 times with *C. variegatus*. All trials were run for 4 h after the pellets were offered to the fish. Results from the experimental trials for each fish species were pooled together for analysis, where the number of replicates corresponded to the number of individual fish available for each species. Replicates of the four pellet types were placed into an equal volume of seawater without the presence of fish for 4 h in order to detect any change in weight due to dissolution in seawater.

#### FIELD TETHERING EXPERIMENT

Juveniles of the two crab species utilized for tethering experiments were collected from their respectively most important 'nursery' habitats. *Taliepus dentatus* (size range 8-11 mm CW), obtained from patches of *Glossophora kunthii* and *Paraxanthus barbiger* (size range: 9-14 mm CW), obtained from cobble patches, were individually tied to a 20 cm long ½ inch ribbed construction bars using 15 cm monofilament line (12 lb. test). A loop of monofilament was placed around the carapace of each individual and the knot secured on the dorsal surface with a drop of Superglue™. All crabs were placed on patches of substrate that were, *a priori* defined as, either safe (cryptic) or unsafe (non-cryptic) in Punta de Tralca at a depth of 10 m MLW. A total of 73 individuals, considering the two crab species, were tethered. Ten bars, each with 1 *T. dentatus*, were randomly placed on patches of *G. kunthii* (cryptic habitat) and 10 on bare rocks (non-cryptic). Similarly, 33 of the tethered *P. barbiger* were placed on patches of shell hash (cryptic habitat) and 20 on bare rocks (non-cryptic). The experiment started at noon on October 11, 2000 and samples were retrieved 24 h later. Predation events could be distinguished from other sources of loss because at least part of the carapace remained attached to the monofilament when it occurred. The integrity of the tethers was ensured, by leaving tethered individuals in tanks with flowing seawater for two days prior the deployment of the experiment. In order to minimize the potential problem of induced predation, individual crabs were placed at least one meter away from each other.

#### STATISTICAL ANALYSES

Parametric statistics were used to compare differences in the abundance of crabs among the different types of substrata. The assumptions of normality, homogeneity of variance, and independence of observations were

tested and transformations were performed when necessary, particularly angular transformation (arcsin of squareroot) when percentages were compared (Sokal & Rohlf 1995). For the field tethering experiment, data were arcsin-transformed and single-factor ANOVAs were utilized to compare the percentage survivorship for each crab species between substrate types and pooling substrate types when comparing survivorship between species. For the multiple-choice feeding experiment, the difference in weight of the pellets before and after the experiment was used to evaluate the consumption rate. Each predatory species was considered separately for differences in the amount of the four pellet types left. In this experiment, variances remained heteroscedastic after transformations, thus, nonparametric Friedman's analysis of variance by ranks was applied to the differences in pellet weight. A significance level of  $P \leq 0.05$  was considered throughout the study.

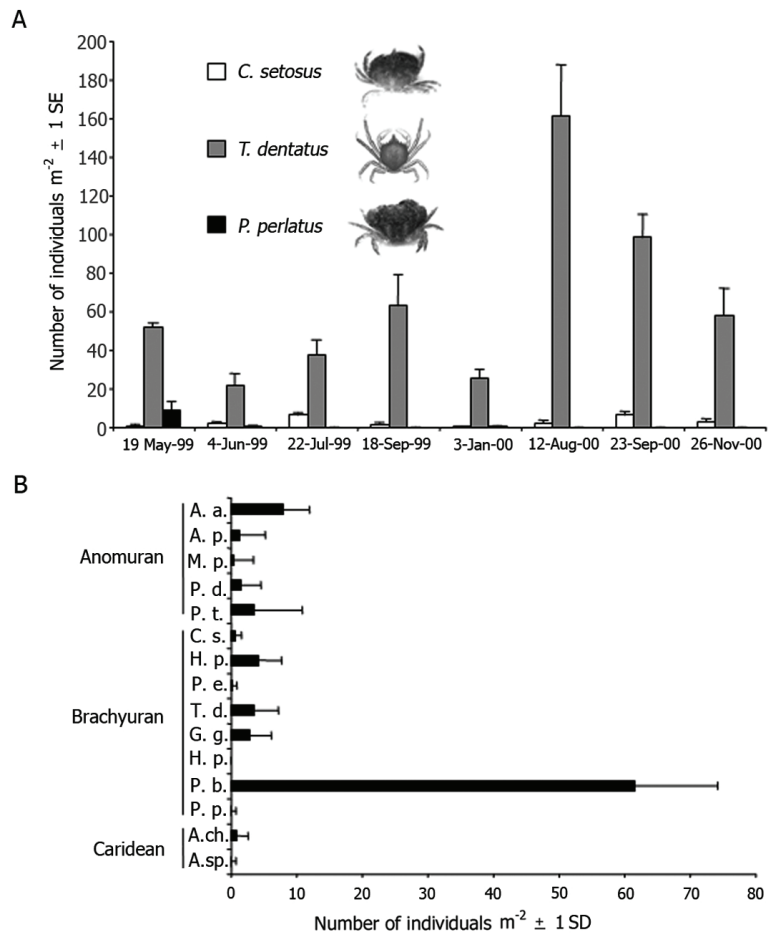
## RESULTS

#### DISTRIBUTION AND ABUNDANCE PATTERNS

Three species of brachyuran crabs were found inhabiting patches of *Glossophora kunthii*, with *Taliepus dentatus* being significantly more abundant than other species surveyed ( $F_{2,155} = 59.4, P < 0.0001$ , Fig. 1A), such as *Cancer setosus* and *Pilumnoides perlatus* during the whole study period (May 1999 to November 2000). In comparison, the higher diversity of decapods in the adjacent cobble patches was highlighted by 15 species (5 Anomurans, 8 Brachyurans and 2 Carideans, Fig. 1B). The abundance of most species was represented by an average of < 10 individuals  $m^{-2}$  with *Paraxanthus barbiger* being the most abundant decapod with *ca.* 60 individuals  $m^{-2}$ .

Comparing its abundance among all substrata considered here *T. dentatus* was more common on patches of *G. kunthii* compared to patches of cobble ( $F_{1,59} = 33.037, P < 0.0001$ , Fig. 2A). Also, when its abundance was standardized for the biomass of the algal substrate, *T. dentatus* densities were significantly higher on *G. kunthii* than on *L. trabeculata* ( $F_{1,79} = 79.140, P < 0.0001$ , Fig. 2B). The average size of individuals showed an inverse relationship with respect to their abundance. Larger, adult individuals were found in lower densities and predominately within *L. trabeculata*, while smaller, juvenile crabs were congregated on *G. kunthii* and cobble substrata ( $F_{2,98} = 102.294, P < 0.0001$ , Fig. 2c).

Figure 1. A) Abundance of three decapod species (*Cancer setosus*, *Talipes dentatus*, and *Pilumnoides perlatus*) on *G. kunthii* patches in the study site of Punta de Tralca sampled on 8 dates between May 1999 and November 2000. B) Pooled average abundance of all decapod species present on cobble-stone substrate in Punta de Tralca during the same period of time. The species names are given in Annex / A) Abundancia de tres especies de decápodos (*Cancer setosus*, *Talipes dentatus*, y *Pilumnoides perlatus*) en parches de *G. kunthii* en el sitio de estudio de Punta de Tralca muestreados en 8 oportunidades entre mayo 1999 y noviembre 2000. B) Abundancia promedio agrupando todas las especies de decápodos presentes en sustratos de bolones y roca en Punta de Tralca durante el mismo período de tiempo. Ver lista de especies en Anexo

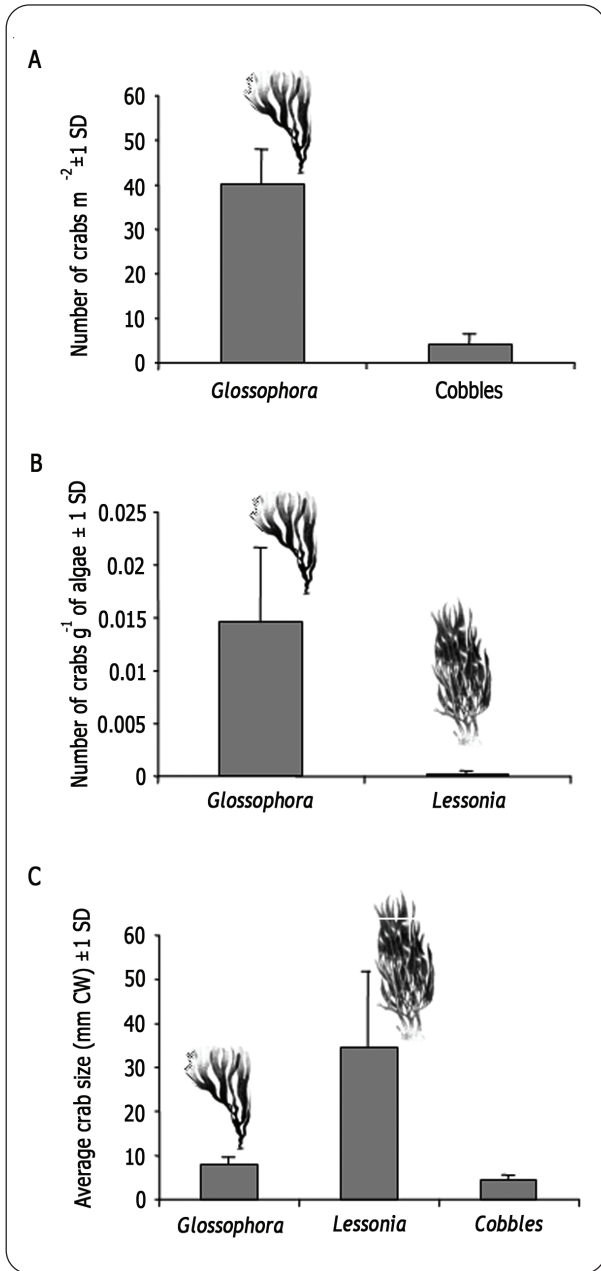


#### BIOASSAY EXPERIMENT

The consumption of pellets prepared with the homogenized *Paraxanthus barbiger* was significantly higher than that of pellets using *Glossophora kunthii* or *Talipes dentatus*. A similar trend was observed for the two predatory fish (six redspotted catshark:  $F_{3,20} = 158.99$ ,  $P < 0.0001$ ; nine surfperch:  $F_{3,32} = 225.9$ ,  $P < 0.0001$ , Fig. 3). In all trials, pellets composed of mussel alone or mussel and *P. barbiger* crabs, were the most preferred food item. Fisher's PLSD post hoc tests further confirmed that pellets composed of mussels alone were consumed in a significantly higher percentage compared to those composed of *P. barbiger*. Nearly 100% of pellets composed of mussels or *P. barbiger* were consumed in experimental trials, while less than 10% of those composed of *T. dentatus* were consumed (Fig. 3).

#### FIELD TETHERING EXPERIMENT

Regardless of the substrate type, predation pressure was significantly different for the two crab species ( $F_{1,68} = 11.13$ ,  $P = 0.0014$ , Fig. 4), with a lower percentage of *Paraxanthus barbiger* surviving ( $50.0 \pm 6.9$ ) compared to *Talipes dentatus* ( $93.7 \pm 6.2$ ). However, when the percentage of surviving crabs of each species was compared according to substrate types, only *P. barbiger* placed on shell-hash showed significantly higher survivorship compared to individuals placed on bare rock ledges ( $F_{1,51} = 6.07$ ,  $P = 0.017$ ), while *T. dentatus* did not experience any significant difference in mortality between the individuals placed inside *Glossophora* patches from those placed on bare rock ledges ( $F_{1,18} = 1.31$ ,  $P = 0.271$ ).



**Figure 2.** *Taliepus dentatus* average abundance in P. de Tralca during the whole study period (May 1999 through November 2000). A) Abundance on *Glossophora* vs. cobble patches over a given surface area. B) Abundance on *Glossophora* vs. *Lessonia* patches per biomass of algae. C) Average crab size on the three substrate types surveyed / Abundancia promedio de *Taliepus dentatus* en P. de Tralca durante todo el período de estudio (mayo 1999 a noviembre 2000). A) Abundancia en parches de *Glossophora* vs. bolones sobre un área determinada. B) Abundancia en parches de *Glossophora* vs. *Lessonia* por biomasa de alga. C) Tamaño promedio de jaibas en los tres sustratos muestreados

## DISCUSSION

Some indirect ecological interactions can be cryptic to casual observation and often require further experimental manipulations to unveil their importance. In our study, *Taliepus dentatus* shows an ontogenetic shift in the use of its natural habitat which bears resemblance to closely related crabs elsewhere (*i.e.*, Hultgren & Stachowicz 2010). Newly settled individuals are found at high densities on patches of the brown kelp *Glossophora kunthii* while older specimens are more frequently found in association with the larger subtidal kelp *Lessonia trabeculata*. Cobblestone habitats, areas commonly inhabited by several other decapod species particularly during their early benthic stages (*e.g.*, Palma *et al.* 1999, 2003, 2006, Pallas *et al.* 2006), contained very few *T. dentatus*. Although, similar specific habitat requirements are common in other species of benthic decapods where ontogenetic habitat switches have also been described (*e.g.*, spider crabs: Hines 1982, American lobsters: Wahle & Steneck 1991, Jonah crabs: Richards 1992).

Even though their specific effect on herbivores is not yet known, noxious secondary metabolites present in *G. kunthii* are likely to have a deterrent effect on consumers that feed on the grazers of the algae (*i.e.*, *T. dentatus*). For this algal species the chemical compounds have been identified as terpenes (Arroyo *et al.* 1991), which are similar to the noxious metabolites found in a related species *Dictyota menstrualis* (Stachowicz & Hay 1999). Although no study has described the secondary metabolites in *L. trabeculata*, phenols have been identified as the main secondary metabolites present in *L. nigrescens*, a related brown algae present in the intertidal and shallow subtidal in these same systems (Martínez 1996). Consequently, adult *T. dentatus* may also derive anti-predator, chemical defenses from their algal hosts, although tissue assays and tethering experiments are needed to confirm whether this is the case.

Several studies have shown that by living and feeding on seaweed which is avoided by fishes many species of mesograzers can significantly lower their susceptibility to predation (*e.g.*, amphipods, polychaetes, Van Dolah 1978, Edgar 1983), which in turn favors these animals to circumvent seaweed chemical defenses (Hay 1992). An extensive body of research has unveiled the indirect and often complex interactions of marine invertebrates and chemically defended seaweed species (see Hay 1996 for review). However, it is worth mentioning that such indirect effect has, to our knowledge, not yet been described for brachyuran decapod species and is perhaps a more pervasive phenomenon than previously expected.

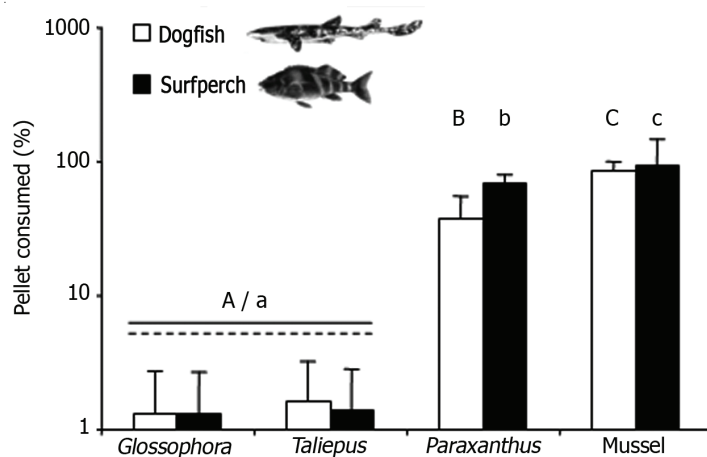


Figure 3. Pellet consumption percentage in the bioassay experiment using different extracts (see methodology for details on pellet preparation). Different bar colors represent the % consumption of pellets by the two different fish species utilized as predators (redspotted catshark, *Schroederichthys chilensis* and surfperch *Cheilodactylus variegatus*). Continuous horizontal lines above bars represent no significant difference for trials with either predatory fish. Different letters above bars represent significant differences ( $P \leq 0.001$ ), capitals for trials with redspotted catshark and lower case for trials with surfperch. % consumption was plotted on  $\log_{10}$  scale in order to visually compare all values given their important differences. Error lines correspond to + 1 SD / Consumo porcentual de pellets en los bioensayos usando diferentes extractos (ver metodología para detalles de la preparación de los pellets). Barras de diferentes colores representan el % de consumo de pellets por las dos especies de peces utilizados como depredadores (pintaroja, *Schroederichthys chilensis* y bilagay *Cheilodactylus variegatus*). Líneas continuas horizontales sobre las barras representan diferencias no significativas en las pruebas con cualquiera de los peces. Diferentes letras sobre las barras representan diferencias significativas ( $P \leq 0,001$ ), mayúsculas para las pruebas con pintaroja y minúsculas para las pruebas con bilagay. El consumo porcentual es expresado en escala  $\log_{10}$  con el objeto de comparar visualmente todos los valores dadas sus importantes diferencias. Líneas representan Error + 1 DE

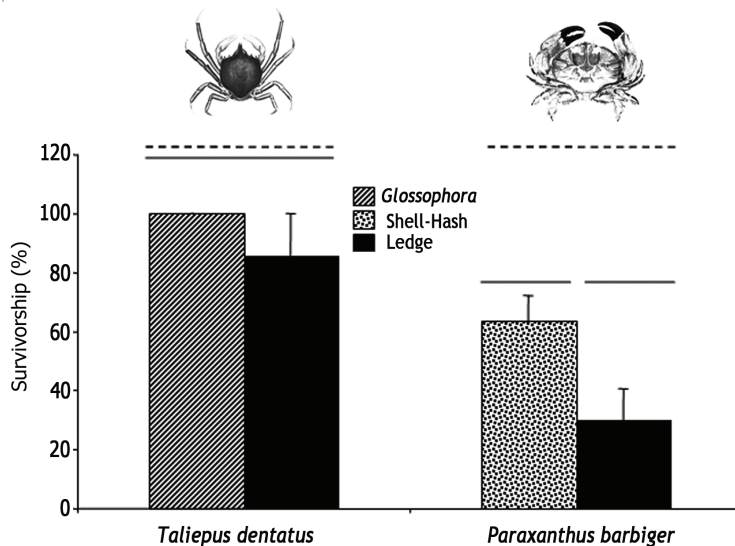


Figure 4. Percentage of crab survivorship in field tethering experiment. Individuals of each crab species were simultaneously placed on different substrate types. *Taliepus dentatus* samples were tethered on *Glossophora* and on exposed bare rock ledge patches while those of *Paraxanthus barbiger* on shell hash and on exposed bare rock ledge patches. Discontinuous horizontal lines above bars represent significant differences (see results). Dashed lines represent the comparison in survivorship between the two crab species, regardless of the habitat on which they were placed. Error bars correspond to + 1 SE / Sobrevivencia porcentual de jaibas en los experimentos de amarre en terreno. Individuos de cada especie de jaiba fueron puestos simultáneamente sobre distintos tipos de sustrato. Los *Taliepus dentatus* fueron amarrados en *Glossophora* en parches de roca desnuda y los *Paraxanthus barbiger* fueron amarrados en conchuelas en parches de roca desnuda. Líneas horizontales discontinuas sobre las barras representan diferencias (ver resultados). Líneas punteadas representan la comparación en sobrevivencia entre las dos especies de jaibas independiente del hábitat en que fueron puestas. Barras representan Error + 1 EE

The bioassay experiment represents indirect evidence that *Glossophora kunthii*, as well as the *Taliepus dentatus* feeding on them, may possess secondary metabolites that actively deter consumers. Although the specific composition of these metabolites is unknown, the presence of secondary metabolites is inferred from our results in that at least two species of common predatory fish avoided consuming pellets of both, *T. dentatus* and *G. kunthii* (Fig. 3).

Additional evidence that supports the idea that *T. dentatus* is chemically defended by consuming *G. kunthii* comes from the results of the field tethering experiment. The parallel use of *Paraxanthus barbiger* was considered a good choice as a control in this experiment since it is a well represented food item in the diet of several carnivorous fish in these systems (Fariña & Ojeda 1993, Palma & Ojeda 2002) without any evidence that it is avoided due to any deterrent chemical compound. The significantly higher survivorship of *T. dentatus* was similar in the two habitat types tested (algae and exposed bare rock). This contrasted with the equally, but lower, survivorship of *P. barbiger* placed on two different substrate types, although crabs placed on shell hash survived more than those placed on bare rock, suggesting that the former substrate represents a more cryptic (sheltered) habitat for this species (Palma *et al.* 2003). This experiment does not quantify the rate of predation that might affect these two decapod species under natural conditions, however, it is an appropriate measurement of the predation pressure potential affecting them when placed within different habitats (Heck & Wilson 1987, Aronson & Heck 1995) and the high survivorship of *T. dentatus* suggests that these crabs contain intrinsic anti-predator defenses that are relatively stronger than those contained in crabs that do not utilize the *G. kunthii* habitats during early life stages.

It has been shown for other decapods which do decorate themselves with noxious algae that their camouflaging behaviors as well as their susceptibility to predators decrease as individuals grow larger (Stachowicz & Hay 1999). In our case, however, predation avoidance should not be considered as the only factor driving the pattern of differential habitat use by *T. dentatus*. In fact, size-specific shifts in food or habitat type have been well documented for many aquatic species as responses to resource availability and predation risk (*e.g.*, Werner & Gilliam 1984, Gosselin 1997). Therefore, future research should focus on a more in-depth understanding of the mechanisms behind the association between *T. dentatus* and *G. kunthii*, particularly to identify the mechanisms

by which this crab incorporates noxious compounds present in *Glossophora* and how this might be a local phenomenon or a widespread trait in this species.

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#### Annex. Abbreviations list / Anexo. Lista de abreviaturas

The 15 species showed in Figure 1B corresponded to three major taxonomic groups (Brachyura, Anomura and Caridea): A.a. (*Allopetrolisthes angulosus*), A.p. (*Allopetrolisthes punctatus*), M.p. (*Megalobrachium peruvianum*), P.d. (*Petrolisthes desmaresti*), P.t. (*Petrolisthes tuberculatus*), C.s. (*Cancer setosus*), H.p. (*Halicarcinus planatus*), P.e. (*Pisoides edwardsi*), T.d. (*Taliepus dentatus*), G.g. (*Gaudichaudia gaudichaudi*), H.p. (*Homalaspis plana*), P.b. (*Paraxanthus barbiger*), P.p. (*Pilumnoides perlatus*), A.ch. (*Alpheus chilensis*), A. sp. (*Alpheus* sp.)

Las 15 especies que se muestran en Figura 1B corresponden a tres grupos taxonómicos mayores (Brachyura, Anomura y Caridea): A.a. (*Allopetrolisthes angulosus*), A.p. (*Allopetrolisthes punctatus*), M.p. (*Megalobrachium peruvianum*), P.d. (*Petrolisthes desmaresti*), P.t. (*Petrolisthes tuberculatus*), C.s. (*Cancer setosus*), H.p. (*Halicarcinus planatus*), P.e. (*Pisoides edwardsi*), T.d. (*Taliepus dentatus*), G.g. (*Gaudichaudia gaudichaudi*), H.p. (*Homalaspis plana*), P.b. (*Paraxanthus barbiger*), P.p. (*Pilumnoides perlatus*), A.ch. (*Alpheus chilensis*), A. sp. (*Alpheus* sp.)