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Behavioral and alimentary aspects of the sea urchin *Paracentrotus gaimardi* (Echinodermata)

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Aspectos comportamentais e alimentares do ouriço-do-mar *Paracentrotus gaimardi* (Echinodermata)

Resumo: *Paracentrotus gaimardi* é um ouriço-do-mar conhecido por sua diversidade de cores, no entanto estudos abordando outros aspectos que não sua coloração ou reprodução são escassos. Assim, este estudo visa contribuir para uma melhor compreensão da biologia de *P. gaimardi*, fornecendo informações relevantes sobre seus hábitos comportamentais e alimentares. Seis indivíduos de duas colorações distintas foram coletados em São Paulo, sudeste do Brasil. Após sete dias de aclimatação, foram observados alguns aspectos comportamentais, bem como a preferência alimentar. Um notável comportamento de cobertura e uma aparente fototaxia negativa foi observado em todos os indivíduos estudados. Eles se alimentaram das algas *Galaxaura* sp., *Padina* sp. e *Ulva lactuta*, mas também foram observados predando a esponja *Hymeniacidon heliophila* e um espécime morto de *Echinometra lucunter*. *Paracentrotus gaimardi* é um herbívoro típico, alimentando-se principalmente de algas, semelhantemente ao já descrito para o seu congênere mediterrâneo *P. lividus*. Porém, *P. gaimardi* também foi observado alimentando-se diretamente de animais vivos e mortos, o que pode ser entendido como uma estratégia para obter nutrientes menos disponíveis no tecido de algas. As informações fornecidas neste estudo indicam que, de forma geral, a biologia de *P. gaimardi* é muito similar à de *P. lividus*, tornando pertinente comparações entre elas.

Palavras chave: Algas, comportamento de cobertura, esponja, predação.

Abstract: *Paracentrotus gaimardi* is a sea urchin well-known by its astonishing color diversity, however, studies addressing aspects other than its coloration variation or reproduction are scarce. Here, this study aims to contribute toward a better understanding of *P. gaimardi* biology, by providing relevant information on its behavioral and feeding habits. Six individuals of two color morphs (gray and green) were collected at São Paulo State, Southeast Brazil. After seven days of acclimation, some behavioral aspects and food preferences were observed. Both color morphs showed a remarkable covering behavior and an apparent negative phototaxis. They fed on the algae *Galaxaura* sp., *Padina* sp., and *Ulva lactuta*, but they were also observed preying on the sponge *Hymeniacidon heliophila* and a dead specimen of *Echinometra lucunter*. *Paracentrotus gaimardi* was a typical herbivore, feeding mostly on algae, similarly to already described to *P. lividus*, its Mediterranean congener. Although, *P. gaimardi* was also observed feeding directly on live and dead animals, which can be understood as a strategy to obtain nutrients less available in algal tissue. The information provided in this study indicates that, in a broad view, *P. gaimardi*'s biology is very similar to that of *P. lividus*.

Key words: Algae, covering behavior, sponge, predation.

Introduction

The genus *Paracentrotus* (Mortensen, 1903) comprises only two sea urchin species, named *P. lividus* (Lamarck, 1816) and *P. gaimardi* (Blainville, 1825), both well-known for their astonishing color diversity (Louise & Benard 1993; Calderon *et al.* 2010). *Paracentrotus lividus,* a species which is restricted to the Northeast Atlantic Ocean – from Scotland and Ireland to southern Morocco and the Canary Island, including all Mediterranean Sea (Boudouresque & Verlaque 2013; Soliman *et al.* 2015) – is one of the most studied echinoids in the world, being used as a model in many fields of biology (Arizza *et al.* 2007, 2013; Boudouresque & Verlaque 2013; Soliman *et al.* 2015; Morgana *et al.* 2016; Basallote *et al.* 2017; Rial *et al.* 2018). Contrary, *P. gaimardi* has a more restricted distribution. It has been recorded on the African coast, from the Gulf of Guinea to Angola, and in south-southeastern Brazil, from Rio de Janeiro to Santa Catarina states (Mortensen 1943; Calderon *et al.* 2010; Xavier 2010; Duarte *et al.* 2016), and the knowledge on its biological characteristics are quite limited.

Regarding the primary biological aspects, such as behaviour and food preference, *P. lividus* has been by far more investigated than *P. gaimardi* (Boudouresque & Verlaque 2007, 2013). For example, it is known that this species can use a wide range of hard and soft materials to cover its test (Crook 2003) and that age and UV light seem to drive this behavior (Crook *et al.* 1999; Verling *et al.* 2002). Similarly, it is also known that *P. lividus'* food preference varies along the year (Lemee *et al.* 1996; Boudouresque & Verlaque 2013), as well as this sea urchin seems to have found a strategy to use the deterrent introduced macroalgae *Caulerpa taxifolia* as a food source (Lemée *et al.* 1996). On the other hand, the studies published so far on *P. gaimardi* have focused on understanding either its color variation and/or reproductive aspects (Ventura & Barcellos 2004; Calderon *et al.* 2009, 2010; Lopes & Ventura 2012; Duarte *et al.* 2016). Consequently, the number of works dealing with aspects other than these are scarce (Villaça & Yoneshigue 1987; Cordeiro *et al.* 2014), and this lack of knowledge is worrisome.

Even though most biological aspects of *P. gaimardi* are poorly known, until 2018 it was considered as a vulnerable species according to Brazilian environmental authorities (Ventura *et al.* 2008; ICMBio 2018). While under this threatened status (*i.e.*, from 2008 to 2018), there was an increase in the number of studies addressing this species (Calderon *et al.* 2009, 2010; Lopes & Ventura 2012; Duarte *et al.* 2016), but only Cordeiro *et al.* (2014) addressed relevant aspects other than color variation or reproduction. In this context, this study aims to contribute toward a better understanding of *P. gaimardi*, by providing relevant information on its behavioral and feeding habits. Based on field and laboratory observations, data on covering behavior and some food items were obtained.

Material and Methods

Six specimens of *Paracentrotus gaimardi* (three grays and three green-colored specimens) found under rocks, were collected by free diving, at a depth of 1.5–2.0 m. Gray specimens were collected in September 2016 and April 2017, while the green ones were gathered in November 2017, at Praia Grande, São Sebastião, São Paulo State, Brazil (23°49'24" S, 45°25'01" W). Gray specimens were transported in a 10L container and transferred to a large aquarium (80L) containing other organisms (*e.g.*, echinoderms and crustaceans) at the *Laboratório de Biologia Celular de Invertebrados Marinhos* (IB–USP). Physicochemical parameters were weekly monitored (Temperature = 24 ± 2°C, Salinity = 34 ± 1 ppt, pH = 8.0 ± 0.1, constant aeration). Gray animals were fed once a week with frozen algae (*Galaxaura* sp. and *Ulva lactuta*) (Queiroz 2018), collected at the same place as the echinoids. Green specimens were maintained in a semi-enclosed system (a 10L aquarium containing one small *E. lucunter*, and supplied with running saltwater pumped-in directly from the sea) at the *Centro de Biologia Marinha* (CEBIMAR–USP), and fed once a week with live *Galaxaura* sp., *Padina* sp., and *U. lactuta*, also collected at the same place as the green individuals. In both cases, after a one-week acclimation period, the behavior

and feeding habits were monitored in a qualitative approach for 45 days. After analysis, all individuals were returned to the sea.

Results

Behavioral aspects

In the field, all specimens of *Paracentrotus gaimardi* were found under rocks, mostly next to sponges, ascidians, or algae and usually covered with debris. All individuals maintained the covering behavior in captivity (**Figure 1A**), using any available material to cover themselves (*i.e.*, rocks, algal blades, and sea urchin spines and tests). They also showed a negative phototaxy (mainly the gray specimens), avoiding the light and looking for sheltered (and darker) places (**Figure 1B**). *Paracentrotus gaimardi* seemed more active at night, crawling over all aquarium substrates during this period. Throughout the day, all specimens spent most of the time hidden among rocks or in the aquarium corners. Aquarium observations showed that, in sandy bottoms, this species can dig and bury itself.

Feeding habits

During the sampling procedures, two gray specimens were caught with algae remains between their teeth. The remaining individuals – one gray and three green – were found under rocks, with no food in the oral aperture. In captivity, the red algae *Galaxaura* sp. (**Figure 1C**) and the green algae *Ulva lactuta* were offered to gray individuals, which fed on both, but the red algae seemed to be preferred because it was eaten first. Additionally, all three gray specimens were also observed feeding on the sponge *Hymeniacidon heliophila* and a dead individual of *Echinometra lucunter* (**Figure 1D–E**). In both situations, the sea urchin showed the same behavioral pattern: they found the animal prey and spent about 30 minutes on it; then disengaged from the victim and went back to their shelters. Green specimens (**Figure 1F**) were fed directly with *Galaxaura* sp., *Padina* sp., and *U. lactuta*. Pieces of these macroalgae were placed in the aquarium and were eaten a while later. Considering the food items offered to the green specimens, *Galaxaura* sp. was the preferred algae since it was always consumed first. Only after eating all the red algae, the green individuals started to eat *Padina* sp. *Ulva lactuta* was usually consumed as the last option. *Gracilaria* sp. and *Dictyota* sp. were also offered, but the echinoids did not feed on them. Two green *Paracentrotus gaimardi* specimens were also observed feeding on dead specimens of *E. lucunter*.

Discussion

In this study, complementary data about the alimentary habits of *Paracentrotus gaimardi* are provided, as well as for the first time some behavioral aspects are described. This species showed a nocturnal activity, associated with a negative phototaxy, as well as a noteworthy covering behavior. Considering the alimentary aspects, it was able to feed on three algae species (*Galaxaura* sp., *Padina* sp., and *Ulva lactuta*) and on live and dead animals: the sponge *Hymeniacidon heliophila* and the echinoid *Echinometra lucunter*.

Paracentrotus gaimardi is usually found in intertidal and sublittoral zones (0–5 m depth – Giordano 1986; Netto 2006), being able to dig small holes on rocks in which it can live along with other conspecific individuals (Giordano 1986; Cordeiro *et al.* 2014). It is also capable of burying itself in soft substrates, as observed in this study. Although *P. gaimardi* has been said to occur in aggregations on top of rocks (Giordano 1986), with different color morphs living in the same microhabitat (Calderon *et al.* 2010; Lopes & Ventura 2012), the gray and green specimens collected during this study were found alone under rocks.

Heaping or covering behavior in *Paracentrotus gaimardi* seems to be as pronounced as in *P. lividus* (Crook *et al.* 1999; Verling *et al.* 2002). In this study, both field and captivity individuals were always covered with debris. Floating particles, UV light, age, among other factors have been said to trigger covering behavior in *P. lividus* (Crook *et al.* 1999; Richner &

Milinski 2000; Verling *et al.* 2002). However, heaping seems to be far more complex and can be modulated not by one factor at a time, but by multiple factors acting at the same time (Dummont *et al.* 2007). Here, no factors were identified as a possible trigger for this behavior.

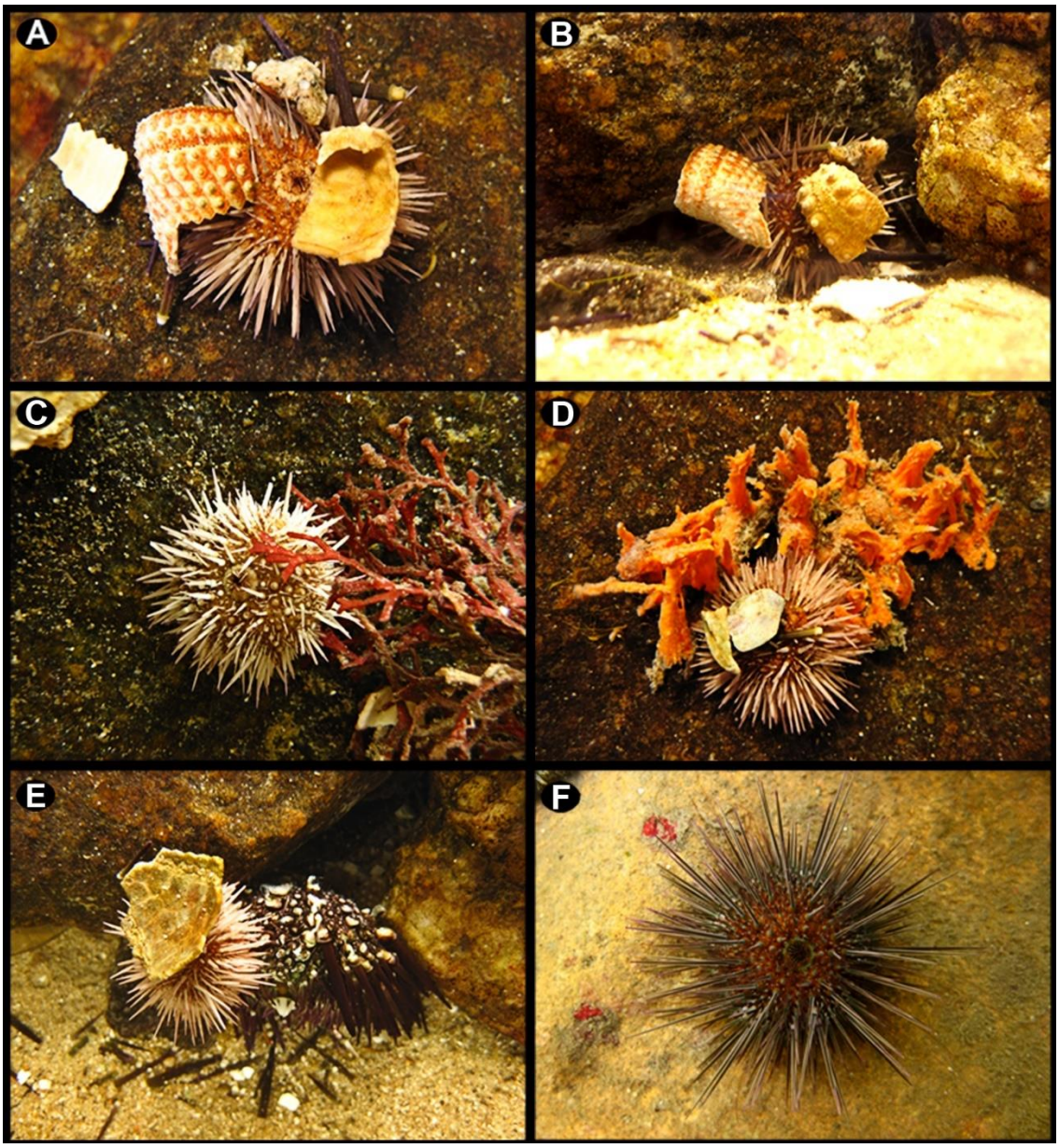

Figure 1. Some biological aspects of the gray and green color morphs of *Paracentrotus gaimardi* observed in the laboratory: **A**. Covering behavior of a gray specimen (2.8 cm test diameter); **B**. Individual hidden among rocks, avoiding strong light; **C–E**. Gray specimen feeding on *Galaxaura* sp., *Hymeniacidon heliophila* and *Echinometra lucunter*, respectively; **F**. Green color morph (3.5 cm test diameter).

Predation was already hypothesized as an explanation to the covering behavior (Milligan 1915; Ebling *et al.* 1966), however, other studies showed that this is likely not the case (Dummont *et al.* 2007; Zhao *et al.* 2014). Indeed, the independence between covering behavior and predation is consistent with our observations on *Paracentrotus gaimardi*, since: (I) it exhibited this behavior even with no predators in the aquarium, and (II) the presence of predators such as crabs and the starfish *Echinaster brasiliensis* did not produce any alterations. Thus, it is clear that even being observed in many sea urchins (Milligan 1915; Mortensen 1943; Millott 1956; Yoshida 1966; Dix 1970), its functional significance is still under debate (Zhao *et al.* 2014; Ziegenhorn 2016).

Paracentrotus lividus has been regarded as an herbivore species with an extensive list of food items, which is comprised mostly of algae (more than 95% – Boudouresque & Verlaque 2013). *Paracentrotus gaimardi* followed the same pattern, and as far as I know, algae were the main item recorded (**Table 1**). Boudouresque & Yoneshigue (1987) reported that *P. gaimardi* can feed on at least 36 different algae species, mostly (62.8%) Rhodophyta. However, brown species seem to be the most preferred by this sea urchin since up to 51% of stomach content can consist of *Sargassum furcatum* (Boudouresque & Yoneshigue 1987). Although the numbers are higher to *P. lividus*, *i.e.* 77 algae species, including 36 red, 22 brown, and 19 green, the pattern is very similar, since most species are Rhodophyta, and brown and green algae have similar amounts (Boudouresque & Verlaque 2013). Still, brown species seem to be the preferred food item of *P. lividus*: 86.36% of the recorded Ochrophyta (19 from 22) were considered "preferred" (Boudouresque & Verlaque 2013).

Table 1. Food items recorded to *Paracentrotus gaimardi*. Legend: a = Boudouresque & Yoneshigue (1987); b = Present study; C = Class; O = Order.

Phylum	Inner taxa	Species
Rhodophyta (Red algae)	Acrochaetiales O	*Acrochaetium* sp. [a]
	Ceramiales O	*Centroceras clavulatum* [a]
		Ceramium codii [a]
		Ceramium gracilimum var. byssoideum [a]
		Ceramium luetzelburgii [a]
		Ceramium sp. [a]
		Ceramium tenuissimum [a]
		Herposiphonia secunda [a]
		Neosiphonia ferulacea [a]
		Polysiphonia or Lophosiphonia sp. [a]
		Polysiphonia scopulorum [a]
	Erythropeltidales O	*Erythrotrichia carnea* [a]
	Nemaliales O	***Galaxaura* sp.** [b]
	Gelidiales O	*Gelidium crinale* [a]
		Pterocladiella capillacea [a]
	Gigartinales O	*Gymnogongrus griffithsiae* [a]
		Wurdemannia miniata [a]
	Corallinales O	*Jania capilaceae* [a]
		Titanoderma sp. [a]
		Fouling Corralinaceae [a]
	Plocamiales O	*Plocamium brasiliense* [a]
	Stylonematales O	*Stylonema alsidii* [a]
Ochrophyta (Brown algae)	Scytosiphonales O	*Colpomenia sinuosa* [a]
	Ectocarpales O	*Ectocarpus rallsiae* [a]
		Feldmannia mitchelliae [a]
	Dictyotales O	***Padina* sp.** [b]
	Fucales O	*Sargassum furcatum* [a]
		Sargassum tribuloides [a]
	Sphacelariales O	*Sphacelaria* sp. [a]
	Phaeophyceae C	Indetermined Phaeophyceae [a]
Chlorophyta (Green algae)	Cladophorales O	*Cladophora* sp. [a]
	Bryopsidales O	*Codium intertextum* [a]
		Codium spongiosum [a]
	Ulvales O	*Ulva fasciata* [a]
		Ulva flexuosa [a]
		Ulva lactuta [b]
		Ulva sp. [a]
		Ulvella viridis [a]
Porifera	Demospongiae C	***Hymeniacidon heliophila*** [b]
Echinodermata	Echinoidea C	***Echinometra lucunter*** [b]

Considering the algae species used in this study, interesting aspects were observed. First, *Galaxaura* sp. is the first species from the family Galaxauracea recorded as food for *Paracentrotus* (Boudouresque & Yoneshigue 1987; Boudouresque & Verlaque 2013); second, *Gracilaria* sp. and *U. lactuta* were avoided by *P. gaimardi*, as also observed in *P. lividus* (Boudouresque & Verlaque 2013); third, *Padina pavonica* and *Dictyota* species were one of the "most preferred" brown algae species to *P. lividus*, however, *P. gaimardi* avoided *Dictyota* sp. Although the data provided here have suggested many similarities in food preference between *P. gaimardi* and *P. lividus,* a more systematic study should be conducted to confirm the laboratory observation described here.

There is no doubt that *Paracentrotus'* diet is based on algal biomass (Boudouresque & Yoneshigue 1987; Boudouresque & Verlaque 2013). Nevertheless, invertebrate fragments were already identified in their gut content (Niell & Pastor 1973; Boudouresque & Yoneshigue 1987). The lack of direct evidence of animal predation by *Paracentrotus* sea urchins may suggest that the invertebrate fragments in *P. gaimardi* and *P. lividus*' guts may have been ingested accidentally during algal consumption. However, in addition to presenting a behavior compatible with the predatory activity, *P. gaimardi* was observed preying directly on *Hymeniacidon heliophila* and *Echinometra lucunter*. Actually, Antarctic Echinidae and Cidaridae can use bryozoans as an important food source (Jacob *et al.* 2003), as well as *Strogylocentrotus droebachiensis* can feed on the mussel *Mytilus edulis* when algal supply is depleted (Briscoe & Sebens 1988). Hence, the data presented here give support to the idea that animal ingestion by *Paracentrotus* echinoids was not by chance.

Presumably, an animal-based diet might improve echinoid's nourishment, providing proteins, fatty acids, and other nutrients less available in algal tissue (Briscoe & Sebens 1988; Barberá *et al.* 2011). Indeed, animal tissue consumption produced an increase in gonad and test growth in *Paracentrotus lividus* (Fernandez & Boudouresque 1998). This alternative is congruent with aquarium observations on *P. gaimardi*: although algal biomass has periodically been offered to *P. gaimardi*, *Hymeniacidon heliophila* and *Echinometra lucunter* may have been used as a supplementary food source.

There is an immense contrast between the extensive knowledge of *Paracentrotus lividus* and the limited available information on *P. gaimardi*. Even the basic biological aspects are poorly known to this later. Thus, this study contributes to a better understanding of *P. gaimardi* biology, showing that many biological aspects are shared with its Mediterranean congener. Here, it is shown that covering behavior is as noteworthy in *P. gaimardi* as it is in *P. lividus* and that in general, algal preferences are similar. Still, *Galaxaura* sp. and *Padina* sp. seem to be good food options for *P. gaimardi* in the laboratory, but maybe its diet should also include some animal protein to supplement its nourishment. Lastly, three species of algae and two invertebrates are added to its list of potential food items (**Table 1**). Under these circumstances, although systematic studies are necessary to confirm the similarities in the biology of *Paracentrotus* sea urchins, this study provides evidence that comparisons between *P. gaimardi* and *P. lividus* are appropriate.

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