



## Feeding habits of the sea urchin *Echinometra lucunter* L. (Echinoidea) in a remote Southwestern Atlantic island, Trindade, Brazil

YARA A. G. TAVARES<sup>1</sup>, NATALIE P. SEMANOVSKI<sup>1</sup>, JÉSSICA C. M. CAMARGO<sup>1</sup>, & FRANCIANE PELLIZZARI<sup>2</sup>

<sup>1</sup> Laboratório de Biologia Marinha, Colegiado de Ciências Biológicas, Universidade Estadual do Paraná. Rua Comendador Correa Júnior, 117, Paranaguá, Paraná, 83203-560. Brasil.

<sup>2</sup> Laboratório de Ficologia e Qualidade de Água Marinha, Colegiado de Ciências Biológicas, Universidade Estadual do Paraná. Rua Comendador Correa Júnior, 117, Paranaguá, Paraná, 83203-560. Brasil.

\*Corresponding author: [yara.tavares@unespar.edu.br](mailto:yara.tavares@unespar.edu.br)

**Abstract:** This investigation analyzed the food contents of *Echinometra lucunter* specimens from Trindade, an oceanic island in the Southwestern Atlantic, between 2014 and 2016. Forty-one macroalgae taxa represented by Rhodophyta (18), Chlorophyta (11), Phaeophyceae (11), four species of Cyanobacteria, and one species of Bacillariophyta were registered. Faunal taxa richness was incipient, mostly represented by Littoriniidae. The echinoids ( $39.8 \pm 6.2$  mm test diameter and  $31.4 \pm 12.4$  g wet weight) showed a predominantly herbivorous diet, mostly for filamentous algae. Seasonality in the sea urchin diet may be strongly associated with macroalgae availability. The feeding behavior of *E. lucunter* in the Brazilian territory suggests a typical trophic generalism with distinct preferences depending on the food availability or morphofunctional groups among distinct populations. Studies focusing on sea urchin feeding habits in remote islands can advance research on the marine ecology of benthic communities in isolated environments.

**Keywords:** Echinoids, Diet, Seaweed, Insular environment, South Atlantic.

**Resumen:** Hábito alimenticio del erizo *Echinometra lucunter* L. (Echinoidea) en una isla remota del Atlántico Sur, Trindade, Brasil. Esta investigación analiza el contenido alimenticio de individuos de *Echinometra lucunter* de Trindade, una isla oceánica del Atlántico Sur, entre los años 2014 y 2016. Fueron registrados 41 taxa de macroalgas representados por Rhodophyta (18), Chlorophyta (11), Phaeophyceae (11), cuatro especies de Cyanobacteria y una de Bacillariophyta. La riqueza de taxa animal fue incipiente, compuesta principalmente de Littoriniidae. Los erizos ( $39.8 \pm 6.2$  mm de diámetro de caparazón y  $31.4 \pm 12.4$  g de peso húmedo) mostraron una dieta predominantemente herbívora, fuertemente asociada a la disponibilidad de macroalgas, principalmente de algas filamentosas. El comportamiento alimenticio de *E. lucunter* en territorio brasileño sugiere un típico generalismo trófico con preferencias específicas para diferentes poblaciones. Estudios centrados en hábitos alimenticios de erizos en islas remotas representan una contribución importante para el conocimiento de ambientes biogeográficamente aislados.

**Palabras clave:** Echinoideos, Dieta, Macroalgas, Ambiente insular, Atlántico Sur

### Introduction

Echinoids are important components of marine benthic trophic webs worldwide (Hay 1984, Rex *et al.* 2006, Blicher *et al.* 2007), often serving as

primary consumers, predators, and eventually representing key species that provide food for higher trophic levels (Prince 1995, Estes *et al.* 2011, Lawrence *et al.* 2013). Echinoid feeding preferences

and their relationships with benthic communities have been extensively studied in several coastal habitats for more than 40 years (Lawrence 1975, Liyana-Pathirana *et al.* 2002, Heflin *et al.* 2012). Sea urchins generally compete for feeding resources with other marine herbivores, consuming mainly a high biomass of seaweed that might lead to the exclusion of other competitors (Kasamatsu 2012). Echinoid grazing activity affects macroalgae coverage and composition considerable, thus studies related to sea urchin feeding are fundamental for understanding the effect of these organisms in marine ecosystems (McClanahan & Muthiga 2001).

*Echinometra* species are commonly rock-boring echinoids that live in sub-to-intertidal ecosystems. Most of them are tropical and are commonly found in shallow waters throughout the West African coast, St. Helena and Sao Tome islands (McCartney *et al.* 2000). The seven species of the genus have omnivorous habits, feeding mainly on macroalgae, and occasionally on other organisms such as sponges, mollusks, and corals (McClanahan & Muthiga 2007).

*E. lucunter* is a tropical-subtropical species with a wide distribution from North Carolina, USA, throughout the Caribbean, and southward to Brazil (McPherson 1969, Hendler *et al.* 1995). This species inhabits diverse ecosystems and is commonly abundant in areas of irregular bottoms and other hard rock substrata, such as beachrock, coral reefs, and seagrass beds (Prince 1995, Lewis & Storey 1984, Ebert *et al.* 2008).

Current knowledge about *E. lucunter* feeding biology along the Brazilian coast is only based on the South and Southeastern populations (Oliveira 1991, Tavares 2004, Mendes & Tavares 2006), and is limited to neritic regions, with no record of *E. lucunter* in offshore environments. In the Brazilian territory, there are five oceanic islands, known as protected marine conservation areas: *Trindade e Martin Vaz*, *Fernando de Noronha*, *São Pedro e São Paulo* archipelagos and *Atol das Rocas* (Serafini *et al.* 2010). These environments have a particular biodiversity due to their biogeographical isolation, which often leads to unique biota with different degrees of endemism (Almeida 2006, Martins *et al.* 2016, Pellizzari *et al.* 2020).

These isolated Brazilian oceanic islands are excellent models for macroecological and phylogenetic studies to understand species composition and biological traits. Recently, Martins *et al.* (2016) updated the inventory of the

Echinodermata group with *E. lucunter*, one of the seven echinoid species listed along Trindade Island. Pellizzari *et al.* (2020) recently listed 60 new records of seaweed and 20 filamentous cyanobacteria from Trindade. Along the island, a total of 141 species of seaweed were identified, mainly among the turfs and algal mats, which as a functional group represent the higher biomass of primary producers in Trindade.

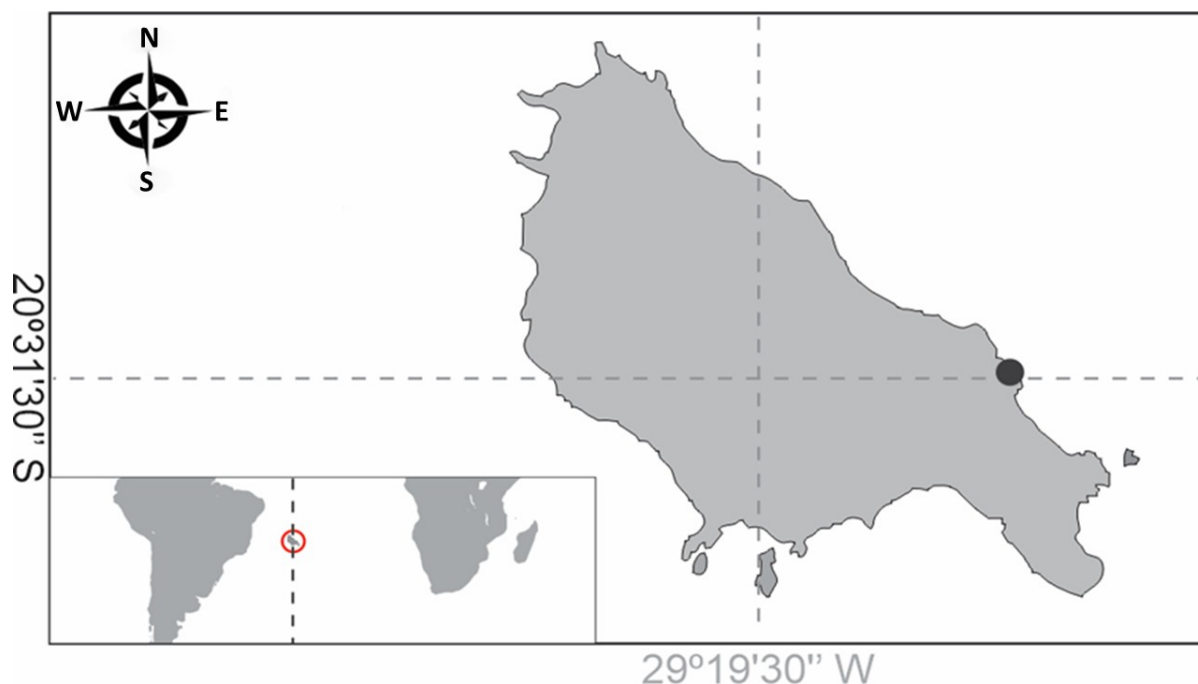
Studies focusing on sea urchins are of extreme importance in remote environments due the possibility to compare them with coastal echinoids feeding habits along the Southern Atlantic, either as an economic resource or as a key-species in these habitats. Thus, considering the absence of similar studies along the Brazilian Oceanic Islands, the present study aims, to provide information about feeding habits of *E. lucunter*, from Trindade island.

### Material and Methods

**Study area:** Trindade Island is located at 20°32'S and 29°21'W, approximately 1.170 km from the Brazilian coast, along a submarine chain (Pires *et al.* 2013). The island is an emergent portion (at a 5.500 m depth) of the Vitoria-Trindade submarine chain (ca. of 1000 km long), and integrates the oriental part of the intersection of two oceanic volcanic chains, facing E-W, that erected from the abyssal zone of the South Atlantic Ocean approximately three million years ago (Alves 1998, Almeida 2002). The island (9.28 km<sup>2</sup>) is surrounded by depths of approximately 5.000 m (Calliari *et al.* 2016, Santos-Silva *et al.* 2018) (Fig.1).

The southeast trade winds prevail with an average speed of 6.6 m. s<sup>-1</sup> and are stronger between July and September (11 m.s<sup>-1</sup>). During the austral winter (April to October), the strongest winds come from extra-tropical cyclones that generate high-speed south and southeast winds (Manso *et al.* 2011, Calliari *et al.* 2016). The region is characterized by high salinity (ca. of 37 psu) and water transparency up to 50 m deep (Alves 1998, Silveira *et al.* 2000). The area is under the influence of the complex circulation of the Subtropical Gyre, receiving influences from the Brazilian, South Atlantic, and South Equatorial currents (Sissini *et al.* 2017) and still receives vortices from the Agulhas Current and Angola-Benguela Front (Pellizzari *et al.* 2020).

The Trindade coastline has reentrances and coves supported by eruptive rocks that are conspicuous around the island (Almeida 2002). The island has 14 beaches, one of them is Andradas Beach (20.5°12'09 S/29.3°07'63"W), the focus of the



**Figure 1.** Map of Trindade Island: The full black circle indicates the sampling site (Andradas Beach). Brazilian coast (left/bellow), the red circle indicates the Trindade Island geographic position in the Southwestern Atlantic Ocean.

present study, which is a typical beachrock located in the eastern sector of the island. This area is characterized by high alkalinity provided by several pyroclasts, crustaceans, and red and calcareous algae reefs that are composed mainly of Rhodophyta (Pires *et al.* 2013, 2016).

**Sampling:** The sampling surveys were performed over three years, during seven cruises: autumn 2014 (April), winter 2014 (July), summer/autumn 2015 (February and April), spring 2015 (October), and summer/autumn 2016 (February and April). The project was supported by the Brazilian Navy ship, and researchers lodged in the ECIT (Trindade Island Scientific Station). Ten to fifteen echinoids were collected at low tides during each sampling cruise. Superficial seawater temperature (SST) and UV radiation were selected as abiotic parameters for comparison with the biological data. SST was measured with a portable/digital field thermometer and UV radiation data were retrieved from the Trindade Island Meteorological Station database (Hydrography and Navigation Office website, Brazilian Navy).

The echinoids were fixed in a 10% formalin solution and then properly stored for transportation to the university laboratories. Each specimen's test diameter was measured (digital caliper: 0.01 mm) and weighed fresh (total wet weight, TWW) using a semi-analytical balance Mark M223 (0.0001 g precision). Then, all the specimens were eviscerated

to remove their whole digestive tracts and separate their gut contents.

The food items were sorted according to their nature (phytological or faunal) under a stereomicroscope (Bel Photonics Ang Global Optics NO106). Faunal and seaweeds taxa were sorted among sea urchin gut content samples, washed and fixed with 4% formalin diluted in seawater for further taxonomic analyses. All items were identified using a stereomicroscope and optical microscopy with phase contrast and an image capture system (Olympus CX31) with previously prepared histological slides.

The vegetative and reproductive features of the algae fragments and remains were used for identification, when possible, at the species level. Nomenclatural information, species distribution, and taxonomic status were described following Guiry & Guiry (1996). Classical morphological taxonomy was performed using comparative material, specialized and illustrated descriptions of the species from the Brazilian Oceanic Islands, southeastern and northeastern Brazilian literature (following Pellizzari *et al.* 2020). The macroalgae morphofunctional groups were classified following Steneck & Dethier (1994) and Littler & Littler (2000).

Gut content composition was analyzed by fauna and seaweed richness (total number of taxa or functional groups) (Dobzhansky & Pavan 1950, Henderson 2001, Magurran 2013) and taxa relative

occurrence frequency categorized using the Dajoz Constancy Index or DCI (Dajoz 1973) as occasional (< 25%), accessory (25-50%), constant (50-75%), and abundant (>75%) taxa using the formula:

$$DCI = \frac{n_i}{N} \times 100$$

where  $n_i$  is the number of appearances of each algae taxa in the gut content and  $N$  is the total number of samples (echinoids *per* season).

In order to compare food selection toward different macroalgae associations, these taxa were grouped into seven morphofunctional groups: filamentous, calcareous articulated, terete, dichotomous foliaceae, foliaceous and vesicular (adapted from Steneck & Dethier 1994).

Food intake during the feeding process was described using a physiological index that considered the temporal condition of the gut content relationships. Thus, the total gut content was weighed, the ash-free content was determined by measuring the weight loss after drying it in an air oven at 70°C for 3 hours and finally igniting it in a muffle furnace at 550°C for 1 hour (Agatsuma *et al.* 2002).

Two repletion indices were calculated: 1) the total repletion index or RI<sub>t</sub> and 2) inorganic gut content repletion index or RI<sub>in</sub> (Guillou & Michel 1994, Privitera *et al.* 2008, Murillo-Navarro & Jiménez-Guirado 2012), as following:

$$RI_t = \frac{TGC/ww}{WBW} \times 100$$

Where TGC/ww is total gut content wet weight, and WBW is wet body weight.

$$RI_{in} = \frac{(TGC/ww - AFGC/ww)}{WBW} \times 100$$

Where AFGC/ww is the ash-free gut content wet weight.

A one-way ANOVA was used to analyze the differences in the repletion index among seasons. Univariate tests using the software STATISTICA for Windows version 8.0 (StatSoft 2007) were conducted. Data normality and homogeneity were tested to ensure compliance with the assumptions of the ANOVA (Zar 1999). Significant differences were further defined using Tukey's test.

Multivariate analysis specifically an ordination technique - principal component analysis or PCA (Henderson 2001) was used to search for relationships between abiotic data (SST and UV radiation), fauna abundance, physiological indexes,

constancy categories relative values of the abundant, accessory and common algae taxa and occasional algae taxa richness (data not-transformed). This approach seeks to present graphically the relationship in terms of food composition between sea urchins gut contents samples through the time. The seasonal and annual categorization was adapted from Pellizzari *et al.* (2020) as follows: 1 (autumn 2014), 2 (winter 2014), 3 (summer and autumn 2015), 4 (spring 2015), and 5 (summer and autumn 2016).

## Results

**Abiotic data:** The abiotic data measured during this study (Table I) presented higher values of superficial seawater temperature (SST) (28.4–29.5°C) and UV radiation (10.1–12.3 mW/cm<sup>2</sup>) during summer/autumn of 2015 and 2016.

**Biotic data:** Ninety-three echinoids, with a mean total weight of 31.4 ±12.4 g (ranging from 45.0 to 84.6 g) and mean test length of 39.8 ± 6.2 mm (47.7 to 58.6 mm) were analyzed. Over the entire studied period, 48 taxa were identified from the echinoid gut contents: 40 seaweeds, four Cyanobacteria, one Bacillariophyta taxa (distributed into five morphofunctional groups), and three faunal invertebrate groups.

Regarding the faunal items, sixty-five marine invertebrate specimens of Littoriniidae not identified ( $n_i$ ) (58) and *Lottia sp.* (Lottiidae) (seven) were identified from the gut contents, besides one specimen of Tanaidacea  $n_i$ . The Dajoz constancy index (DCI) categorized all of them as accessory or occasional at least once during the sampling period (Table II).

Among the seaweed found in the sea urchin gut contents, 18 taxa of Rhodophyta, the most representative group (Ceramiaceae, Champiaceae, Corallinaceae, Cystocloniaceae, Dasyaceae, Delesseriaceae, Gelidiaceae, Gigartinaceae, Lithophyllaceae, Lomentariaceae, and Rhodomelaceae), 11 taxa of Phaeophyceae (Acinetosporaceae, Asteronemataceae, Dictyotaceae, and Sphacelariaceae), 11 taxa of Chlorophyta (Udoteaceae, Bryopsidaceae, Cladophoraceae, Caulerpaceae, Boodleaceae, Siphonocladaceae, and Ulvaceae), four taxa of Cyanobacteria (Oscillatoriaceae and Microcoleaceae) and one taxa of Bacillariophyta were identified (Table III). Some representative taxa are presented in Figure 2.

Filamentous specimens showed greater richness (29 taxa) compared to other groups, followed by terete or fleshy specimens (11 taxa).

**Table I.** Abiotic data monitored *in situ* at Andradas Beach (Trindade Island, Brazil) from 2014 to 2016. SST: superficial seawater temperature in Celsius degree, UV: Ultraviolet radiation in milliwatts per square centimeter.

	2014			2015		2016	
	autumn	winter	summer	autumn	spring	summer	autumn
<b>SST (°C)</b>	20.8	22.6	28.4	28.0	25.0	29.5	29.0
<b>UV (mW/cm<sup>2</sup>)</b>	5.0	5.7	10.2	6.0	9.5	12.3	10.1

**Table II.** Seasonal relative occurrence of marine invertebrate registered in the gut contents of *Echinometra lucunter* from Trindade Island (Andradas Beach) Brazil, sampled between 2014 and 2016. ni: not identified, n: number of gut contents with faunal item registered, N: number of echinoids *per sample*.

Species/morphotypes	2014			2015		2016	
	autumn	winter	summer	autumn	spring	summer	autumn
<b><i>Lottia</i> sp.</b>	33,3	-	-	7,7	-	-	-
<b>Littorinidae ni</b>	-	-	35,7	25,0	21,4	26,6	-
<b>Tanaidacea ni</b>	8,3	-	-	-	-	-	-
<b>n:N</b>	5:12	0:15	5:14	4:13	3:14	4:15	0:10

The remaining groups together represented 6 taxa (Fig. 3).

**Statistical analysis:** Faunistic organisms (marine invertebrate) were the most representative organisms from the summer 2015 (n=21) and 2016 (n=18). Fewer than 10 individuals were identified from the autumn 2015 (n=8) and 2014 (n=7), and the spring 2015 (n=5). None of the invertebrates were registered during the winter of 2014 and autumn 2016. Littorinidae ni (n=51) was the most abundant taxa (DCI >75%) and *Lottia* sp. and Tanaidacea ni. were categorized as occasional (DCI <25%).

The seasonal richness of macroalgae and Cyanobacteria/Bacillariophyta were 20 spp. in almost all the austral seasons. A higher number of species were registered during the autumn and winter 2014 (21 spp. and 25 spp., respectively). Lower richness was observed during the summer 2015 (8 spp.) and autumn 2016 (14 spp.). Rhodophyta were the most representative group (ca. of 10 spp.), except during the summer 2015 (3 spp.) (Fig. 4).

The Dajoz constancy index (DCI) categorized a great majority of macroalgae and Cyanobacteria/Bacillariophyta as occasional (DCI <25%) among Rhodophyta (16 spp.), Chlorophyta (10 spp.), Phaeophyceae (10 spp.), Cyanobacteria (4 spp.) and Bacillariophyta (1 sp.). Only *J. adhaerens*, a calcareous branched form, was categorized as abundant (DCI >75%). The other five filamentous

specimens were categorized as constant (50 < DCI <75%) (*Sphacelaria* sp. and *C. clavulatum*) and accessory (25 < DCI <50%) (*Polysiphonia* sp., *L. majuscula*, and *Caulerpa* spp).

Seasonally, the following items were abundant in the sea urchin gut contents: *J. adhaerens* (during autumn, winter of 2014 and summer, autumn of 2015), *Centroceras clavulatum* (autumn and winter of 2014) and *Sphacelaria* sp. (summer, autumn and spring of 2015) (DCI >75%) (Fig. 5).

*Polysiphonia* sp., *Caulerpa* spp., *Sphacelaria* sp. represented constant taxa (50 < DI <75%) during the winter 2014 as well as *J. adhaerens* during the spring 2015, and summer and autumn 2016 and *C. clavulatum* (autumn 2016). Among the accessory taxa, *C. clavulatum* (summer and autumn 2015) and *Lyngbya majuscula* (summer/autumn 2015/2016) were the most representative (DCI between 40-50%).

The total repletion index (IRt) (annual mean±sd: 2.28±4.30) showed no variation (p<0.05) among all the samples, and the inorganic content repletion index (IRin) (0.61±0.48) ranged from 0.23% (autumn 2016) to 1.14% (spring 2015). A higher mean value during this month represents a significant difference among other seasons/years (F = 7.80; p <0.00001) (Figs. 6a-6b).

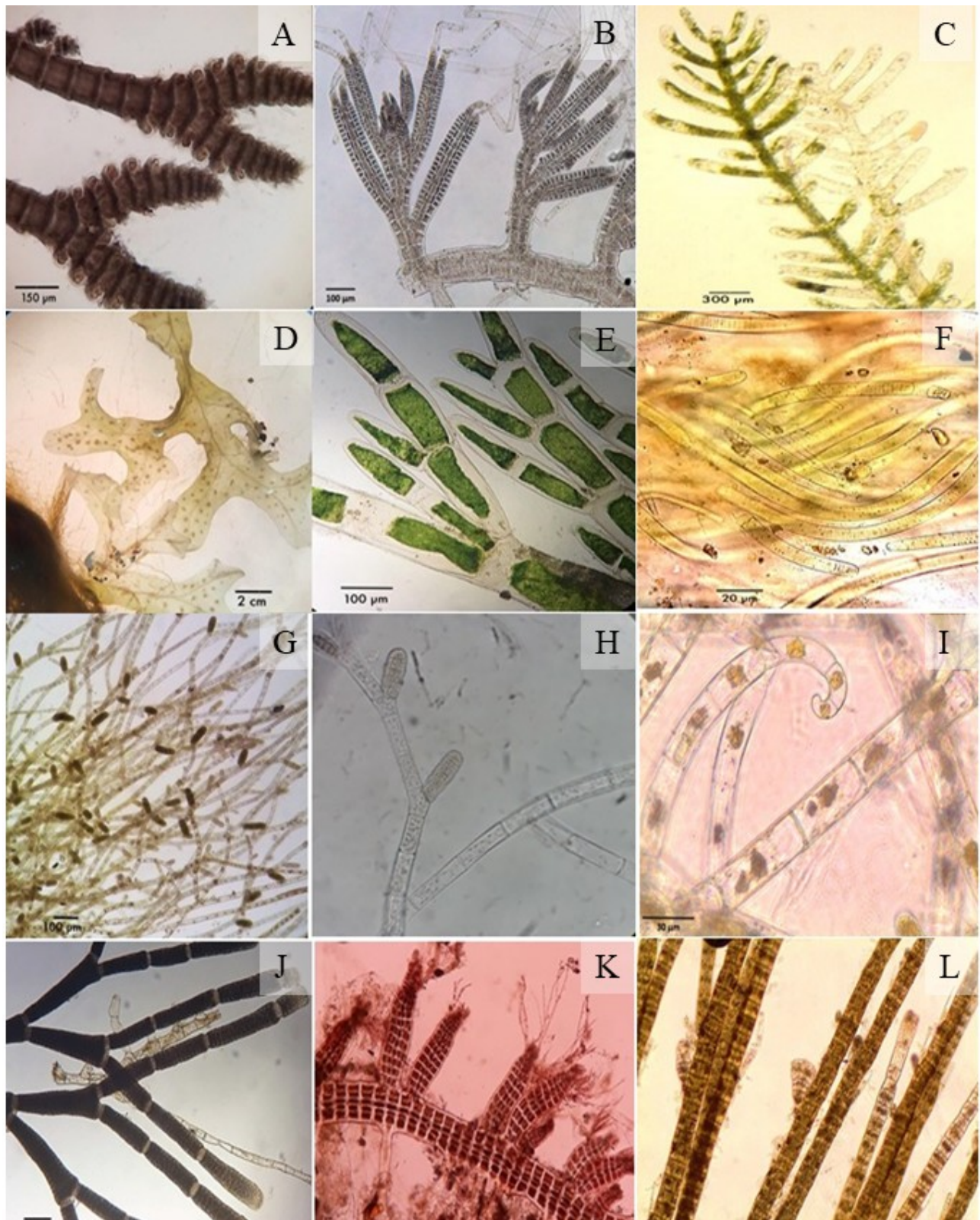
The PCA indicated that the first two dimensions (or factors 1 and 2) accounted for 77.5% of the whole variability of ecological, physiological,

**Table III.** List of macroalgae and Cyanobacteria/Bacillariophyta species and their respective morphofunctional groups registered in the gut contents of *Echinometra lucunter* from Trindade Island (Andradas Beach) from 2014 to 2016. F: Filamentous, CA: Calcareous Articulated, FOL: Foliaceous, T: Terete, V: Vesicular.

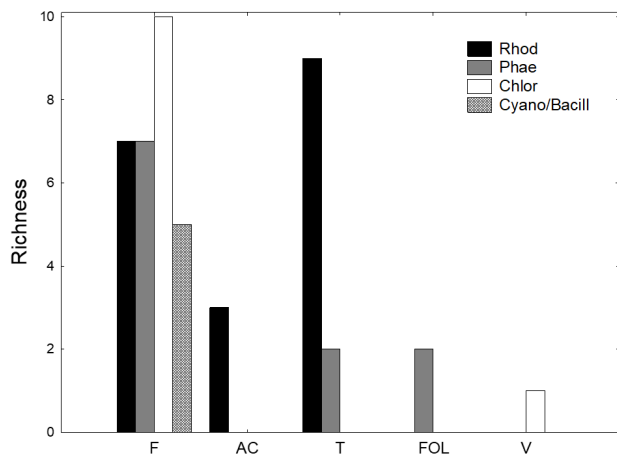
<b>Cyanobacteria/Bacillariophyta</b>		
<b>Oscillatoriaceae</b>	<b>Microcoleaceae</b>	<b>Asterionellopsidaceae</b>
<i>Lyngbya majuscula</i> (Gomont, M; 1892) <sup>F</sup>	<i>Sirocoleum</i> sp. <sup>F</sup>	<i>Asterionellopsis</i> sp. <sup>F</sup>
<i>Phormidium</i> sp. <sup>F</sup>		
<i>Oscillatoria</i> sp. <sup>F</sup>		
<b>Rhodophyta</b>		
<b>Ceramiales</b>	<b>Dasyaceae</b>	<b>Lomentariaceae</b>
<i>Ceramium</i> sp. <sup>F</sup>	<i>Heterosiphonia</i> sp. <sup>F</sup>	<i>Ceratodictyon</i> sp. <sup>T</sup>
<i>Centroceras clavulatum</i> (Montagne, 1846) <sup>F</sup>	<b>Delesseriaceae</b>	<b>Rhodomelaceae</b>
<b>Cystocloniaceae</b>	<i>Taenioma</i> sp. <sup>F</sup>	<i>Chondria</i> sp. <sup>T</sup>
<i>Hypnea</i> sp. <sup>T</sup>	<b>Gelidiaceae</b>	<i>Chondrophycus</i> sp. <sup>T</sup>
<b>Corallinales</b>	<i>Gelidium</i> sp. <sup>T</sup>	<i>Herposiphonia</i> sp. <sup>F</sup>
<i>Arthrocardia</i> sp. <sup>CA</sup>	<b>Gigartinales</b>	<i>Laurencia</i> sp. <sup>T</sup>
<i>Jania adhaerens</i> (J.V. Lamouroux, 1816) <sup>CA</sup>	<i>Chondracanthus</i> sp.	<i>Palisada</i> sp. <sup>T</sup>
<b>Champiaceae</b>	<b>Lithophyllaceae</b>	<i>Polysiphonia</i> sp. <sup>F</sup>
<i>Champia</i> sp. <sup>F</sup>	<i>Amphiroa</i> sp. <sup>CA</sup>	
<b>Phaeophyceae</b>		
<b>Acinetosporaceae</b>	<b>Bachelotiaceae</b>	<b>Ectocarpaceae</b>
<i>Feldmannia</i> sp. <sup>F</sup>	<i>Bachelotia</i> sp. <sup>F</sup>	<i>Ectocarpus</i> sp. <sup>F</sup>
<i>Hincksia</i> sp. <sup>F</sup>	<b>Dictyotaceae</b>	<b>Scytosiphonaceae</b>
<b>Asterocladaceae</b>	<i>Dictyota</i> sp. <sup>FOL</sup>	<i>Chnoospora</i> sp. <sup>T</sup>
<i>Asterocladon</i> sp. <sup>F</sup>	<i>Dictyopteris</i> sp. <sup>FOL</sup>	<b>Sphacelariaceae</b>
<b>Asteronemataceae</b>	<i>Padina</i> sp. <sup>FOL</sup>	<i>Sphacelaria</i> sp. <sup>F</sup>
<i>Asteronema</i> sp. <sup>F</sup>		
<b>Chlorophyta</b>		
<b>Udoteaceae</b>	<b>Cladophoraceae</b>	<b>Boodleaceae</b>
<i>Boodlopsis pusilla</i> (Taylor, W. R., 1953) <sup>F</sup>	<i>Cladophora</i> sp. <sup>F</sup>	<i>Cladophoropsis membranacea</i> (Børgesen, F., 1905) <sup>F</sup>
<i>Penicillus</i> sp. <sup>F</sup>	<i>Chaetomorpha</i> sp. <sup>F</sup>	<b>Siphonocladaceae</b>
<b>Bryopsidaceae</b>	<b>Caulerpaceae</b>	<i>Dictyosphaeria</i> sp. <sup>V</sup>
<i>Bryopsis</i> sp. <sup>F</sup>	<i>Caulerpa</i> sp. <sup>F</sup>	<i>Ulva chaetomorphoides</i> <sup>F</sup> (Hayden, H. S. & Blomster, J., 2003)
	<i>Caulerpa verticillata</i> (Agardh, J. G., 1847) <sup>F</sup>	
	<i>Caulerpa ambigua</i> (Okamura, K; 1897) <sup>F</sup>	

and abiotic factors (Fig. 7). The first plane from the 2-D plot was strongly correlated with SST, UV radiation, fauna abundance (S), richness of occasional algae taxa, and the most representative

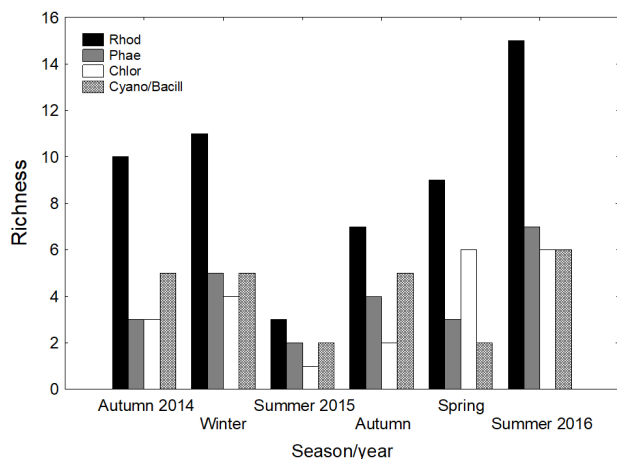
macroalgae species (*J. adhaerens*, *C. clavulatum*, *Polysiphonia* sp., *Caulerpa* spp., and Cyanobacteria *L. majuscula*). The second axis also showed a strong relationship with *Sphacelaria* sp. and IRin. Data



**Figure 2.** Some representative algal taxa of *Echinometra lucunter* gut content from Trindade island (Andradas Beach): (A) *Centroceras clavulatum*; (B) *Taenomia* sp.; (C) *Caulerpa* sp.; (D) *Dictyota delicatula*.; (E) *Cladophora* sp.; (F) *Lyngbya majuscula*; (G) *Feldmania* sp.; (H) *Feldmania* sp. filament; (I) *Asteronema breviarticulatum*; (J) *Jania adhaerens*.; (K) *Polysiphonia* sp.; (L) *Sphacelaria* sp. (Source: Melo, J. and Ito, C.).

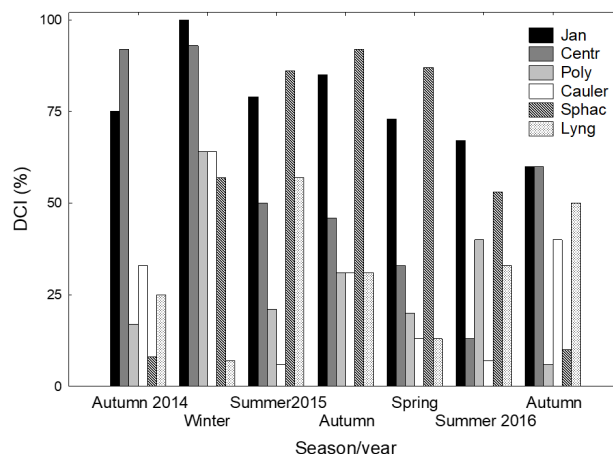


**Figure 3.** Richness of five morphofunctional groups of macroalgae and Cyanobacteria/Bacillariophyta registered in the gut contents of *Echinometra lucunter* from Trindade Island (Andradas Beach), Brazil from 2014 to 2016. F: filamentous; CA: calcareous articulated; T: Terete; FOL: foliaceous; V: vesicular; Rhod: Rhodophyta; Phae: Phaeophyceae; Chlor: Chlorophyta; Cyano/Bacill: Cyanobacteria/Bacillariophyta.



**Figure 4.** Seasonal richness of macroalgae and Cyanobacteria/Bacillariophyta taxa of *Echinometra lucunter* gut content from Trindade Island (Andradas Beach), sampled between 2014 and 2016. Rhod: Rhodophyta; Phae: Phaeophyceae; Chlor: Chlorophyta; Cyano/Bacill: Cyanobacteria/Bacillariophyta.

analysis revealed that two groups were negatively related: group I (SST + UV + fauna abundance + richness of occasional algae taxa + *L. majuscula*) to group II (*C. clavulatum* + *Caulerpa* spp. + *Polysiphonia* sp. + *J. adhaerens*). Group III, formed by *Sphacelaria* sp. and IRin, was completely isolated.



**Figure 5.** Seasonal relative occurrence of macroalgae and Cyanobacteria (DCI >25%) registered in the gut contents of *Echinometra lucunter* from Trindade Island (Andradas Beach), Brazil, sampled between 2014 and 2016. Jan: *Jania adhaerens*; Cent: *Centroceras clavulatum*; Cauler: *Caulerpa* spp.; Sphac: *Sphacelaria* sp.; Lyng: *Lyngbya majuscula*.

## Discussion

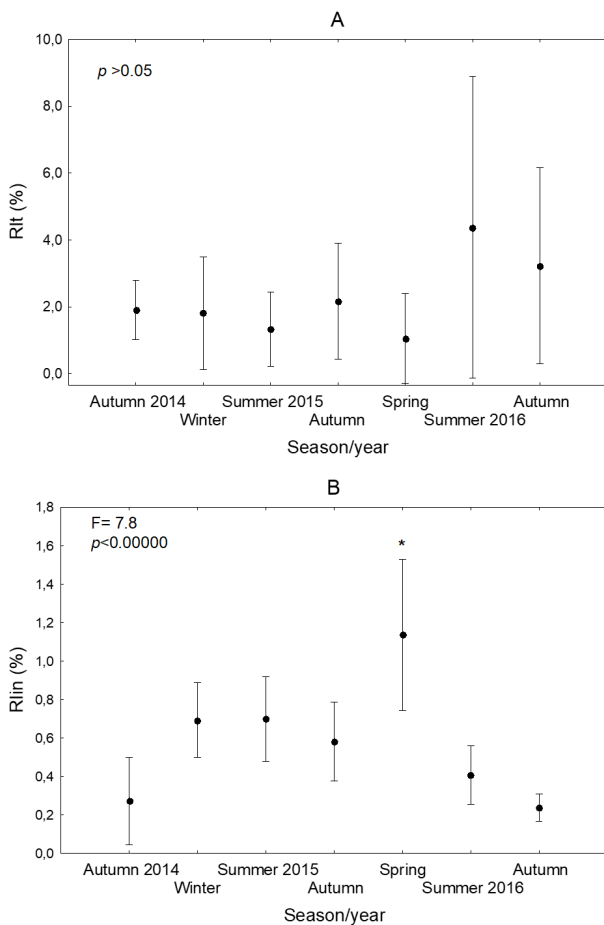
In the present study, the feeding habits of *E. lucunter* from Trindade in a South Atlantic insular environment, was investigated. *E. lucunter* showed a predominantly herbivorous diet, mostly composed by filamentous macroalgae and Cyanobacteria.

Along the latitudinal gradient (from United State to Brazil) the species, a dominant rock-boring sea urchin, was classified as herbivore (McPherson 1969, Oliveira 1991, Mendes & Tavares 2006) and sometimes as facultative omnivore with a tendency for herbivory (Tavares 2004, Reyes-Luján *et al.* 2015) (Annex, Table A-I).

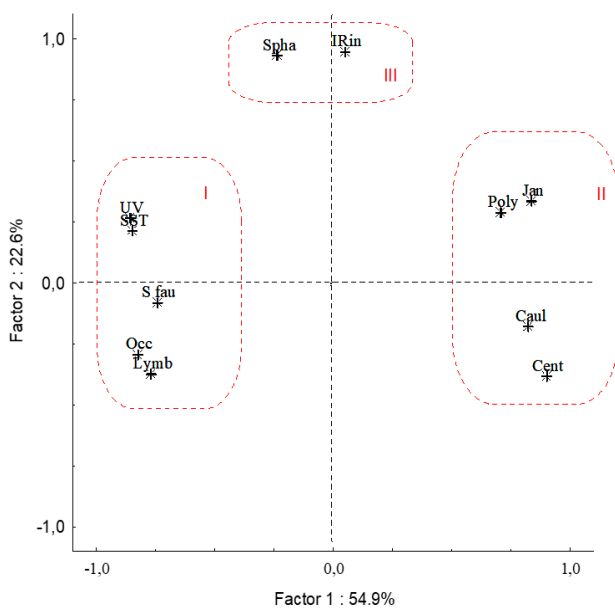
*E. lucunter* populations ingest predominantly macroalgae items, mostly Rhodophyta in coral reefs, with the expressive presence of crustose and calcareous articulated forms (*Jania* spp.). Mendes & Tavares (2006) also reported that in beachrock environments, there was a greater representativity of filamentous groups (*Ceramium* sp., *C. clavulatum*, and *Polysiphonia* sp.) or terete forms (*Gelidium* sp. and *Hypnea* sp.). The presence of Cyanobacteria taxa in *E. lucunter* gut content was only registered in Venezuela (Reyes-Luján *et al.* 2015) and Trindade populations.

Filamentous macroalgae and Cyanobacteria are quite abundant and have a higher richness in Trindade throughout the year, according to Pellizzari *et al.* (2020). The higher biomass and richness of filamentous marine Cyanobacteria is associated with abiotic changes around the globe, including remote islands in Antarctica (Pellizzari *et al.* 2017). Thus, if





**Figure 6.** One-way ANOVA results for total reptile index - IRt (A) and inorganic content reptile index - IRin (B) of *Echinometra lucunter* from Trindade Island (Andradas Beach), Brazil, sampled from 2014 to 2016. Significant season difference (\*) is indicated.



**Figure 7 (opposite).** Plot of principal component analysis (PCA) for feeding features of *Echinometra lucunter* plotted by seasons: Dajoz categories (abundant, accessory and common algae taxa), ecological parameter (richness), physiological index and abiotic factors (SST and UV radiation). Caul: *Caulerpa* spp.; Cent: *Centroceras clavulatum*; Jan: *Jania adhaerens*; Lymb: *Lyngbya majuscula*; Poly: *Polysiphonia* sp.; Spha: *Sphacelaria* sp.; Occ: richness of occasional algae taxa; S.fau: fauna abundance; IRin: inorganic content Repletion Index; SST: superficial seawater temperature, UV: ultraviolet radiation.

there is higher availability of these resources, it is also expected that consumption could increase. *E. lucunter* populations showed strong trophic opportunistic behavior (herbivorous or omnivorous), grazing preferentially upon the available benthic community, and following the seasonal occurrence of food items in the field (McLean 1967, Lawrence & Sammarco 1982, Lewis & Storey 1984, Blevins & Johnsen 2004, Mendes & Tavares 2006). In the present study, the high representativity of macroalgae items might indicate the great availability of food items in this insular environment. A recent update of the seaweed inventory from Trindade Island has identified 161 taxa that are mainly composed of Rhodophyta (36%) and Chlorophyta (34%), followed by Phaeophyceae (17%) and filamentous Cyanobacteria (12%) (Pellizzari *et al.* 2020). Rhodophyta predominance (Rhodomelaceae, Ceramiaceae, and Corallinaceae) compared to other groups is the main feature of the insular benthic algae community broadly described in this area (Sissini *et al.* 2017, Pellizzari 2019, Pellizzari *et al.* 2020). Moreover, these authors report that encrusting species and other turf species (Ceramiaceae and filamentous taxa from Bryopsidales covering articulated calcareous specimens) are among the most dominant morphofunctional species and have the highest biomass of the primary producers on Trindade Island.

The large number of filamentous forms as the main food content could be explained by the high disponibility of turf assemblages commonly found along the intertidal and subtidal coasts of all latitudes (Pellizzari *et al.* 2020). These algae associations, turfs, are composed by smaller size filamentous and terete algae (McClanahan & Muthiga 2007).

According to Cheroske *et al.* (2000) and Connell *et al.* (2014), turf associations are composed of small and delicate forms of branched filaments or blades (<1 mm diameter), including green and red

seaweed, such as *Cladophora*, Ulvales and *Polysiphonia*. Turfs can form persistent aggregations conforming substrates with bases formed by geniculate corallines, and they are covered with terete and foliaceous specimens such as *Laurencia* and *Dictyota* (Pellizzari *et al.* 2020). Thus, the large number of filamentous specimens present in *E. lucunter* gut content from Trindade Island might be related to the presence of turf assemblages, which are quite common in oceanic oligotrophic areas; consequently, the higher availability of these delicate filamentous shapes, not observed in the previously studied Brazilian coastal areas (Pellizzari *et al.* 2020).

An interannual change in diet items (species) was observed between spring-summer of 2015 and summer-autumn of 2016, with a predominance of the constant and accessory taxa *Sphacelaria sp.* and *L. majuscula*, followed by the decline of red species: *J. adhaerens* (calcareous articulated) and *C. clavulatum* (filamentous). This might reflect the opportunistic behavior of *E. lucunter* influenced by *in situ* food availability as well as the sea urchin preference for specific algal items. Although abundant and accessory algae taxa were conspicuous species, the species fluctuations observed were likely due to the seasonal variation in seaweed assemblages, corroborated by the previous inventory of Trindade Island (Pellizzari 2019).

According to Mendes & Tavares (2006), *E. lucunter* populations from the southeastern Brazilian coast, in contrast to our results (where *E. lucunter* populations grazed mainly on filamentous forms), consumed leathery, corticated, and crustose algae forms, revealing a completely different diet trend. To these authors, echinoid feeding behavior depends on algal availability, most likely following the seasonal occurrence and distribution of seaweed species in the field, which opposes the results found in the present study, where *E. lucunter* seems to show some level of preference, feeding on specific groups/species even though there is a large variety of algal taxa available, although further studies focusing on the algae biomass in the field must be done.

In addition, *E. lucunter* diet variations might be associated with trophic plasticity behavior, resulting in a broad diet choice due to the higher trophic niches of the populations along the latitudinal gradient, which was also observed for *Tetrapygyus niger* from Chilean intertidal communities (Navarrete *et al.* 2008). Trophic plasticity is widespread in wild populations and might explain some differences in sea urchin diets

(McLean 1967, Grunbaum *et al.* 1978, Beddingfield & McClintock 1998, Mendes & Tavares 2006, Navarrete *et al.* 2008, Lawrence *et al.* 2013, Rodríguez-Barreras *et al.* 2016).

This has also been corroborated by studies related to the grazing activities of many sea urchin populations such as *Evechinus chloroticus* (Wing *et al.* 2008), *Tripneustes gratilla* (de Loma *et al.* 2002, Väitilingon *et al.* 2003, Stimson *et al.* 2007), *Arbacia lixula* and *Paracentrotus lividus* (Bulleri *et al.* 1999, Wangensteen *et al.* 2011), *A. punctulata* and *Lytechinus variegatus* (Cobb & Lawrence 2005, Souza *et al.* 2008).

Differences in the habitats occupied by *E. lucunter* populations could also reflect their feeding habit plasticity and their ability to use multiple local food resources (Navarrete *et al.* 2008, Lawrence *et al.* 2013, Rodríguez-Barreiras *et al.* 2016). The seasonality observed in *E. lucunter* food contents at Andradas Beach might be associated with food availability; however, selecting specific functional groups (by species, shape or size) to be ingested. Thus, as suggested by Navarrete *et al.* (2008), while omnivorous generalist echinoids might use opportunistic strategies to obtain food resources, they are able to select among the taxa available, exhibiting some level of food preference. This corroborates the hypothesis that echinoids are typical trophic generalist organisms able to choose food items based on their greater abundance, diversity and/or palatability (Beddingfield & McClintock 1999, Mills *et al.* 2000, de Loma *et al.* 2002, Mendes & Tavares 2006). Moreover, echinoids with feeding plasticity should have a more complex trophic status, distinct from a typical primary consumer, and these could be applied to *E. lucunter* from Trindade island.

Knowledge of the behavioral mechanisms of echinoid feeding preferences in relation to the physiological aspects of digestion are fundamental to understanding sea urchin biology and ecology (Trenzado *et al.* 2012, Lawrence *et al.* 2013, Rodríguez-Barreras *et al.* 2016). Several studies have reported on the ingestion of hard substrata during grazing activity, suggesting constraints strongly imposed by the limited mobility of tropical-subtropical *Echinometra* species, such as *E. viridis* (McPherson 1969, McClanahan 1998), *E. mathaei* (McClanahan & Kurtis 1991, Mills *et al.* 2000), and *E. lucunter* (McLean 1967, Grunbaum *et al.* 1978, Ventura *et al.* 2003, Mendes & Tavares 2006). All populations living in beachrock and reef environments have their guts filled with a high

proportion of calcium carbonate from biogenic sediments as well as endolithic Cyanobacteria (Lawrence & Sammarco 1982, Lewis & Storey 1984, Blevins & Johnsen 2004).

Generally, in the digestive tract, the gut is considered to be the first site of nutrient accumulation (Lawrence & Sammarco 1982, Beddingfield & McClintock 1998, Väitilingon *et al.* 2003). The relative contribution of animal and algal matter in the gut may be quantified by the addition of the standardized feeding indices (repletion index) of all food ingested (cumulative feeding) (Klumpp *et al.* 1993, Maharavo *et al.* 1994, Wangensteen *et al.* 2011). Variations in the repletion index may lead to the facultative presence of substratum and must be interpreted with caution since, in some situations, this may coincide with the burrowing process during foraging activity (Lawrence & Sammarco 1982, Mills *et al.* 2000) and, therefore, cannot truly represent the food weight ingested (Lawrence 1975, de Loma *et al.* 2002). On the other hand, occasional increases in RI during a specific period of the year could also suggest a greater consumption of certain calcareous Rhodophyta (articulate or encrusting), as suggested by Murillo-Navarro & Jiménez-Guirado (2012).

In the present study, the total gut contents did not vary over time. However, in the PCA, the inorganic matter index was related to the occurrence of brown algae *Sphacelaria* sp., suggesting high ingestion of this species in addition to carbonate material (from eroded substrate or from calcareous algae). Thus, gut content wet weight could also be reflected by the magnification of burrowing behavior, which justifies the less accurate analysis of the feeding process using the repletion index without separating the ash fraction.

Sea urchin feeding preferences can also be explained by biological (age, nutritional status) and environmental (hydrodynamic, light, temperature, among other water parameters) effects, as well as the associative effects between food shape or the presence of attractants or stimulants in the food presented to the animal (Lawrence *et al.* 2013, Rodríguez-Barreras *et al.* 2016). Preferential feeding is often related to the nutritional value of food types and/or the presence of chemical substances in food that attract or repel echinoids (Beddingfield & McClintock 1998, 1999, Väitilingon *et al.* 2003).

One of the most characteristic descriptions of *E. lucunter* feeding behavior is the avoidance of less palatable forms of fleshy (terete) algae (Prince 1995, McClanahan 1998, Reyes-Luján *et al.* 2015).

Chemical defenses, usually produced by several seaweed species, such as the *Laurecia* complex and Dictyotales (Rhodophyta and Phaeophyceae, respectively) are one of the best-studied intrinsic properties that determine which species are preferred, avoided or indifferent to the grazers. Also, many marine Chlorophyta can produce chemical defenses (secondary metabolites) against herbivores (McClintock & Baker 2001, Amsler 2008). An experimental study by Erickson *et al.* (2006) suggested that *E. lucunter* is more sensitive to species of Chlorophyta (including Bryopsidales, *Ulva*, *Caulerpa* and *Halimeda*) that produce chemical defenses that inhibit herbivory.

Among brown seaweeds, those belonging to the genus *Dictyota* are known to produce lipophilic metabolites that can act as echinoid deterrents (Souza *et al.* 2008). Additionally, Vergés *et al.* (2011) concluded that morphology and fine-scale structural defenses are the primary determinants of sea urchin feeding behavior, suggesting macroalgae shape (functional groups) as the major choosing characteristic for echinoids, rather than nutrient content and chemical compounds. This might explain the specific preference of *E. lucunter* for branched calcareous and filamentous specimens, not depending on a specific algae group.

Under controlled conditions, Cruz-Rivera & Paul (2002) tested the feeding preferences of *E. mathaei* for autotrophic organisms as *Lyngbya majuscula* (Cyanobacteria), and they registered very low consumption of it. Like many eukaryotic algae, some marine Cyanobacteria may also have chemical defenses against macroherbivores (Pennings *et al.* 1997, Nagle & Paul 1998, 1999). However, according to Capper *et al.* (2016), *E. lucunter* is not inhibited by Cyanobacteria chemical compounds, emphasizing that this species might be well adapted to tolerate variations in metabolite production. Souza *et al.* (2008) discussed that the feeding preference of *L. variegatus* is probably controlled by chemicals, in association with seaweed features such as morphological structure. Our findings are in close agreement with theirs, which could be attributed to *E. lucunter*'s strong capacity to overgrow other species, as argued by Mendes & Tavares (2006).

Grazers organisms, such as sea urchins, as well as seaweeds, integrate a complex trophic system (Bustamante *et al.* 1995). Both are sensitive to abiotic changes at medium and large scales. Seasonal variations in surface seawater temperature, salinity, pH, and oceanic circulation patterns, which directly impact seaweed distribution, modify the

entire marine community structure, and consequently, herbivorous feeding rates (Rodríguez-Barreras *et al.* 2016, Pellizzari 2019, Nielsen & Navarrete 2004). Thus, changes in herbivorous echinoid feeding preferences may be related to the feeding resource fluctuations caused by these environmental conditions (Navarrete *et al.* 2008, Pellizzari *et al.* 2020).

Considering the abiotic data measured during the sampling period, superficial seawater temperature and UV radiation range presented differences between winter and summer. As suggested by Pellizzari (2017, 2019) in the last decade, abiotic changes have been reported to drive changes in marine communities, such as macroalgae richness and diversity, in intertidal zones around the globe (Tanaka *et al.* 2012, Duarte *et al.* 2013, Sangil *et al.* 2012). In contrast to data reported in coastal areas, species rarity, reduction and replacement of biomass, local extinctions or the predominance/substitution of specific groups of macroalgae has not been observed in Trindade Island (Pellizzari *et al.* 2020).

Oceanic islands represent only 5% of terrestrial earth coverage (Israel *et al.* 2010). Therefore, insular biodiversity is more vulnerable when compared to coastal environments due their interaction specificities with biotic and abiotic parameters and their geographic restrictions; they are more susceptible to contrasting conditions that may affect local populations and potentialize adaptative pressures (Serafini *et al.* 2010, Sjøtun *et al.* 2015).

Current global changes are inducing shifts in seaweed assemblages and ecosystem functionality. In addition, the occurrence of alien species is the second main cause of biodiversity loss, right after global climate changes (Serafini *et al.* 2010, Pellizzari 2019, Pellizzari *et al.* 2020). The direct impact of global climatic thermal rise is presumed to be minor due to the wide temperature tolerance of macroalgae, but the high richness of macroalgae make trophic web responses unpredictable (Israel *et al.* 2010). Thus, oceanic thermohaline changes may enhance turf algae biomasses to substitute for fleshy (terete) or foliose thalli, which implicates the opening of new trophic niches for the echinoids.

Additionally, anomalous oceanic circulation patterns may induce the rupture of biogeographic limits, favoring the expansion of alien species (Pellizzari *et al.* 2020). Specifically, considering macroalgae blooms and the global alien species increase, in the last decade, several new occurrences

were reported on Trindade Island due to the increasing number of opportunistic green seaweeds, such as Ulvales, Cyanobacteria and Bacillariophyta.

Although it is quite far from the coast, Trindade Island is connected to the mainland by seamounts, which probably contributes to the great species richness on this island (Martins *et al.* 2016, Sissini *et al.* 2017, Pellizzari 2019, Pellizzari *et al.* 2020). In addition to the high seaweed richness of Trindade Island, among the South Atlantic Oceanic Islands, Trindade endemism is low, suggesting the potential role of oceanic currents and seamounts as stepping-stones in the transoceanic dispersal of species to remote islands (Pellizzari *et al.* 2020).

Finally, there is a demand for further studies to investigate specific factors that may contribute to knowledge on meteorological and oceanographic changing events in Trindade Island, which influence and regulate the functioning of these model ecosystems, as well as the biology of the invertebrate benthic species that inhabit this biodiversity hotspot. Therefore, further studies should focus on the association of algal biomass and the function of burrowing animals, such as echinoids, to contribute to knowledge on benthic communities in this biogeographically isolated environment.

### Acknowledgements

We are grateful to Secretariat of the Interministerial Commission for the Resources of the Sea (SECIRM) logistical support via Brazilian Navy vessels. We thank to MSc. Michele Santos-Silva and colleagues of Laboratory of Phycology and Marine Water Quality (coordinator: Dr. FM Pellizzari) for the help in identifications and photographs. JCM Camargo thanks to Araucária Foundation for providing financial support by projects fellowship (No. 947/2013 and 006/2016 ID 4113201318202-9). YAG Tavares thanks CNPq (403940/2012-5) for financial support to the ProTrindade Project (Diversity and bioactivity of macroalgae of the Trindade Island and São Pedro and São Paulo Archipelago in front of climatic changes/ coordinator: Dr. FM Pellizzari).

### References

- Agatsuma, Y., Yamada, Y. & Taniguchi, K. 2002. Dietary effect of the boiled stipe of brown alga *Undaria pinnatifida* on the growth and gonadal enhancement of the sea urchin *Strongylocentrotus nudus*. **Fisheries Science**, 68(6): 1274-1281.

- Almeida, F. 2006. Ilhas oceânicas brasileiras e suas relações com a tectônica atlântica. **Terrae Didactica**, 2(1): 3-18.
- Almeida, F. F. M. 2002. A ilha da Trindade. Pp. 369-377. In: Schobbenhaus, C., Campos, D. A., Queiroz, E. T., Winge, M. & Berbert-Born, M. (eds). **Sítios geológicos e paleontológicos do Brasil**. DNPM/CPRM, Brasília, 523 p.
- Alves, R. J. V. 1998. **Ilha da Trindade & arquipélago Martin Vaz: um ensaio geobotânico**. Serviço de Documentação da Marinha, Brazil, 144 pp.
- Amsler, C. D. (Ed.). 2008. **Algal chemical ecology**. Springer, Berlin, 313 p.
- Beddingfield, S. & McClintock, J. 1998. Differential survivorship, reproduction, growth and nutrient allocation in the regular echinoid *Lytechinus variegatus* (Lam.) fed natural diets. **Journal of Experimental Marine Biology and Ecology**, 226(2): 195-215.
- Beddingfield, S. D. & McClintock, J. B. 1999. Food resource utilization in the sea urchin *Lytechinus variegatus* in contrasting shallow water microhabitats of Saint Joseph Bay, Florida. **Gulf of Mexico Science**, 17(1): 27-34.
- Blevins, E. & Johnsen, S. 2004. Spatial vision in the echinoid genus *Echinometra*. **Journal of Experimental Biology**, 207(24): 4249-4253.
- Blicher, M., Rysgaard, S. & Sejr, M. 2007. Growth and production of sea urchin *Strongylocentrotus droebachiensis* in a high-Arctic fjord, and growth along a climatic gradient (64 to 77 N). **Marine Ecology Progress Series**, 341: 89-102.
- Bulleri, F., Benedetti-Cecchi, L. & Cinelli, F. 1999. Grazing by the sea urchins *Arbacia lixula* L. and *Paracentrotus lividus* Lam. in the Northwest Mediterranean. **Journal of Experimental Marine Biology and Ecology**, 241(1): 81-95.
- Bustamante, R. H., Branch, G. M. & Eekhout, S. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. **Ecology**, 76(7): 2314-2329.
- Calliari, L. J., de Souza-Pereira, P., Short, A. D., Sobral, F. C., Machado, A. A., Pinheiro, Y. G. & Fitzpatrick, C. 2016. Sandy Beaches of Brazilian Oceanic Islands. Pp. 543-571. In: Short, A. D. & Klein, da F. A. H. (eds.). **Brazilian Beach Systems**. Springer, Switzerland, 609 p.
- Capper, A., Erickson, A. A., Ritson-Williams, R., Becerro, M. A., Arthur, K. A. & Paul, V. J. 2016. Palatability and chemical defences of benthic cyanobacteria to a suite of herbivores. **Journal of Experimental Marine Biology and Ecology**, 474: 100-108.
- Cheroske, A. G., Williams, S. L. & Carpenter, R. C. 2000. Effects of physical and biological disturbances on algal turfs in Kaneohe Bay, Hawaii. **Journal of Experimental Marine Biology and Ecology**, 248(1): 1-34.
- Cobb, J. & Lawrence, J. 2005. Diets and coexistence of the sea urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) along the central Florida gulf coast. **Marine Ecology Progress Series**, 295: 171-182.
- Connell, S. D., Foster, M. S. & Airoidi, L. 2014. What are algal turfs? Towards a better description of turfs. **Marine Ecology Progress Series**, 495: 299-307.
- Cruz-Rivera, E. & Paul, V. J. 2002. Coral reef benthic cyanobacteria as food and refuge: diversity, chemistry and complex interactions. **Proceedings of 9th International Coral Reef Symposium**, Bali, Indonesia, 515-520.
- Dajoz, R. 1973. **Ecologia Geral**. Vozes, São Paulo, 472 p.
- de Loma, T. L., Conand, C., Harmelin-Vivien, M. & Ballesteros, E. 2002. Food selectivity of *Tripneustes gratilla* (L.) (Echinodermata: Echinoidea) in oligotrophic and nutrient-enriched coral reefs at La Reunion (Indian Ocean). **Bulletin of Marine Science**, 70(3): 927-938.
- Dobzhansky, T. & Pavan, C. 1950. Local and seasonal variations in relative frequencies of species of *Drosophila* in Brazil. **The Journal of Animal Ecology**, 19(1): 1-14.
- Duarte, L., Viejo, R. M., Martínez, B., de Castro, M., Gómez-Gesteira M. & Gallardo T. 2013. Recent and historical range shifts of two canopy-forming seaweeds in North Spain and the link with trends in sea surface temperature. **Acta Oecologica**, 51: 1-10.
- Ebert, T. A., Russell M. P., Gamba G. & Bodnar A. 2008. Growth, survival, and longevity estimates for the rock-boring sea urchin *Echinometra lucunter* (Echinodermata, Echinoidea) in Bermuda. **Bulletin of Marine Science**, 82: 381-403.
- Erickson, A. A., Paul, V. J., Van Alstyne, K. L. & Kwiatkowski, L. M. 2006. Palatability of macroalgae that use different types of

- chemical defenses. **Journal of Chemical Ecology**, 32(9): 1883-1895.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington T. E. *et al.* 2011. Trophic downgrading of planet Earth. **Science**, 333: 301-306.
- Guillou, M., & Michel, C. 1994. The influence of environmental factors on the growth of *Sphaerechinus granularis* (Lamarck) (Echinodermata: Echinoidea). **Journal of Experimental Marine Biology and Ecology**, 178(1), 97-111.
- Guiry, M. D. & Guiry, G. M. 1996. **AlgaeBase**. World-wide electronic publication. URL <http://www.algaebase.org>. (Accessed 05/02/2020).
- Grunbaum, H., Bergman, G., Abbott, D. P. & Ogden, J. C. 1978. Intraspecific agonistic behavior in the rock-boring sea urchin *Echinometra lucunter* (L.) (Echinodermata: Echinoidea). **Bulletin of Marine Science**, 28(1): 181.
- Hay, M. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? **Ecology**, 65: 446-454.
- Heflin, L. E., Gibbs, V. K., Powell, M. L., Makowsky, R., Lawrence, A. & Lawrence, J. 2012. Effect of diet quality on nutrient allocation to the test and Aristotle's lantern in the sea urchin *Lytechinus variegatus* (Lam.). **Journal of Shellfish Research**, 31: 867.
- Henderson, P. A. 2001. **Ecological Methods**. Wiley Online Library Encyclopedia of Life Sciences © 2001, John Wiley & Sons, Ltd., accessible at <https://www.els.net>. (Accessed 12/01/2020).
- Hendler, G., Miller, I. E., Pawson, D. L. & Kier, P. M. 1995. **Sea stars, sea urchins, and aliens: echinoderms of Florida and the Caribbean**. Smithsonian Institution Press, Washington, D.C., 391 p.
- Israel A., Einav R. & Seckbach, J. (Eds.). 2010. **Seaweeds and their role in Globally Changing Environments**. Springer Science & Business Media B.V., 478 p.
- Kasamatsu, L. K. 2012. Análise espaço-temporal da composição da dieta, preferência alimentar e desenvolvimento de gônadas de *Lytechinus variegatus* (Lam.) no infralitoral rochoso da enseada de Parati-Mirim (Paraty, RJ) **PhD. Dissertation**. Universidade de São Paulo, São Paulo, Brazil, 130 p.
- Klumpp, D. W., Salita-Espinosa, J. T. & Fortes, M. D. 1993. Feeding ecology and trophic role of sea urchins in a tropical seagrass community. **Aquatic Botany**, 45: 205-229.
- Lawrence, J. 1975. On the relationships between marine plants and sea urchins. **Oceanography Marine Biology Annual Review**, 13: 213-286.
- Lawrence, J. M. & Sammarco, P. W. 1982. Effects of feeding on the environment: Echinoidea. Echinoderm nutrition. **Echinoderms: Proceedings of the International Conference**, Tampa Bay, Florida, USA, 499-519.
- Lawrence, J., Lawrence, A. & Watts, S. 2013. Feeding, digestion and digestibility of sea urchins. Pp. 135-154. *In*: Lawrence J. (Eds), **Developments in Aquaculture and Fisheries Science**. Elsevier, United Kingdom, 509 p.
- Lewis J. B. & Storey G. S. 1984. Differences in morphology and life history traits of the echinoid *Echinometra lucunter* from different habitats. **Marine Ecology Progress Series**, 15: 207-211.
- Littler D.S. & Littler M. M. 2000. **Caribbean reef plants: an identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico**. OffShore Graphics, Inc., Washington, DC, 543 p.
- Liyana-Pathirana, C., Shahidi, F. & Whittick, A. 2002. The effect of an artificial diet on the biochemical composition of the gonads of the sea urchin (*Strongylocentrotus droebachiensis*). **Food Chemistry**, 79: 461-472.
- Magurran, A. E. 2013. **Measuring biological diversity**. Blackwell Publishing, Oxford, UK, 215 p.
- Maharavo, J., Régis, M. B., & Thomassin, B. A. (1994). Food preference of *Tripneustes gratilla* (L.) (Echinoidea) on fringing reef flats off the NW coast of Madagascar (SW Indian Ocean). Echinoderms through time. **Proceedings of the Eighth International Echinoderm Conference**, Dijon, France, 769-774.
- Manso, V. A., Menor, E. A., Valença, L. M. M., Neumann, V. H. M. L., Pereira, N. S., Junior, C. F. A. S. & Silva, E. R. M. 2011. Morfodinâmica de praias setentrionais da Ilha de Fernando de Noronha. **Journal of Integrated Coastal Zone Management**, 11(3): 327-339.

- Martins, L., Souto, C., Braga, J. & Tavares, M. 2016. Echinozoidea and Holothurozoidea (Echinodermata) of the Trindade and Martin Vaz Archipelago, off Brazil, with new records and remarks on taxonomy and species composition. **Journal of the Marine Biological Association of the United Kingdom**, 98(3): 521-555.
- McCartney, M. A., Keller, G. & Lessios, H. A. 2000. Dispersal barriers in tropical oceans and speciation in Atlantic and eastern Pacific sea urchins of the genus *Echinometra*. **Molecular Ecology**, 9(9): 1391-1400.
- McClanahan T. R. & Muthiga, N. A. 2001. The ecology of *Echinometra*. **Developments in Aquaculture and Fisheries Science**, 32: 225-244.
- McClanahan, T. & Kurtis, J. 1991. Population regulation of the rock-boring sea urchin *Echinometra mathaei*. **Journal of Experimental Marine Biology and Ecology**, 147: 121-146.
- McClanahan, T. R. 1998. Predation and the distribution and abundance of tropical sea urchin populations. **Journal of Experimental Marine Biology and Ecology**, 221(2), 231-255.
- McClanahan, T.R. & Muthiga, N. A. 2007. Ecology of *Echinometra*. Pp. 297-317. *In*: Lawrence J. (Ed.). **Edible Sea Urchins: Biology and Ecology**. Elsevier, United Kingdom, 509 p.
- McLean, R. F. 1967. Erosion of burrows in beachrock by the tropical sea urchin, *Echinometra lucunter*. **Canadian Journal of Zoology**, 45(4): 586-588.
- McClintock, J. B. & Baker, B. J. (Eds.). 2001. **Marine chemical ecology**. CRC press, Florida, 624 p.
- McPherson, B. F. 1969. Studies on the biology of the tropical sea urchins, *Echinometra lucunter* and *Echinometra viridis*. **Bulletin of Marine Science**, 19: 194-213.
- Mendes, C. & Tavares, C. 2006. The relation of algal availability and food preferences in the field diet of the echinoid *Echinometra lucunter* on a rocky shore in southeast Brazil. **Journal of Coastal Research**, 39: 1197-1201.
- Mills, S. C., Peyrot-Clausade, M. & Fontaine, M. F. 2000. Ingestion and transformation of algal turf by *Echinometra mathaei* on Tiahura fringing reef (French Polynesia). **Journal of Experimental Marine Biology and Ecology**, 254: 71-84.
- Murillo-Navarro, R. & Jiménez-Guirado, D. 2012. Relationships between algal food and gut and gonad conditions in the Mediterranean sea urchin *Paracentrotus lividus* (Lam.). **Mediterranean Marine Science**, 13(2): 227-238.
- Nagle, D. G. & Paul, V. J. 1998. Chemical defense of a marine cyanobacterial bloom. **Journal of Experimental Marine Biology and Ecology**, 225(1): 29-38.
- Nagle, D. G. & Paul, V. J. 1999. Production of secondary metabolites by filamentous tropical marine cyanobacteria: ecological functions of the compounds. **Journal of Phycology**, 35(6): 1412-1421.
- Navarrete, A. H., Camus, P. A. & Opazo, L. F. 2008. Variación ambiental y patrones di etarios del erizo negro *Tetrapygus niger* en costas intermareales rocosas del norte de Chile. **Revista Chilena de Historia Natural**, 81(3): 305-319.
- Nielsen, K. J. & Navarrete, S. A. 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. **Ecology Letters**, 7(1): 31-41.
- Oliveira, M. 1991. Survival of seaweeds ingested by three species of tropical sea urchins from Brazil. **Hydrobiologia**, 222: 13-17.
- Pellizzari F. M., Silva M. C., Medeiros A., Oliveira, M. C., Yokoya, N. S., Pupo, D. & Colepicolo, P. 2017. Diversity and spatial distribution of seaweeds in the South Shetland Islands, Antarctica: an updated database for environmental monitoring under climate change scenarios. **Polar Biology**, 40: 1671-1685.
- Pellizzari, F. 2019. Monitoramento da diversidade de macroalgas na ilha da Trindade: conservação e implicações ecológicas, frente as mudanças climáticas. Pp. 43-64. *In*: Rodrigues T., Neto J. & Galvao D. (Eds.). **As Ciências do mar em todos os seus aspectos**. Atena Editora, Ponta Grossa, Brazil, 164 p.
- Pellizzari, F., Osaki, V. S. & Santos-Silva, M. 2020. New records of seaweeds and filamentous cyanobacteria from Trindade Island: an updated checklist to support conservation guidelines and monitoring of environmental changes in the Southern Atlantic archipelagos. **Scientia Marina**, 83: 1-16.
- Pennings, S. C., Pablo, S. R. & Paul, V. J. 1997. Chemical defenses of the tropical benthic marine cyanobacterium *Hormothamnion*

- enteromorphoides: diverse consumers and synergisms. **Limnology and Oceanography**, 42(5): 911-917.
- Pires, G. L. C., Bongioiolo, E. M., Geraldés, M. C., Renac, C., Santos, A. C., Jourdan, F. & Neumann, R. 2016. New <sup>40</sup>Ar/<sup>39</sup>Ar ages and revised <sup>40</sup>K/<sup>40</sup>Ar data from nephelinitic-phonolitic volcanic successions of the Trindade Island (South Atlantic Ocean). **Journal of Volcanology and Geothermal Research**, 327: 531-538.
- Pires, G. L. C., Mansur, K. L. & Bongioiolo, E. M. 2013. Geoconservação da Ilha da Trindade: Principais Aspectos e Potencial de Uso. **Anuário do Instituto de Geociências**, 36: 96-104.
- Prince, J. 1995. Limited effects of the sea urchin *Echinometra mathaei* (de Blainville) on the recruitment of benthic algae and macroinvertebrates into intertidal rock platforms at Rottneest Island, Western Australia. **Journal of Experimental Marine Biology and Ecology**, 186: 237-258.
- Privitera, D., Chiantore, M., Mangialajo, L., Glavic, N., Kozul, W. & Cattaneo-Vietti, R. 2008. Inter- and intra-specific competition between *Paracentrotus lividus* and *Arbacia lixula* in resource-limited barren areas. **Journal of Sea Research**, 60(3), 184-192.
- Rex, M., Etter, R. & Morris, J., Crouse, J., McClain, C. R., Johnson, N. A., Stuart, A. T., Deming, J. W., Thies, R., Avery, R. 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. **Marine Ecology Progress Series**, 317: 1-8.
- Reyes-Luján, J., Barrios, J., Arrieché, D., Zapata-Vivenes, E., Salgado, W. & Lodeiros, C. 2015. Dieta del erizo negro *Echinometra lucunter* (Echinometra: Echinoidea) en el Nororiente de Venezuela. **Revista de Biología Tropical**, 63: 233-242.
- Rodríguez-Barreras, R., Cuevas, E., Cabanillas-Terán, N. & Branoff, B. 2016. Understanding trophic relationships among Caribbean sea urchins. **Revista de Biología Tropical**, 64(2): 837-848.
- Sangil, C., Sansón, M., Afonso-Carrillo, J., Herrera, R., Rodríguez, A., Martín-García, L. & Díaz-Villa, T. 2012. Changes in subtidal assemblages in a scenario of warming: proliferations of ephemeral benthic algae in the Canary Islands (eastern Atlantic Ocean). **Marine Environmental Research**, 77: 120-128.
- Santos-Silva, M. C., Machado, E. C., Wallner-Kersanach, M., Camargo, M. G., Andrade, C., Sá, F. & Pellizzari, F. 2018. Background levels of trace elements in brown and red seaweeds from Trindade, a remote island in South Atlantic Ocean. **Marine Pollution Bulletin**, 135: 923-931.
- Serafini, T. Z., de França, G. B. & Andriquetto-Filho, J. M. 2010. Ilhas oceânicas brasileiras: biodiversidade conhecida e sua relação com o histórico de uso e ocupação humana. **Journal of Integrated Coastal Zone Management**, 10(3): 281-301.
- Silveira, I. C. A., Schmidt, A. C. K., Campos, E. J. D., de Godoi, S. S. & Ikeda, Y. 2000. A corrente do Brasil ao largo da costa leste brasileira. **Revista Brasileira de Oceanografia**, 48(2): 171-183.
- Sissini, M., Horta, P. A. & Pellizzari, F. 2017. Macroalgas da Ilha da Trindade. Pp. 157-165. In: Campos, T. (Eds), **PROTRINDADE: 10 anos de Pesquisa**. SECIRM, Brasília, Brazil, 200 p.
- Sjøtun, K., Husa, V., Asplin, L. & Sandvik, A. D. 2015. Climatic and environmental factors influencing occurrence and distribution of macroalgae a fjord gradient revisited. **Marine Ecology Progress Series**, 532: 73-88.
- Souza, C., Oliveira, A. & Pereira, R. 2008. Feeding preference of the sea urchin *Lytechinus variegatus* (Lam.) on seaweeds. **Brazilian Journal of Oceanography**, 56: 239-247.
- STATSOFT, INC. 2007. **Statistica** - data analysis softwaresystem version 7, accessible at [www.statsoft.com](http://www.statsoft.com). (Accessed 03/08/2007)
- Steneck, R. S. & Dethier, M. N. 1994. A functional group approach to the structure of algal-dominated communities. **Oikos**, 69: 476-498.
- Stimson, J., Cunha, T. & Philippoff, J. 2007. Food preferences and related behavior of the browsing sea urchin *Tripneustes gratilla* (L.) and its potential for use as a biological control agent. **Marine Biology**, 151(5): 1761-1772.
- Tanaka, K., Taino, S., Haraguchi, H., Prendergast, G. & Hiraoka, M. 2012. Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. **Ecology and Evolution**, 2(11): 2854-2865.
- Tavares, Y. A. G. 2004. Biologia reprodutiva dos equinóides *Echinometra lucunter* (L.) e *Arbacia lixula* (L.) na Ilha da Galheta, litoral



- paranaense, Brasil. **PhD. Thesis**, Universidade Federal do Paraná, Paraná, Brasil, 219 p.
- Trenzado, C. E., Hidalgo, F., Villanueva, D., Furné, M., Díaz-Casado, M. E., Merino, R. & Sanz, A. 2012. Study of the enzymatic digestive profile in three species of Mediterranean sea urchins. **Aquaculture**, 344: 174-180.
- Väitilingon, D., Rasolofonirina, R. & Jangoux, M. 2003. Feeding preferences, seasonal gut repletion indices, and diel feeding patterns of the sea urchin *Tripneustes gratilla* (Echinodermata: Echinoidea) on a coastal habitat off Toliara (Madagascar). **Marine Biology**, 143(3): 451-458.
- Ventura, C. R. R., Varotto, R. S., Carvalho, A. L. P. S., Pereira, A. D., Alves, S. L. S. & MacCord, F. S. 2003. Interpopulation comparison of the reproductive and morphological traits of *Echinometra lucunter* (Echinodermata: Echinoidea) from two different habitats on Brazilian coast. Pp. 289-293. In Féral, J. P. & David, B. (Eds.). **Echinoderms Research**. Lisse, Swets and Zeitlinger, 352 p.
- Vergés, A., Alcoverro, T. & Romero, J. 2011. Plant defense and the role of epibiosis in mediating within-plant feeding choices of seagrass consumers. **Oecologia**. 166: 381–390.
- Wangensteen, O., Turon, X., García-Cisneros, A., Recasens, M., Romero, J. & Palacín, C. 2011. A wolf in sheep's clothing: carnivory in dominant sea urchins in the Mediterranean. **Marine Ecology Progress Series**, 441: 117-128.
- Wing, S., McLeod, R., Clark, K. & Frew, R. 2008. Plasticity in the diet of two echinoderm species across an ecotone: microbial recycling of forest litter and bottom-up forcing of population structure. **Marine Ecology Progress Series**, 360: 115-123.
- Zar, J. H. 1999. **Bioestatistical Analysis**. 4th ed. New Jersey: Prentice-Hall, 1999. 361 p.

Received: October 2020

Accepted: December 2020

Published: Decembre 2020