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Ecologia alimentar e sobreposição de nicho trófico entre duas espécies de ouriços-do-mar na ilha de Santa Catarina, Sul do Brasil

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O presente trabalho em nível de mestrado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de mestre em Ecologia.

____
Coordenação do Programa de Pós-Graduação

____
Prof. Dr. Renato Hajenius Aché de Freitas
Orientador

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RESUMO

Ouriços-do-mar atuam como moduladores da abundância, composição e riqueza de macroalgas nos sistemas bentônicos rasos. Em comunidades que abrigam mais de uma espécie, a compreensão de fatores como a utilização e compartilhamento de recursos tróficos são aspectos centrais para o entendimento da dinâmica dos ecossistemas em que elas estão inseridas. Na ilha de Santa Catarina, no Sul do Brasil, as espécies *Echinometra lucunter* e *Paracentrotus gaimardi* ocupam a mesma faixa de habitat, onde são encontradas principalmente nas áreas mais rasas dos costões rochosos (1-3 metros). Para identificar se um dos fatores que permite a coexistência dessas espécies é o particionamento de recursos tróficos, esse trabalho se propôs a investigar o conteúdo estomacal de vinte (20) indivíduos de cada espécie, provindos de dois locais diferentes (costões do Gravatá e Matadeiro), de modo a verificar se o particionamento alimentar das espécies se modificaria em relação a diferenças na composição dos ambientes. Utilizando análises de nível taxonômico e morfológico na identificação do conteúdo estomacal, e o índice de Pianka para verificar o grau de sobreposição trófica entre as espécies em cada local, averiguou-se que, apesar dos costões apresentarem diferenças na composição bentônica, a aquisição de recursos se manteve similar entre as espécies nos dois locais com ambas sendo classificadas como herbívoras generalistas, apresentando baixo grau de dissimilaridade na obtenção de recursos tróficos. Os resultados encontrados indicam que as espécies possuem como principal fator modulador da dieta a disponibilidade de recursos. E a alta sobreposição trófica ocorre pelo comportamento generalista das espécies, que utilizam e compartilham os recursos disponíveis no ambiente.

Palavras-chave: Bentos. Ecologia trófica. *Echinometra lucunter*. *Paracentrotus gaimardi*.

ABSTRACT

Sea urchins play a key role in shallow rocky shores, acting as modulators of abundance, density and species composition of macroalgae. In communities that host more than one species, understanding how trophic resources are used and partitioned is a key aspect of understanding the ecosystem's dynamics in which they are inserted. In Santa Catarina island, Southern Brazil, *Echinometra lucunter* and *Paracentrotus gaimardi* show a high spatial overlap, in the upper (1-3 m) subtidal zone. To evaluate if one of the factors that allows the coexistence of these species is the partitioning of trophic resources, this study aimed to investigate the stomach contents of twenty (20) individuals of each species, coming from two sites (Gravatá and Matadeiro rocky shores) to verify feeding patterns of the species. Using taxonomic and morphological levels in identifying stomach contents and Pianka index to assess the degree of trophic overlap between species in each site. Despite the differences in benthic composition, the feeding patterns of both species were similar in both sites with the species being classified as generalist herbivores. The species showed a low degree of dissimilarity in the acquisition of trophic resources, and a high trophic overlap. The results indicate that the main influencing factor of the feeding patterns was the availability of resources. The high trophic overlap occurs due to the generalist behavior of the species, which use and share the resources available in the environment.

Keywords: Benthos. Trophic ecology. *Echinometra lucunter*. *Paracentrotus gaimardi.*

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1.0 INTRODUÇÃO GERAL

Nicho pode ser definido como a relação de um indivíduo ou de uma população com todos os aspectos de seu ambiente, e dessa forma, representa o “ espaço ecológico” das espécies dentro das comunidades (RICKLEFS, 1996). O conceito de nicho busca explicar como as espécies estariam interagindo e sendo limitadas pelo seu meio abiótico - nicho Grinelliano - ou pelo seu meio biótico - nicho Eltoniano - (SOBERÓN, 2007; SOBERÓN & NAKAMURA, 2009). Hutchinson, em 1957, propôs que os limites de atividades de cada espécie estariam, na verdade, sendo influenciados por um hiperespaço multidimensional, na qual fatores biológicos (bióticos), físicos e químicos (abióticos) estariam juntamente limitando a distribuição das espécies no ambiente (PINTO-COELHO, 2006; CORNELL, 2012).

Pode-se dizer que a teoria do nicho decorre da visão darwinista de que duas espécies em coexistência devem ocupar espaços ecológicos distintos (SEXTON et al., 2017). E que a competição interespecífica estaria agindo como um limitador ambiental, onde segundo Hutchinson, o Nicho Fundamental (com ausência de competidores) seria diminuído ou limitado por uma espécie competidora, chamando este de Nicho Realizado (SOBERÓN, 2007; CORNELL, 2012). Na década de 1960 o conceito de nicho Hutchinsoniano foi alterado, sobretudo, porque o modelo não previa sobreposição entre diferentes espécies, pois as mesmas eram vistas competindo por valores únicos de um fator ambiental em cada posição do hiperespaço, o que levaria sempre, segundo o modelo, à exclusão da espécie com menor poder competitivo (WHITTAKER, 1973; CORNELL, 2012; POCHEVILLE, 2015).

Os ecólogos Levins e MacArthur, em 1967, inseriram o princípio de amplitude de nicho que veio reformular o conceito de Nicho Fundamental de Hutchinson, modificando o paradigma da exclusão competitiva. O fracionamento de recursos ou ambientes organizados ao longo da dimensão do nicho, como utilização em diferentes proporções de alimentos de tamanho diferentes ou o tempo gasto em diferentes micro-habitats se tornaram a amplitude do nicho (CORNELL, 2012).

A sobreposição de nicho veio para se referir à utilização de alguns mesmos tipos de recursos por duas ou mais espécies, sendo que à medida que a sobreposição aumentasse a competição também deveria aumentar (SCHOENER, 1974; ABRAMS, 1980). Pianka (1974) apontou que o modo como as espécies particionam recursos dentro de uma comunidade pode agir como um forte modulador ambiental, pois é um fator-chave para permitir a coexistência entre elas. Assim, mesmo que haja sobreposição de nicho, ela deve ser parcial ou mínima, possibilitando que as espécies que coexistem possam obter recursos de maneira satisfatória para a manutenção de suas populações no ambiente (PIANKA, 1974; SCHOENER, 1974).

Desse modo, a identificação dos fatores que permitem a coexistência de espécies vem ganhando cada vez mais relevância nos estudos ecológicos, sobretudo, por buscar compreender os processos que levam a sustentação da biodiversidade nos ecossistemas (SCHOENER, 1974; RODRÍGUEZ-BARRERAS et al*.,* 2016; LIEDKE et al*.,* 2018). O entendimento das relações tróficas vem então a ser fundamental para o entendimento da dinâmica dos ecossistemas, principalmente em ambientes marinhos, onde uma grande diversidade de espécies aparenta ocupar posições tróficas semelhantes (VANDERKLIFT et al., 2006; SPTIZ et al., 2011; RODRÍGUEZ-BARRERAS et al*.,* 2016).

Usualmente é visto diferenças no tamanho das presas, na forma de captação e na área de forrageio das espécies que, *a priori*, aparentam ter um aspecto alimentar semelhante (RIBI et al., 1977; CONTRERAS & CASTILLA, 1987; SPITZ et al., 2011). Em alguns casos é possível notar diferenciação alimentar entre estágios ontogenéticos em uma mesma população, ao modo de evitar a competição intraespecífica e diminuir a sobreposição de nicho entre diferentes faixas etárias (BRANDL et al., 2020). Há casos onde é possível enxergar alargamento e retração do nicho alimentar das espécies conforme as modificações de padrões ambientais (TAVARES, 2004), o que pode gerar uma maior sobreposição do nicho trófico e aumento do processo competitivo por recursos, principalmente em situações onde a oferta de alimento se torna limitada (CASTRO-SOUZA & BOND-BUCKUP, 2004).

Ouriços-do-mar desempenham um importante papel nos ambientes bentônicos marinhos (BIRKELAND, 1989; STENECK, 2020), atuando na manutenção da biodiversidade dos ecossistemas tropicais (BELLWOOD et al., 2004) e temperados (STENECK et al., 2002), modulando a abundância, densidade e composição das espécies dos produtores primários como macroalgas (LAWRENCE, 1975; MCCLANAHAN, 1992; JOHANSSON et al., 2010) e gramas marinhas (KLUMPP et al., 1993), sobretudo atualmente, onde a sobrepesca está reduzindo drasticamente a população de outros herbívoros marinhos (HUGHES et al., 2007).

Por possuírem esse importante papel estruturador, diversos estudos vêm buscando identificar como as diferentes espécies de ouriços-do-mar utilizam e compartilham os recursos tróficos nas diferentes comunidades em que habitam ao redor do globo (e.g. CONTRERAS & CASTILLA, 1987; VANDERKLIFT et al., 2006; HIRATSUKA & UEHARA, 2007; CABANILLAS-TERÁN et al., 2016; RODRÍGUEZ-BARRERAS et al., 2016), verificando como as variações ambientais e na disponibilidade de recursos tróficos (e.g. VILLAÇA, 1988; GUILLOU & LUMINGAS, 1999; YATSUYA & NAKAHARA, 2004; CABANILLAS-TERÁN et al., 2016; GIL et al., 2021) podem afetar o hábito alimentar, o nicho trófico (CABANILLAS-TERÁN et al., 2019) e o particionamento de recursos entre espécies que coexistem em diferentes comunidades (RODRÍGUEZ-BARRERAS et al., 2020).

De modo geral, as assembleias de ouriços-do-mar são caracterizadas por uma baixa riqueza (2 a 5 espécies), mas com populações muito grandes que podem chegar a dezenas de indivíduos por metro quadrado (VANDERKLIFT et al*.,* 2006; HIRATSUKA & UEHARA, 2007; CORDEIRO et al*.,* 2014; RODRÍGUEZ-BARRERAS et al., 2016; LABBÉ-BELLAS et al., 2016). Nos costões rochosos rasos das regiões Sul e Sudeste do Brasil – pertencentes a província biogeográfica do Atlântico Sudoeste Temperado Quente (SPALDING et al., 2007), são quatro as principais espécies de ouriço-do-mar encontradas compondo as assembleias no bentos, sendo elas: *Echinometra lucunter* (Linnaeus, 1758), *Paracentrotus gaimardi* (Blainville, 1825), *Arbacia lixula* (Linnaeus, 1758) e *Lytechinus variegatus* (Lamarck, 1816) (OLIVEIRA, 1991; SÁNCHEZ-JÉREZ et al., 2001; TAVARES, 2004; CORDEIRO et al., 2014).

Em Santa Catarina, Sul do Brasil, com exceção de *L. variegatus* (encontrada em baixa abundância e densidade no estado), os recifes rochosos rasos mantêm esse padrão com *E. lucunter*, *P. gaimardi* e *A. lixula* ocorrendo em elevada abundância, dominando as assembleias de ouriços-do-mar no local (XAVIER, 2010; LABBÉ-BELLAS et al., 2016; MARTINS, 2016). Na ilha de Santa Catarina o padrão da distribuição dessas espécies nas regiões do infralitoral (região permanentemente imersa) nos costões indica uma divisão na ocupação de habitat, movida pela alteração do gradiente físico. A espécie *A. lixula* ocorre em altas densidades nas regiões mais profundas do que 3 metros nos costões da ilha, enquanto as outras duas espécies estão em maiores densidades acima disso (MARTINS, 2016). Esse padrão de distribuição é também encontrado no Rio de Janeiro (CORDEIRO et al., 2014) e em São Paulo (SÁNCHEZ-JÉREZ et al., 2001), indicando que *A. lixula* responde positivamente ao aumento da profundidade no ambiente, crescendo em maiores valores de abundância e biomassa nas áreas inferiores a 3 metros de profundidade.

Por outro lado, assim como em outros costões rochosos rasos ao longo da costa do Sul e Sudeste brasileira (CORDEIRO et al., 2014; LABBÉ-BELLAS et al., 2016), *E. lucunter* e *P. gaimardi* possuem um padrão similar de ocupação de habitat (nicho espacial), nos costões da ilha de Santa Catarina, onde ambas habitam as regiões superiores do infralitoral, sendo encontradas em maiores densidades nas regiões entre 1,5 até 3 metros de profundidade (MARTINS, 2016). Tanto *E. lucunter* (OLIVEIRA, 1991; REYES-LUJÁN et al., 2015, TAVARES et al., 2020) quanto *P. gaimardi* (QUEIROZ, 2020) são reconhecidamente espécies de hábito herbívoro, apresentando baixa ingestão de material animal (TAVARES, 2004; VILLAÇA, 1988, TAVARES et al., 2020). Sendo assim, a compreensão de como as espécies estão utilizando e compartilhando os recursos tróficos nos ambientes onde ambas ocorrem se torna necessária. A ilha de Santa Catarina se mostra então um importante sítio para avaliar a ecologia alimentar de *E. lucunter* e *P. gaimardi***,** sobretudo, por se tratar de um local onde elas são encontradas em densidades populacionais similares, com esse padrão sendo observado em diferentes costões na ilha (MARTINS, 2016).

Desse modo, o atual trabalho teve como objetivo geral: verificar através de um recorte sazonal (verão) se o particionamento de recursos tróficos é um dos fatores que permite a coexistência das espécies; 1) investigando o conteúdo estomacal de vinte (20) indivíduos de cada espécie provindos de dois locais diferentes (costões do Gravatá e Matadeiro); 2) identificando se há - e quais - as diferenças de disponibilidade de recursos tróficos entre os locais, e se elas afetam a dieta e o particionamento de nicho trófico entre as espécies. Esperando-se encontrar: 1) diferenças do hábito alimentar entre ambas as espécies ao modo de diminuir ou evitar a sobreposição de nicho trófico; 2) a disponibilidade de recursos tróficos presentes nos costões atuando como moduladora da dieta das espécies, influenciando na aquisição dos recursos alimentares.

1.0.1 REFERÊNCIAS BIBLIOGRÁFICAS

ABRAMS, P. Some comments on measuring niche overlap. **Ecology,** v. 61, p. 44-49, 1980.

BELLWOOD, D.R.; HUGHES T.P.; FOLKE C.; NYSTROM M. Confronting the coral reef crisis. **Nature**, v. 429, p. 827–832, 2004.

BIRKELAND, C. The influence of echinoderms on coral-reef communities. **Echinoderm Studies**, v. 3, p. 1-79, 1989.

BRANDL, S.J; CASEY, J.M; MEYER, C.P. Dietary and habitat niche partitioning in congeneric cryptobenthic reef fish species. **Coral Reefs**, v. 39, p. 305–317, 2020.

CABANILLAS-TERÁN, N; LOOR-ANDRADE, P; BARRERAS, R. R; CORTÉS, J. Trophic ecology of sea urchins in coral-rocky reef systems, Ecuador. **PeerJ**, v. 4, p. 1-20, 2016.

CABANILLAS-TERÁN, N; HERNÁNDEZ-ARANA, H.A; RUIZ-ZÁRATE, H.A; VEGA-ZEPEDA, A; SANCHEZ-GONZALEZ, A. *Sargassum* blooms in the Caribbean alter the trophic structure of the sea urchin *Diadema antillarum*. **PeerJ,** v.7, p. 1-32, 2019.

CASTRO-SOUZA, T; BOND-BUCKUP, G. O nicho trófico de duas espécies simpátricas de Aegla Leach (Crustacea, Aeglidae) no tributário da bacia hidrográfica do Rio Pelotas, Rio Grande do Sul, Brasil. **Revista Brasileira de Zoologia**, v. 21, p. 805–813, 2004.

CONTRERAS, S; CASTILLA, J.C. Feeding behavior and morphological adaptations in two sympatric sea urchin species in central Chile. **Marine Ecology Progress Series**, v. 38, p. 217-224, 1987.

CORDEIRO, C.A.M.M.; HARBORNE, A.R.; FERREIRA, C.E.L. Patterns of distribution and composition of sea urchin assemblages on Brazilian subtropical rocky reefs. **Marine Biology**, v. 161, p. 2221-2232, 2014.

CORNELL, H. Niche Overlap. p.489-497. In book: **Encyclopedia of Theoretical Ecology**, Publisher: University of California Press, Editors: A. Hastings and L. J. Gross. 2012.

GIL, G.D; BORASO, A.L; LOPRETTO, E.C; ZAIXSO, H.E. Depth-related plasticity in the diet composition of *Pseudechinus magellanicus* (Echinoidea, Temnopleuridae) in nearshore environments off central Patagonia, Argentina. **Aquatic Ecology**, v. 55, p. 589-606, 2021.

GUILLOU, M.; LUMINGAS, L. J. L. Variation in the reproductive strategy of the sea urchin *Sphaerechinus granularis* (Echinodermata: Echinoidea) related to food availability. **Journal of the Marine Biological Association of the United Kingdom,** v. 79, p. 131-136, 1999.

HUGHES, T.P; BELLWOOD, D. R; FOLKE, C.S; MCCOCK, L. J; PANDOLFI, J.M. No-take areas, herbivory and coral reef resilience. **Trends in Ecology & Evolution**, v. 22, p. 1–3, 2007.

HIRATSUKA, Y; UEHARA, T. Feeding Ecology of Four Species of Sea Urchins (Genus *Echinometra*) in Okinawa. **Bulletin of Marine Science**, v. 81, p. 85–100, 2007.

JOHANSSON, C.L.; BELLWOOD, D.R.; DEPCZYNSKI, M. Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia. **Marine Ecology Progress Series**, v. 414, p. 65-74, 2010.

KLUMPP, D.W; ESPINOSA, J.T.S; FORTES, M.D. Feeding ecology and trophic role of sea urchins in a tropical seagrass community. **Aquatic Botany**, v. 45, p. 205-229, 1993.

LABBÉ-BELLAS, R; CORDEIRO, C.A.M.M; FLOETER, S.R; SEGAL. B. Sea urchin abundance and habitat relationships in different Brazilian reef types. **Regional Studies in Marine Science**, v. 8, p. 33-40, 2016.

LAWRENCE, J.M. On the relationship between marine plants and sea urchins. **Oceanography and Marine Biology**: An Annual Review, v. 13, p. 213-286, 1975.

LIEDKE A.M.R; BONALDO R.M; SEGAL.B; FERREIRA C.E.L; NUNES, L.T; BURIGO, A.P; BUCK, S; OLIVEIRA-SANTOS, L.G.R; FLOETER. S. Resource partitioning by two syntopic sister species of butterflyfish (Chaetodontidae). **Journal of the Marine Biological Association of the United Kingdom**, v. 98, p.1767–1773, 2018.

MARTINS, L.F. **Abundância de ouriços-do-mar em costões rochosos rasos de Santa Catarina**. Monografia (bacharelado em Oceanografia) - Universidade Federal de Santa Catarina. Florianópolis, p.37. 2016.

MCCLANAHAN, T.R. Resource utilization, competition, and predation: a model and example from coral reef grazers. **Ecological modelling**, v. 61, p. 195-215, 1992.

OLIVEIRA, C.M. Survival of seaweeds ingested by three species of tropical sea urchins from Brazil. **Hydrobiologia**, v. 222, p. 13–17, 1991.

PIANKA, E. R. Niche Overlap and Diffuse Competition. **PNAS**, v. 71, p. 2141-2145, 1974.

PINTO-COELHO, R. M. **Fundamentos de Ecologia.** Artmed 2° ed. 2006.

POCHEVILLE, A. The Ecological Niche: History and Recent Controversies. Chapter: The Ecological Niche: History and Recent Controversies. p.547-586. In Book: **Handbook of Evolutionary Thinking in the Sciences**, Publisher: Springer, Editors: Thomas Heams, Philippe Huneman, Guillaume Lecointre, Marc Silberstein. 2015.

QUEIROZ, V. Behavioral and alimentary aspects of the sea urchin *Paracentrotus gaimardi* (Echinodermata). **Pesquisa e Ensino em Ciências Exatas e da Natureza**, v. 4, e1482, 2020.

REYES-LUJÁN, J; BARRIOS, J; ARRIECHE, D; ZAPATA-VÍVENES, E; SALGADO, W; LODEIROS, C. Dieta del erizo negro *Echinometra lucunter* (Echinometra: Echinoidea) en el Nororiente de Venezuela. **Biología Tropical**, v. 63, p. 233-242, 2015.

RIBI, G; SCHÃRER R; OCHSNER P. Stomach Contents and Size-Frequency Distributions of Two Coexisting Sea Star Species, *Astropecten aranciacus* and *A. bispinosus*, with Reference to Competition. **Marine Biology**, v. 43, p. 181-185, 1977.

RICKLEFS, R. **A Economia da Natureza**. Guanabara Koogan, 3° ed. 1996.

RODRÍGUEZ-BARRERAS, R; CUEVAS, E; CABANILLAS-TERÁN, N; BRANOFF, B. Understanding trophic relationships among Caribbean Sea urchins. **Biologia Tropical**, v. 64, p. 837-848, 2016.

RODRÍGUEZ-BARRERAS, R; VITORINO, F.G; PRAEBEL, K; WANGENSTEEN, O.S. DNA metabarcoding unveils niche overlapping and competition among Caribbean sea urchins. **Regional Studies in Marine Science**, v. 40, 2020.

SÁNCHEZ-JÉREZ, P; CESAR, A; CORTEZ, F.S; PEREIRA, C.D.S; SILVA, S.L.R. Distribución Espacial de las Poblaciones de Erizos Más Abundantes de la Costa Sudeste Del Litoral de São Paulo (Brasil). **Ciencias Marinas**, v. 27, p. 139-153, 2001.

SCHOENER, T.W. Resource Partitioning in Ecological Communities. **Science**, v. 185, p. 27-39, 1974.

SEXTON, J.P; MONTIEL, J. SHAY, J.E; STEPHENS, M R; SLATYER, R. A. Evolution of Ecological Niche Breadth. **Annual Review of Ecology, Evolution, and Systematic**, v. 48, p 183-206, 2017.

SOBERÓN, J. Grinnellian and Eltonian niches and geographic distributions of species. **Ecology Letters**, v. 10, p. 1115-1123, 2007.

SOBERÓN, J; NAKAMURA, M. Niches and distributional areas: Concepts, methods, and assumptions. **PNAS**, v. 106, p. 19644-19650, 2009.

SPALDING, M.D; FOX, H.E; ALLEN, G.R; DAVIDSON, N; FERDAÑA, Z.A; FINLAYSON, M; HALPERN, B.S; JORGE, M.A; LOMBANA, A; LOURIE, S.A; MARTIN K.D; MCMANUS, E; MOLNAR, J; RECCHIA, C.A; ROBERTSON, J. Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. **BioScience**, v. 57, p. 573-583, 2007.

SPITZ, J; CHEREL, Y; BERTIN S; KISZKA, J; DEWZ, A; RIDOUX, V. Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. **Deep-Sea Research**, v. 58, p. 273–282, 2011.

STENECK, R.S; GRAHAM, M.H; BOURQUE, B.J; CORBETT, D; ERLANDSON, J.M; ESTER, J.A; TEGNER, M.J. Kelp forest ecosystem: biodiversity, stability, resilience and their future. **Environment Conservation**, v. 29, p. 436–459, 2002.

STENECK, R.S. Regular sea urchins as drivers of shallow benthic marine community structure. In: LAWRENCE. J.M. **Sea Urchins: Biology and Ecology**. Elsevier. Fourth Edition, 43, 2020.

TAVARES, Y. A. G. **Biologia reprodutiva dos equinóides *Echinometra lucunter* (Linnaeus, 1758) e *Arbacia lixula* (Linnaeus, 1758) na Ilha da Galheta, litoral paranaense, Brasil.** Tese (Doutorado) - Universidade Federal do Paraná. Curitiba, p.129. 2004.

TAVARES, Y.A.G; SEMANOVSCHI, N.P; CAMARGO, J.C.M; PELLIZZARI, F. Feeding habits of the sea urchin *Echinometra lucunter* L. (Echinoidea) in a remote Southwestern Atlantic island, Trindade, Brazil. **Pan-American Journal of Aquatic Sciences**, v. 15, p. 303-319, 2020.

VANDERKLIFT, M.A; KENDRICK, G.A; SMITH, A.J. Differences in trophic position among sympatric sea urchin species. **Estuarine, Coastal and Shelf Science**, **v.** 66, p.291–297, 2006.

VILLAÇA, R.C. **Le Phytobenthos Infralittoral des Biotopes Sciaphiles dans la Région d'Upwelling de Cabo Frio (Brésil)**. EssesDoct. Univ. Aix-Marseille II, p. 217. 1988.

WHITTAKER, R. H; LEVIN, S. A; ROOT, R. B. Niche, habitat, and ecotope. **American Naturalist**, v. 10, p. 321–338, 1973.

XAVIER, L.A.R. Inventário dos equinodermos do estado de Santa Catarina, Brasil. **Brazilian Journal of Aquatic Science and Technology**, v. 14, p.73-78, 2010.

YATSUYA, K; NAKAHARA, H. Diet and stable isotope ratios of gut contents and gonad of the sea urchin *Anthocidaris crassispina* (A. Agassiz) in two different adjacent habitats, the *Sargassum* area and Corallina area. **Fisheries Science**, v. 70, p. 285-292, 2004.

2.0 CAPÍTULO ÚNICO: FEEDING PATTERNS AND TROPHIC NICHE OVERLAP BETWEEN TWO SEA URCHIN SPECIES IN SANTA CATARINA ISLAND, SOUTHERN BRAZIL

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2.0.1 Abstract

ABSTRACT

Sea urchins play a key role in shallow rocky shores, acting as modulators of abundance, density and species composition of macroalgae. In communities that host more than one species, understanding how trophic resources are used and partitioned is a key aspect of understanding the ecosystem's dynamics in which they are inserted. In Santa Catarina island, Southern Brazil, *Echinometra lucunter* and *Paracentrotus gaimardi* show a high spatial overlap, in the upper (1-3 m) subtidal zone. To evaluate if one of the factors that allows the coexistence of these species is the partitioning of trophic resources, this study aimed to investigate the stomach contents of twenty (20) individuals of each species, coming from two sites (Gravatá and Matadeiro rocky shores) to verify feeding patterns of the species. Using taxonomic and morphological levels in identifying stomach contents and Pianka index to assess the degree of trophic overlap between species in each site. It was found that despite the differences in benthic composition, the feeding patterns of both species were similar in both sites with the species being classified as generalist herbivores. The species showed a low degree of dissimilarity in the acquisition of trophic resources, and a high trophic overlap. The results found indicate that the main influencing factor of the feeding patterns was the availability of resources. The high trophic overlap occurs due to the generalist behavior of the species, which use and share the resources available in the environment.

Key-words: Benthos; Trophic ecology; *Echinometra lucunter*; *Paracentrotus gaimardi*

2.1 Introduction

Trophic ecology is one of the most relevant areas for understanding mechanisms driving species coexistence (Spitz et al., 2011; Liedke et al., 2018; Kent and Sherry, 2020). It also helps understanding species ecosystem functions (Rosumek et al., 2018; Hayden et al., 2019), particularly in marine ecosystems where several species have similar trophic positions (Ribi et al., 1977; Spitz et al., 2011; Fernandez et al., 2017; Liedke et al., 2018; Brandl et al., 2020). The co-occurrence of species may be possible due to differences in resource partitioning associated with differences in feeding behavior that limit the trophic overlap (Pianka, 1974; Cornell, 2012). Thus, resources partitioning can be one of the main drivers for explaining how species can coexist in communities with high biodiversity (Pianka, 1973; Schoener, 1974). The shallow reef habitats, for example, harbor great animal richness (Vanderklift and Kendrick, 2004; Floeter et al., 2007; Aued et al., 2018), being some taxa, such as the sea urchins, mostly associated with this environment (McPherson, 1969; Lawrence and Sammarco, 1982; Labbé-Bellas et al., 2016; Steneck, 2020).

Most often, sea urchins species live in assemblages, which can support a certain number of species, usually ranging from two to five (Bulleri et al., 1999; Guidetti et al., 2004; Vanderklift and Kendrick, 2004; Cordeiro et al., 2014; Labbé-Bellas et al., 2016). They play a key role in marine communities (Birkeland, 1989; Johansson et al., 2010), characterized as primarily herbivorous (Lawrence et al., 2020) often acting as modulators of abundance, density and species composition of macroalgae (Carpenter, 1988, 1990; McClanahan, 1992) and seagrass (Klumpp et al., 1993). They are key in maintaining biodiversity in both tropical (Sammarco, 1982; Bellwood et al., 2004) and temperate (Steneck et al., 2002) shallow benthic marine ecosystems.

Having such an important function, several studies have tried to understand the relationships of sea urchins and their environments (Klumpp et al., 1993; Vanderklift et al., 2006; Calderon et al., 2007), and how this influences their trophic ecology and feeding behavior (Larson et al., 1980). Depth gradients (Gil et al., 2021), seasonality (Agatsuma et al., 2000; Reyes-Luján et al., 2015; Tavares et al., 2020), and stochastic events (Navarrete et al., 2008; Cabanillas-Terán et al., 2019) were investigated and demonstrated that the sea urchins species can show great trophic plasticity, adapting their dietary pattern to environmental conditions and resource availability. In some cases, expanding their trophic level from herbivory to omnivory (Tavares, 2004), or even changing the feeding methods, in some environments acting as a passive grazer capturing drift algae and in others as a biofilm grazer (Gil et al., 2021).

In addition, several studies have evaluated how coexisting species with potentially similar diets use and partition the feeding resources (Vásquez et al., 1984; Contreras and Castilla, 1987; Vanderklift et al., 2006; Rodríguez-Barreras et al., 2016). In some cases, it is possible to verify trophic differentiation to avoid or minimize competition (Privitera et al., 2008). *Arbacia lixula,* for example, was classified from omnivorous to carnivorous in Southeastern Brazil where it cohabits shallow rocky shores with *Echinometra lucunter* and *Lytechinus variegatus,* both herbivorous species (Oliveira, 1991). However, in the Mediterranean, *A. lixula* shows a herbivorous feeding pattern, but shares the same habitat with only one species, *Paracentrotus lividus* (Bulleri et al., 1999; Privitera et al., 2008). Dietary differentiation can also occur regarding food capturing mode, as described by Contreras and Castilla (1987). In shallow Chilean rocky shores, these authors studied two sympatric herbivorous sea urchin species, *Loxechinus albus* and *Tetrapygus niger*, and observed that the first one was specialized in capturing drift algae while *T. niger* had basically a scraping feeding habit.

Thus, trophic overlap and resource partitioning can vary between sites depending on differences in the availability of resources and environmental composition (Cobb and Lawrence 2005; Privitera et al., 2008 Cabanillas-Terán et al., 2016; Rodríguez-Barreras et al., 2020). On the West Coast of Central Florida (USA), Cobb and Lawrence (2005) found differences in the dietary pattern of *Arbacia punctulata* (omnivorous) with cohabiting the same sites with *Lytechinus variegatus* (herbivorous). Throughout the study, in different seasons and locations, the availability of resources varied. In the low supply of algal material, *A. punctulata* presented unimpressive consumption of this material, acting like a carnivore. But in situations of algal material is not limited, the species increased consumption of this resource, overlapping the consumption of algal material with *L. variegatus*.

In Southeastern and Southern Brazil, the shallow rocky shores are inhabited by three coexisting sea urchin species: *A. lixula*, *E. lucunter* and *Paracentrotus gaimardi* (Cordeiro et al., 2014; Labbé-Bellas et al., 2016). *E. lucunter* and *P. gaimardi* show high spatial overlap in the upper (1-3 m) subtidal zone with high abundances and density (Cordeiro et al., 2014). *A. lixula* is more abundant and increases in density in regions deeper than 3-meter depth (Sánchez-Jérez et al., 2001), indicating differentiation of the spatial niche between the species with *E. lucunter* and *P. gaimardi*.

Thus, we investigate whether the trophic niche differentiation can be a factor that allows the coexistence of both sea urchin species *E. lucunter* and *P. gaimardi* in Santa Catarina island, Southern Brazil. To identify how environmental factors influence the partitioning of food resources between the species we: 1) analyzed both species diets; 2) verified if differences in benthic composition influenced their diet and, consequently, the trophic niche partition between those species**.**

2.2 Material and methods

2.2.1 Study Area

Santa Catarina island (27º 35' S; 48º 32' W) is located on Southern Brazilian coast (Figure 1). During the austral summer, the island is under influence of tropical waters from Brazil Current and South Atlantic Central Water, while the Plata River plume and the Sub-Antarctic Water are prevalent during the winter (Piola et al., 2000, 2005; Pereira et al., 2009). Regional sea surface temperature ranges from 17°C to 20°C approximately during the winter, and from 23°C to 27°C approximately in the summer (Carvalho et al., 1998; Segal et al., 2017). The local shallow benthic community is mainly composed of turf algae and frondose macroalgae (Aued et al., 2018). The sampling sites, Gravatá (27°36’46S; 48°25’59W) and Matadeiro (27°45’ 25S; 48°29’37W) were classified as semi-exposed rocky shores, susceptible to wave action from east and northern quadrant winds (Carvalho et al., 1998).

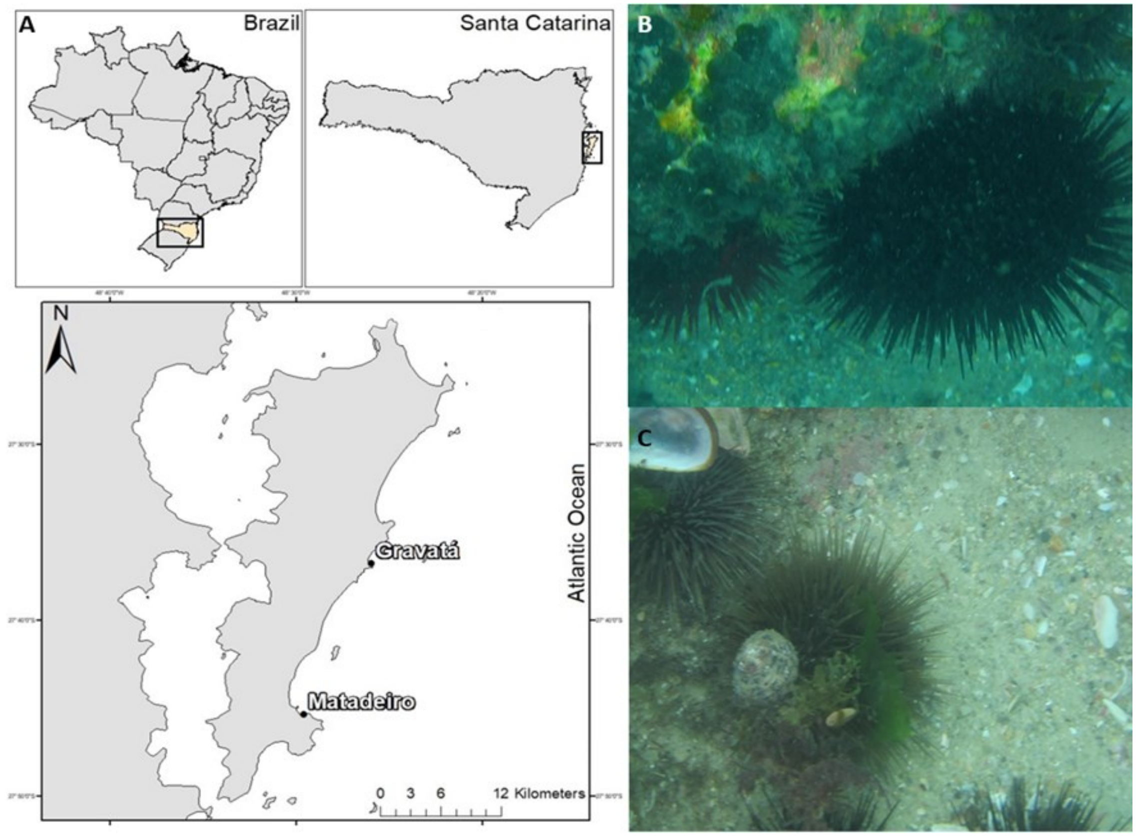

Fig.1. A: Map from Santa Catarina island indicating both sampling sites. B: *Echinometra lucunter*. C: *Paracentrotus gaimardi*. Photos: Tainá Gaspar.

2.2.2 Sea urchins sampling

The sea urchin species, *E. lucunter* and *P. gaimardi*, were collected (n = 10 of each) in both sites Matadeiro and Gravatá in January, during the austral summer of 2020, at shallow depths (2-3 m) during low tide. Sampling occurred in the early morning hours (7:30 a.m. – 9:00 a.m.). Only individuals of > 2 cm in test diameter were collected to avoid the influence of ontogenetic changes in feeding patterns as suggested by Larson et al., (1980) and Cabanillas-Terán et al., (2016). The sampled individuals were conditioned individually in zip-lock bags, covered by ice and taken to the laboratory.

2.2.3 Sites characterization

To characterize the benthic community, we used a set of fifteen 25x25 cm photo quadrats, haphazardly placed in the same area where sea urchins were collected. The images were analyzed using the *photoQuad* software (Trygonis and Sini, 2012). To identify the components of the benthic cover, 50 points were randomly scattered over each image and the organisms below each point were identified at the lowest taxonomic level, either using proper literature (e.g. Littler and Little, 2000; Horta, 2001; Nassar, 2012, Lindner, 2018). Algae species were grouped in: articulated calcareous algae (ACA), corticated, crustose, filamentous, foliose and leathery, following Steneck and Dethier (1994) morphological groups classification. The epilithic algae matrix formed thick mats < 2 cm tall were classified as "turf" (Connell et al., 2014; Longo et al., 2015). Animal groups were classified according to phylum except for cnidarians that were separate in zoanthids and other cnidarian (anemone B*unodosoma* sp.). The bare substrate was also classified as bare rock and sediment (SED), composed of sand and gravel.

To identify the turf components, we scraped the substrate using 5 quadrats (10x10 cm) haphazardly placed in the same sampling area with five replicates in each site (Longo et al., 2015). In the lab, the turf was sifted with a three-level sieve (710, 500, and 425 µm) and washed with distilled water to separate the sediment from the organic matter. Only the macroalgae were used to characterize the turf components. The animal component was not considered for diversity or biomass analyses in this study. The algae species were separated in morphological groups and were kept in the oven for drying (50°±10°C for 48 hours) to determine the dry weight and measure their relative biomass (Reyes-Luján et al., 2015).

2.2.4 Sea urchin laboratory processing

In the laboratory, sea urchins were fixed and conserved in saline formaldehyde 10% until dissection and had their carapace diameter without spines measured with a digital caliper. Each individual was carefully dissected, had the gut removed, and the wet weight measured using an analytical scale. An indirect analysis of intake was measured using the repletion index (RI), adapted from Guillou and Lumingas (1999):

$$RI = \frac{wet\ \ weight\ of\ gut\ contents}{wet\ body\ \ weight} \times 100$$

After weighing, individual gut content was homogenized and partitioned into two equal portions. One portion was used to quantify the inorganic gut content index (IGCI), adapted from

Tavares, 2004), and the other was used in diet analysis. To identify the intake of organic matter, one portion was put to dry for four days (60°±10°C) and had its dry weight measured by the end of this period. The dried matter was then burned in a muffle furnace for 550°C for two hours and weighted to calculate the IGCI using the formula:

$$IGCI = \frac{ash\ weight}{dry\ gut\ content\ weight} \times 100$$

The difference of the inorganic matter percentage was used to identify the amount of ingested organic matter (organic matter index or OMI).

2.2.5 Diet analysis

For the analysis of the gut content, we used a stereomicroscope and optical microscope to identify all items to the lowest taxonomic group possible using the proper literature (e.g. Littler and Littler, 2000; Horta, 2001; Brusca and Brusca, 2007; Nassar, 2012; Lindner, 2018), and consulting taxonomic experts when necessary.

After the sorting, the organic identifiable items were put in a Petri dish (over a graph paper 1 mm^2) and compressed to 1 mm of height with a histological glass supported by two small glass slides 1 mm. The volume (mm^3) of an item was measured by counting the number of grid cells occupied by the items (Liedke et al., 2016, 2018). We also used the frequency of items and volume to calculate the food index (IAi) proposed for Kawakami and Vazzoler (1980) as follows:

$$\%IAi = \frac{(Fi\,.Vi)}{\sum_{x=1}^{n}(Fi.Vi)}$$

In which, *Fi* represents the total number of stomachs with a given type of prey, *i* is relative to all stomachs, and V*i* is the relative volume of the prey in relation to all prey volumes in the stomachs of all individuals. We calculated the IAi according to taxa levels (IAi_t) and morphological approach (IAi_m) for verifying whether these aspects showed influences in food intake by sea urchins species.

2.2.6 Niche Overlap

The niche overlap was measured using taxonomic and morphological groups to identify patterns of similarity in resource utilization in each site, applying the Pianka's index (1973):

$$Ojk=\sum Pij\ Pik / \sqrt{(\sum Pij \sum Pik)}$$

where O_{jk} = Pianka's measure of niche overlap index between species *j* and *k*; p_{ij} = proportion of resource *i* of the total resources used by species *j*; p_{ik} = proportion of resource *i* of the total resources used by species *k*. The Pianka's index ranges from 0 to 1, where the closer to 1, the larger is the niche overlap between the species, and values > 0.6 indicate a high overlap (Pianka, 1973).

2.2.7 Statistical analysis

We used a Student's t-test or Wilcoxon test to verify differences in intraspecific test size and RI between sites. Also used t-test to verify intra and interspecific differences in the OMI, replacing occasional outlier values for the sample general means (Tukey, 1977). The diet composition was compared between species and sites using the taxa in a two-way ANOVA (Gotelli and Ellison, 2013). Assumptions of normality (t-test and ANOVA) and homogeneity (ANOVA) were tested by Shapiro-Wilk (Royston, 1995) and Bartlett's tests (Bartlett, 1937), respectively.

Non-metric multidimensional scaling (nMDS) and one-way analyses of similarity (ANOSIM) using Bray-Curtis dissimilarities (999 permutations) were performed to investigate differences in the diet composition using morphological groups (Clarke, 1993; Anderson and Walsh, 2013). The percentage similarity analysis (SIMPER) was applied *a posteriori* to check the morphological groups that differed between species (Clarke, 1993).

We tested a null model using the algorithm *RA3* to evaluate the Pianka's index significance (Winemiller and Pianka, 1990). We also compared the observed result of the Pianka's index with the mean of 999 randomized. If the p-value is significantly lower (< 0.05) we assumed that the niche overlap is greater than expected by chance (Albrecht and Gotelli, 2001).

Differences in the benthic cover composition were assessed using PERMANOVA (Euclidean distance and 999 permutations) followed by a SIMPER analysis for identifying components contributing to differences between sites (Clarke, 1993; Anderson and Walsh, 2013). The PERMDISP test for homogeneity of dispersion was done to validate the PERMANOVA results checking for groups' dispersion (Anderson and Walsh, 2013). Principal component analysis (PCA) was used to visualize associations between benthic components.

All analyses were performed in the R software (R core team, 2020) using the packages “EcoSimR” (Gotelli et al., 2015), “ggplot2” (Wickham, 2016), “plyr” (Wickham, 2011), “reshape2” (Wickham, 2007) and “vegan” (Oksanen et al., 2020) using a 95% confidence level indicating significance with a 0.05 alpha level.

2.3 Results

2.3.1 Sea urchins' attributes

Paracentrotus gaimardi individuals were larger in Gravatá (44.6 ± 3.08 mm) than Matadeiro *(*41.26 ± 3.03 mm) ($t = 2.48$, $p < 0.05$), but *E. lucunter* did not show differences in size between sites (Gravatá: 57.84 ± 9.05 mm; Matadeiro: 57.24 ± 10.47 mm; $t = 0.13$, $p > 0.05$). The RI also did not vary between sites for *E. lucunter* ($t = 1.12$, $p > 0.05$) or *P. gaimardi* ($w = 72$, $p > 0.05$). The OMI in gut content was significantly larger for *E. lucunter* ($t = -3.39$, $p < 0.001$) and *P. gaimardi* ($t = -3.03$, $p < 0.001$) at Matadeiro than in Gravatá, but was similar for species within sites ($p > 0.05$, Figure 2).

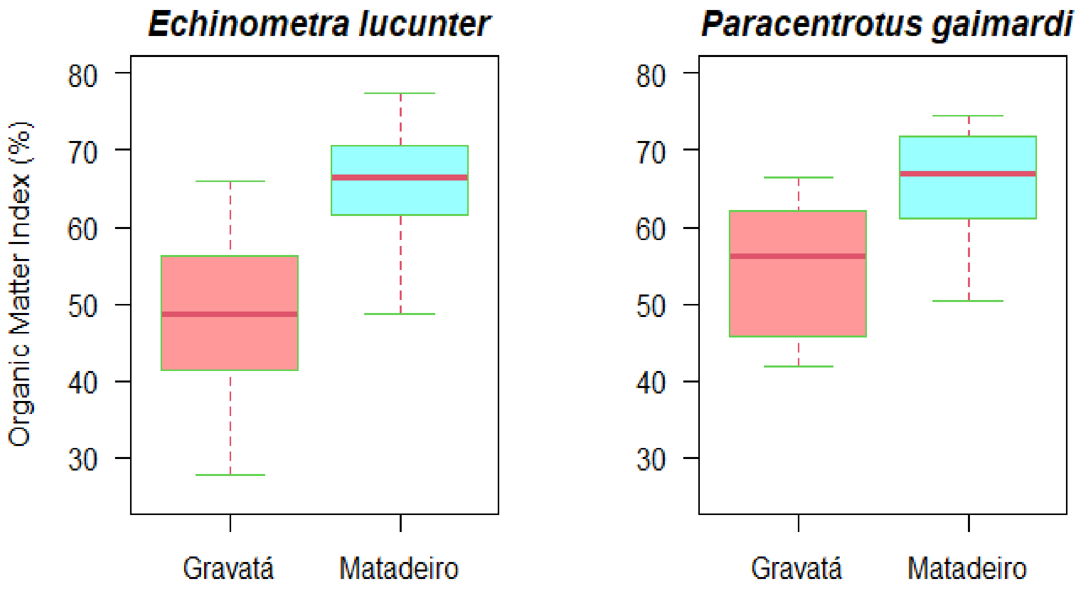

Fig. 2. Average amount of organic material (organic matter index) found in the plot of both species at the two sites.

2.3.2 Resource availability

We recorded a total of 21 taxa across both sites and grouped them in 13 categories to characterize the environments (Figure 3). A total of 16 algae taxa of six morphological groups were recorded in both sites (Table S1). The dominant macroalgae species (excluding turf algae) in Gravatá was *Sargassum spp.* (28.6%), followed by *Jania* sp. (16%), *Hypnea pseudomusciformis* (11%), *Pterocladiella capillacea* (10.5%), *Canistrocarpus cervicornis* (9.3%), and *Codium intertextum* (7%). Matadeiro was mostly covered by crustose coralline algae (CCA; 28.7%), *Codium intertextum* (24.6%), *H. pseudomusciformis (*19.8%) and *P. capillacea* (8.5%).

The invertebrate macrofauna was dominated by sea urchins and cnidarians (represented by *Bunodosoma* sp.). sponges (*Tedania ignis*) and zoanthids were found only in Gravatá site (Table S1).

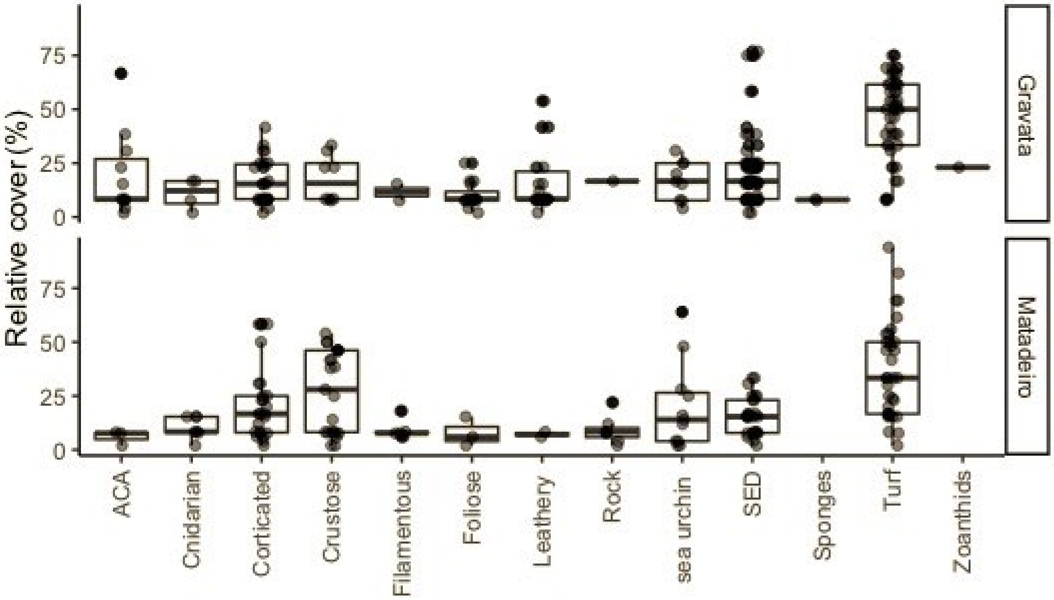

Fig. 3. The relative benthic cover of Gravatá and Matadeiro, Santa Catarina, Brazil. The bars represent the median, the two hinges indicate from 25% to 75% of data and two whiskers mean 95% of confidence intervals. ACA: articulate calcareous algae; SED: sand and gravel.

The PERMANOVA showed differences in the benthic cover composition between the sites ($F = 6.08$, $R2 = 0.17$, $p = 0.001$) (Figure 4). A contrast SIMPER showed that the difference was caused by the high concentration of SED ($p < 0.01$) and the leathery *Sargassum* spp. ($p < 0.01$) in Gravatá, and the crustose algae ($p < 0.01$) and rock ($p < 0.05$) in Matadeiro. For ACA and foliose algae groups, the difference between sites was marginally significant ($p = 0.06$). There was no significant difference between sites for sea urchins ($p = 0.08$) and cnidarian ($p = 0.54$) in benthic cover. In the same way, the relative cover for corticated and filamentous algae did not differ between sites ($p = 0.37$ and $p = 0.12$ respectively). The turf was the main component in both sites, in Gravatá representing 42% of total benthic cover and 38% in Matadeiro. ACA dominated biomass turf in both sites (Figure 5), but the species richness was dominated by red corticated and filamentous algae in both sites (S2 Table).

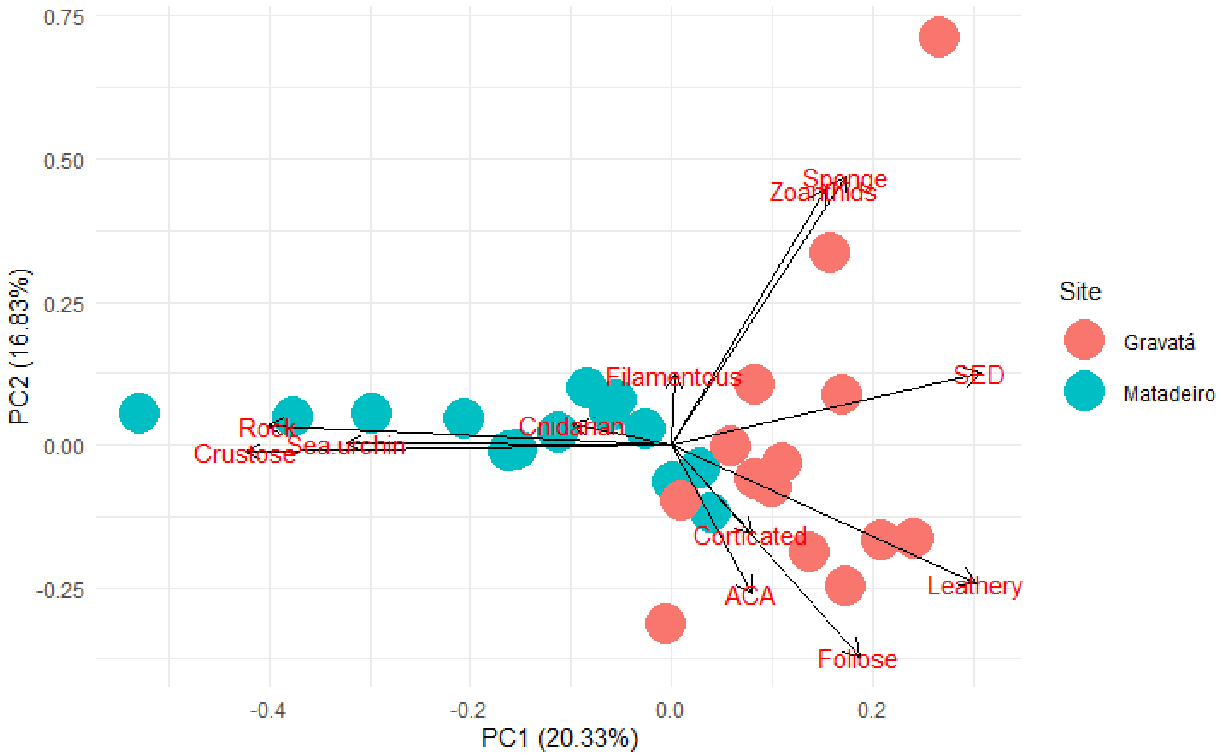

Fig. 4. Principal component analysis (PCA) showing the main compositions of benthos in each site. ACA: articulated calcareous algae. SED: sediment.

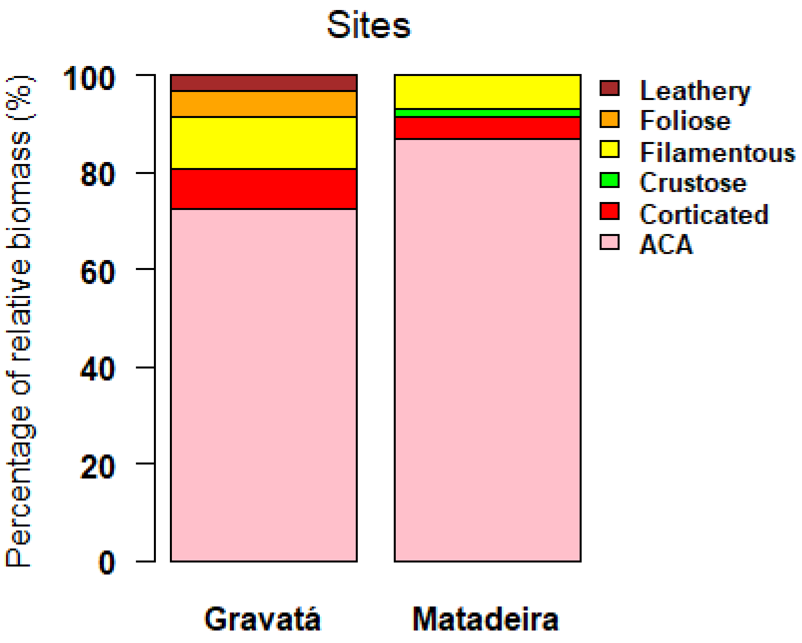

Fig. 5. Biomass relative in percentage of morphological groups in turf algal complexes in each site. ACA: articulated calcareous algae.

2.3.3 Diet analysis

2.3.3.1 Taxonomic composition

A total of 38 taxa were identified in the stomach contents for both sites and species (S3 Table). Thirty-four and 30 taxa items were found in gut content of sea urchins from Gravatá and Matadeiro, respectively. The mean taxa richness was higher in Gravatá site ($F = 44.6$, $p < 0.001$), but did not differ between species ($F = 0.60$, $p > 0.05$) or in interaction between species and site ($F = 1.36$, $p > 0.05$).

The IAi using taxonomic groups showed that both species had diverse diets in Gravatá, ingesting more taxa and in larger quantities than in Matadeiro (Figure 6, S3 Table). In Gravatá, there was no dominance of a particular algae. *E. lucunter* gut content exhibited a similar contribution of Corallinales (18.3%), *Pterocladiella capillacea* (17.4%), *Ulva* spp. (15.5%), *Hypnea* spp. (14.3%) and *Codium* spp. (13.8%). Intake of animal taxa was low (< 1%), although frequent (found in 100% of stomachs). In *P. gaimardi* gut content, Corallinales (26.7%) and *Sargassum* spp. (25.8%) were dominant, followed by *Hypnea* spp. (11.9%) and *Ulva* spp. (9.2%). Still, bivalves (mollusk) and peracarida (crustacean) were found in 70% of *P. gaimardi* stomachs, and showed relative contribution of 1.5% and 1.3% in diet, respectively.

In Matadeiro, *Hypnea* spp. (35.4%) and *P. capillacea* (33.1%) were the main components of *E. lucunter* diet, followed by *Codium* spp. (11.2%), Corallinales (6.6%) and *Ulva* spp. (5.7%) (Figure 6, S3 Table). The intake of animal taxa was low, as in the Gravatá site. No animal item represented > 0.5% in the food index (IAi_t). *P. gaimardi* from the Matadeiro site had a clear domain of *Hypnea* spp. (49.6%) in its diet. *P. capillacea* (13.3%), *Centroceras clavulatum* (9.5%) and *Ulva* spp. (9%) also appeared frequently in stomachs. In this site, Peracarida (3.1% in IAi_t) had a high frequency of occurrence in gut content of *P. gaimardi* (80%).

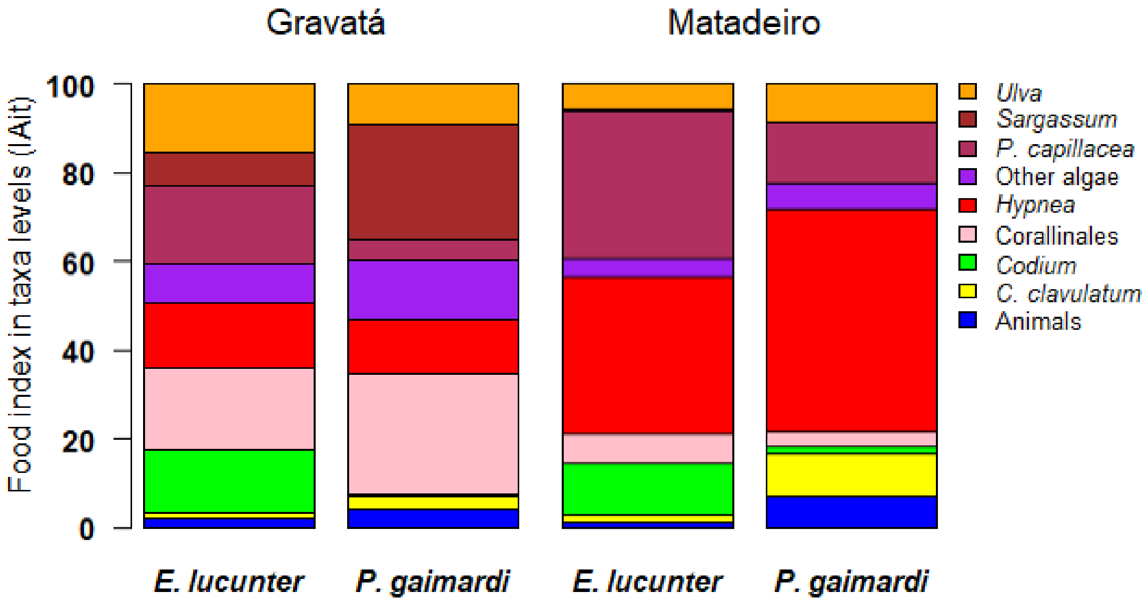

Fig. 6. Food index in taxa levels (IAi_t) for *Echinometra lucunter* and *Paracentrotus gaimardi* in both Gravatá and Matadeiro sites. Items with IAi less than 5% were grouped into large groups (animals and other algae) for better graphical visualization.

2.3.3.2 Morphological analyses

Codium spp. had more than one species in the environment (Matadeiro) from different morphological groups (see S1 Table), but it was not possible to differentiate them by analyzing the stomach content, so they were classified together (Figure 7).

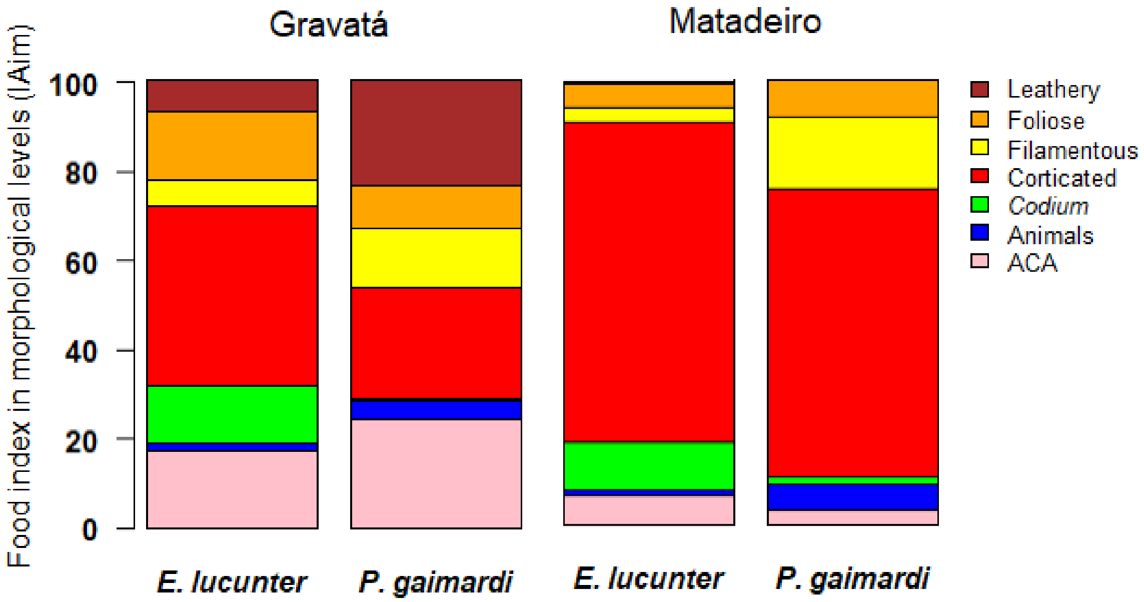

Fig. 7. Food index in morphological levels (IAi_m) for *Echinometra lucunter* and *Paracentrotus gaimardi* in both Gravatá and Matadeiro sites. Items with IAi less than 5% were grouped into large groups (animals) for better graphical visualization.

Echinometra lucunter showed a large consumption of corticated (39.7%), followed by ACA (17.1%), foliose (15.1%), *Codium* spp. (13%), leathery (6.8%) and filamentous (6.1%). *P. gaimardi* had three groups dominating the gut content and exhibiting a similar contribution: corticated (24.7%), ACA (24.2%) and leathery (23.4%), followed by filamentous (13.2%) and foliose (9.5%). ANOSIM showed differences in feeding patterns (R = 0.49, p = 0.001). The SIMPER showed the groups that contributed to this difference were *Codium* spp. ($p < 0.01$) more consumed by *E. lucunter*, and leathery ($p < 0.01$) and filamentous (p = 0.001) most consumed by *P. gaimardi*. Despite the difference pointed out by ANOSIM, the nMDS showed a high degree of niche overlap between the species in Gravatá (Figure 8A).

In Matadeiro, the corticated algae dominated the IAi_m of both species. In *E. lucunter* gut 72% of the stomach contents was constituted by corticated, following for *Codium* spp. (10.7%), ACA (6.3%) and foliose (5.6%). In *P. gaimardi*, the corticated was 64.5% of the stomach contents, filamentous (16.1%) and foliose (8%) were the second and third most abundant morphological groups respectively. The ANOSIM (R = 0.33, p = 0.001) showed a low difference in feeding patterns in the Matadeiro site. SIMPER pointed crustose algae ($p < 0.05$) as more consumed for *E. lucunter* and, filamentous algae ($p = 0.001$), hydroid ($p < 0.05$) and crustacean ($p < 0.05$), more consumed for *P. gaimardi,* as responsible for this difference. The nMDS showed a high degree of overlap between the species (Figure 8B).

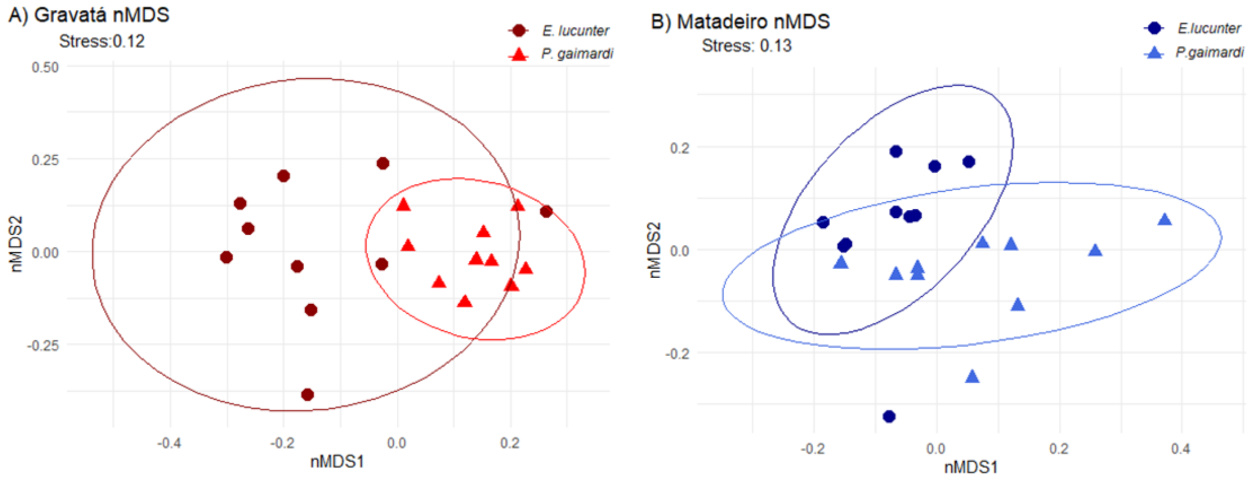

Fig. 8. nMDS using Bray-Curtis dissimilarity between *E. lucunter* and *P. gaimardi* in Gravatá and Matadeiro sites.

2.3.4 Pianka's index

The Pianka's index indicated a high feeding pattern overlap at both sites, using both morphological and taxonomic groups (Table 1).

Table 1
Pianka's niche overlap index and null model per site using morphological food index/taxonomic food index (IAi).

	Pianka's index	Null model	P-value
Gravatá	0.82/0.72	0.33/0.20	p<0.01/p<0.01
Matadeiro	0.97/0.85	0.15/0.12	p<0.05/p<0.01

2.4 Discussion

Our results support the evidence that the *E. lucunter* and *P. gaimardi* are typical herbivorous species, during summer, in Southern Brazil (with unimpressive ingestion of animal material), showing a high trophic overlap due to this similar feeding pattern.

Along the Brazilian coast, the feeding patterns of *E. lucunter* appear to differ according to the availability of food resources. Several authors classified *E. lucunter* as herbivore (Oliveira, 1991; Mendes and Tavares, 2006; Tavares et al., 2020). However, the species has already been described as omnivorous with a tendency for herbivory in the coldest seasons of the years when algae resources were limited (Tavares, 2004). On rocky shores from Venezuela, *E. lucunter* was described as an opportunistic omnivore (Reyes-Luján et al., 2015), while in Puerto Rico the species maintained a herbivore behavior, even in different sites and in the presence of co-occurring species (Rodríguez-Barreras et al., 2016). As expected, our data support the description of *E. lucunter* as a generalist herbivore (McClanahan and Muthiga, 2020) with a lower preference for animal items than other sea urchin species (McClintock et al., 1982). In our study, the low ingestion of animal material may indicate incidental capture while grazing on macroalgae (Vanderklift et al., 2006; Hiratsuka and Uehara, 2007), because the most of animal material in the gut content (sponges and cnidarians in Gravatá site and mollusks in the Matadeiro site) were conspicuous components of the epifauna.

Paracentrotus gaimardi was described as herbivorous during the summer, becoming omnivorous during the winter in Southeastern Brazil (Villaça, 1988). Queiroz (2020) confirmed the feeding behavior of the species as typically herbivore, just like the congeneric species *Paracentrotus lividus* (Boudouresque and Verlaque, 2020). Isotopic analysis in different sites with different proportions and availability of resources demonstrated that the *P. lividus* presented a low trophic level, being clearly a herbivorous species (Wangensteen et al., 2011). The presence of animal material such as sponge, cnidarian, mollusk and bryozoan was constantly found in *P. lividus* gut content, but in low proportions, and related to accidental ingestion (Boudouresque and Verlaque, 2020), which appears to be the same pattern found in our study. The high frequencies of crustaceans (peracarida) in the *P. gaimardi* gut content in Matadeiro site may be linked with the abundance of these animals on the red macroalgae *Hypnea* spp. (Nascimento and Rosso, 2007), the most consumed algae.

The high contribution in stomach content of the common algae species in the subtidal benthic community in both sites demonstrates that active grazing is the main source used to obtain food (Hiratsuka and Uehara, 2007). The availability of resources in the field is known as the main driver of the diversity of items found in the stomach contents of sea urchins' herbivores species (Vásquez et al., 1984; Cobb and Lawrence, 2005; Murillo-Navarro and Jiménez-Guirado, 2012; Gil et al., 2021), followed by anti-herbivore adaptation, such as chemical and morphological aspects in algae (Cobb and Lawrence, 2005; Souza et al., 2008; Bianco et al., 2010; Vergés et al., 2011). For example, the foliose *Canistrocarpus cervicornis* had a low consumption ($IAi_t < 0.5$ for both species), despite being an important component of benthos in Gravatá. Thus, it is considered as avoided for sea urchin species. Chemical compounds (e.g. diterpenes in *C. cervicornis*) that serve as deterrents against herbivores are the factors that lead to this avoided behavior of feeding by sea urchins for this species (Bianco et al., 2010). However, selectivity also seems to occur, especially in environments where the food supply is not limited (Larson et al., 1980; Boudouresque and Verlaque, 2020). On the coast of Chile, the most consumed algae, by the species *Tetrapygus niger* is the Chlorophyta *Ulva rigida*, even though this not being the most abundant algae in the benthic community (Navarrete et al., 2008). In Argentina, the algae *Ceramium virgatum*, *Lophurela hookeriana*, *Streblocadia camptoclada* and *Chaetomorpha linum* were highly consumed although less available in the field than other algae species (Gil et al., 2021).

The different intake of *Sargassum* spp. between *P. gaimairdi* and *E. lucunter* in Gravatá may be related to food preferences. Mendes and Tavares (2006) showed a low degree of preference in *Sargassum* consumption in the field for *E. lucunter*. Some species of *Sargassum* produce polyphenols (Steinberg, 1986) and *E. lucunter* may be more sensitive to this compound than *P. gaimardi.* Algae from the genus *Codium* was less preferred by *Paracentrotus* genus, or even considered avoided (Boudouresque and Verlaque, 2020). For *E. lucunter*, *Codium* had a high consumption, when a variety of algae was offered in multiple-choice feeding assays (Erickson et al., 2006) or a complement resource in the field (Mendes and Tavares, 2006). Thus, it could explain this difference in the acquisition of these resources by both species in this study.

The crustose coralline algae (CCA) were not consumed on any of the sites, despite being the dominant algae group (not considering turf) in Matadeiro. Mendes and Tavares (2006), verified in the field that the most avoided algae group by *E. lucunter* was CCA. Being less susceptible to herbivory, possibly to morphological aspects that make grazing and assimilation difficult (Little et al., 1983), and with the availability of resources more susceptible to grazing and high caloric values (e.g. corticated) (Little et al., 1983), the consumption of these algae would be contrary to the optimal foraging theory (Hughes, 1980).

On the other hand, the filamentous algae were significantly consumed, mainly by *P. gaimardi* (S4 Table). The fact that this algae group is unrepresentative in the environment (especially in Gravatá where they are found basically in turf) may indicate a preference for this morphological group (Mendes and Tavares, 2006) possibly caused by low resistance to herbivory (Little et al., 1983).

Articulated coralline algae (ACA) had higher consumption in Gravatá than the Matadeiro site for both species. This difference was possibly responsible for the difference in the organic matter index (OMI) (higher in the Matadeiro). As they have calcified cortex (Little and Little, 2000), the increase in consumption of this algae naturally increases the amount of inorganic material consumed by sea urchins (Murillo-Navarro and Jiménez-Guirado, 2012), making the OMI lower than in sites where there is a low intake of this morphological group. However, this difference in consumption was not different between species in the same site.

That difference in ACA consumption appears to be related to its availability in the field (Murillo-Navarro and Jiménez-Guirado, 2012; Gil et al., 2021). Despite being an important component of turf (greater biomass), the aggregation of ACA has already been recognized as least preferred or negatively selected for sea urchin species when other sources of resources such as flesh macroalgae are available in the field (Hiratsuka and Uehara, 2007; McClanahan and Muthiga, 2020). However, in the field, the ACA was the third preferred morphological group by *E. lucunter* in Rio de Janeiro, Brazil (Mendes and Tavares, 2006). Larson et al. (1980) showed the *Corallina officinalis* (ACA) were significantly preferred over other non-calcareous algae species by *Strongylocentrotus droebachiensis* in Maine, USA. Accidental consumption can also be taken into account due to the proximity to another food item (Hiratsuka and Uehara, 2007; Gil et al., 2021).

Commonly, sea urchins have morphological variations (e.g. relative larger Aristotle's lantern or smaller test size) in sites with resource limitation or greater competition (Black et al., 1984, 1992; Ebert 1968; Levitan, 1991). In our study, the *E. lucunter* did not differ in test size between sites, and *P. gaimardi* had a larger relative test size in Gravatá (site with the biggest OMI). In addition, it is common to find lower RI values in sea urchins that live in environments with a low supply of resources, when compared to those that live in sites with a greater supply of food (Guillou and Lumingas, 1999; Cobb and Lawrence, 2005; Reyes-Lújan et al. 2015). In our study the intraspecific RI of species did not vary between sites, indicating that there is no limitation in trophic resources at sites. Furthermore, it is common in environments with low availability of resources that species that cohabit in the same place do not overlap their diets, avoiding competition (Cobb and Lawrence, 2005; Privitera et al., 2008; Wangensteen et al., 2011).

Our analysis showed that the differences in feeding patterns between species were not sufficient to indicate a trophic niche partitioning even using different metrics analyses (IAi_t and IAi_m). Brandl et al. (2020) pointed out that as analysis resolution increases niche overlap should decrease. Our results suggest this pattern, but even at lower resolutions, the trophic niche overlap remained high (Pianka's index >0.6) between species in both sites, indicating a high similarity in the trophic position for *E. lucunter* and *P. gaimardi* in Santa Catarina Island, Southern Brazil.

Nonetheless, high trophic similarity cannot be used to indicate that both species have the same structuring role in communities either. Sammarco (1982) found in Jamaica that two sea urchin species, *Diadema antillarum* and *Echinometra viridis*, affected differently the benthic composition, with the first acting homogeneously in the environment, while *E. viridis*, even at high densities, created only patches algal-free. In general, niche overlap (in our case, trophic niche) measures were designed to understand the degree of the utilization of common resources between species, and also should not be used to measure the degree of competition between species (Lawlor, 1980).

Although several studies reported that the trophic dissimilarity is one of the main drivers that allow the coexistence among sea urchins species (Contreras and Castilla, 1987; Cobb and Lawrence, 2005; Privitera et al., 2008; Wangensteen et al., 2011; Cabanillas-Terán et al., 2016; Rodríguez-Barreras et al., 2016), the high consumption of the same resources by more than one species is related to their high availability in the environment and does not seem to be a limiting factor (Vásquez et al., 1984; Vanderklift et al., 2006; the present study).

In Okinawa (Japan), four *Echinometra* species have the same feeding types and preferences for the same resources, but they occur in segregated habitats (Hiratsuka and Uehara, 2007). In Chile, three of four sea urchin species strongly overlap their trophic niche feeding high proportions of the kelp *Macrocystis pyrifera,* but there is no overlap in microhabitat utilization, except for two of them (Vásquez et al., 1984). Although recent studies have indicated distribution patterns (Cordeiro et al., 2014) and habitat relationships (Labbé-Bellas et al., 2016) for both *E. lucunter* and *P. gaimardi,* future studies that assess the microhabitats use - e.g. substrate slope, crevices - (Bulleri et al., 1999) can elucidate this apparent high spatial overlap (Cordeiro et al., 2014; Labbé-Bellas et al., 2016) and trophic niche between species in the superficial subtidal zones in shallow rocky shores.

We also should not underestimate the high feeding plasticity of sea urchin species (Wing et al., 2008; Rodríguez-Barreras et al., 2016; Gil et al., 2021). Especially in situations of high abundance of resources (Vanderklift et al., 2006; Oliveira et al., 2021), the generalist feeding patterns tend to reduce the competitive potential between species and, at the same time, increase the apparent trophic niche overlap (Schoener, 1971). Then, studies that take into account, as well other aspects of the niche dimensions, such as microhabitats' use, and feeding patterns in temporal scale (seasonal scale) can provide a more specific perspective on the relationship between *E. lucunter* and *P. gaimardi*.

2.5 Conclusion

E. lucunter and *P. gaimardi* had a high trophic niche overlap, caused by the high consumption of algal material, being first-order consumers (herbivores). The feeding pattern of both species is primarily influenced by the availability of resources, and to some degree, for morphological and chemical aspects of the algae, causing sea urchins to avoid it. The distinction between sites (availability of resources) did not exert significant changes in the degree of food partitioning between species. Thus, the generalist herbivore feeding pattern and the high supply of trophic resources indicate that there is no direct competition between species. In addition, other dimensions of the niche must be analyzed, in order to have a better understanding of the mechanisms that allow the coexistence of both species in the shallow rocky shores.

Ethical consideration

This study was conducted following Brazilian legislation, under the permit SISBIO #64318-3 (ICMBIO/MMA – Brazilian Ministry of Environment).

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2.6 References

Agatsuma, Y.A., Nakata, A.K., Matsuyama, K.E., 2000. Seasonal foraging activity of the sea urchin *Strongylocentrotus nudus* on coralline flats in Oshoro Bay in south-western Hokkaido, Japan. Fisheries Science. 66(2), 198-203. https://doi.org/10.1046/j.1444-2906.2000.00035.x

Albrecht M., Gotelli, N.J., 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia. 126, 134–141. https://doi.org/10.1007/s004420000494

Aued, A.W., Smith, F., Quimbayo, J.P., Cândido, D.V., Longo, G.O., Ferreira, C.E.L., Witman, J.D., Floeter, S.R., Segal, B., 2018. Large-scale patterns of benthic marine communities in the Brazilian Province. PLOS ONE. 13(6), e0198452. https://doi.org/10.1371/journal.pone.0198452

Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs. 83(4), 557-574. https://doi.org/10.1890/12-2010.1

Bartlett, M.S., 1937. Properties of sufficiency and statistical tests. Proceedings of the royal society of London. 160, 268–282. https://doi.org/10.1098/rspa.1937.0109

Bellwood, D., Hughes, T., Folke, C., Nystrom, M., 2004. Confronting the coral reef crisis. Nature. 429, 827–833. https://doi.org/10.1038/nature02691

Bianco, E.M., Teixeira, V.L., Pereira, R.P., 2010. Chemical defenses against herbivory by sea urchin from tropical marine seaweed. Brazilian Journal of Oceanography. 53, 213-218. https://doi.org/10.1590/S1679-87592010000300004

Birkeland, C., 1989. The influence of echinoderms on coral-reef communities. Echinoderm studies. 3, 1-79.

Black, R., Johnson, M.S., Trendall, J.T., 1982. Relative size of Aristotle's Lantern in *Echinometra mathaei* occurring at different densities. Marine Biology. 71, 101-106. https://doi.org/10.1007/BF00396997

Black, R., Cood, C., Hebbert, D., Vink, S., Burt., 1984. The functional significance of the relative size of Aristotle's lantern in the sea urchin *Echinometra mathaei* (de blainville). Journal of Experimental Marine Biology and Ecology provides. 77, 81-97. https://doi.org/10.1016/0022-0981(84)90052-2

Brandl, S.J., Casey, J.M., Meyer, C.P., 2020. Dietary and habitat niche partitioning in congeneric cryptobenthic reef fish species. Coral Reefs. 39, 305-317. https://doi.org/10.1007/s00338-020-01892-z

Boudouresque, C.F., Verlaque, M. 2020. Chapter 26 – *Paracentrotus lividus* in: Lawrence, M.J (Ed.), Sea Urchins: Biology and Ecology. Developments in Aquaculture and Fisheries Science, Elsevier, Volume 43, pp. 447-485. https://doi.org/10.1016/B978-0-12-819570-3.00026-3

Brusca, R.C., Brusca, G.S., 2007. Invertebrados, segunda ed. Guanabara Koogan, Rio de Janeiro.

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, 81-95. https://doi.org/10.1016/S0022-0981(99)00073-8

Cabanillas-Terán, N., Loor-Andrade, P., Barreras, R.R., Cortés, J., 2016. Trophic ecology of sea urchins in coral-rocky reef systems, Ecuador. PeerJ. 4, e1578. https://doi.org/10.7717/peerj.1578

Cabanillas-Terán, N., Hernández-Arana, H.A., Ruiz-Zárate, M., Vega-Zepeda, A., Sanchez-Gonzalez, A., 2019. *Sargassum* blooms in the Caribbean alter the trophic structure of the sea urchin *Diadema antillarum*. PeerJ. 7, e7589. https://doi.org/10.7717/peerj.7589

Calderon, E.N., Zilberberg, C., Paiva, P.C., 2007. The possible role of *Echinometra lucunter* (Echinodermata: Echinoidea) in the local distribution of *Darwinella* sp. (Porifera: Dendroceratida) in Arraial do Cabo, Rio de Janeiro State, Brazil. Porifera Research: Biodiversity, Innovation and Sustainability. 211-217.

Carpenter, R.C., 1988. Mass mortality of a Caribbean sea urchin: Immediate effects on community metabolism and other herbivores. PNAS. 85, 511-514. https://doi.org/10.1073/pnas.85.2.511

Carpenter, R.C., 1990 Mass mortality of *Diadema antillarum*. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Marine Biology. 104, 67-77. https://doi.org/10.1007/BF01313159

Carvalho, J.L., Schettini, C.A., Ribas, T.M., 1998. Estrutura termohalina do litoral centro-norte catarinense. Brazilian Journal of Aquatic Science and Technology. 2, 181-197 https://doi.org/10.14210/bjast.v2n1.p181-197

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology. 18, 117-143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Cobb, J. Lawrence, J.M., 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., Airoldi, L., 2014. What are algal turfs? Towards a better description of turfs. Marine Ecology Progress Series. 495, 299–307. https://doi.org/10.3354/meps10513

Contreras, S., Castilla, J.C., 1987. Feeding behavior and morphological adaptations in two sympatric sea urchin species in central Chile. Marine Ecology Progress Series. 38, 217-224.

Cordeiro C.A.M.M., Harborne, A.R., Ferreira, C.E.L., 2014. Patterns of distribution and composition of sea urchin assemblages on Brazilian subtropical rocky reefs. Marine Biology. 161, 2221-2232. https://doi.org/10.1007/s00227-014-2500-0

Cornell, H.V., 2012. Niche overlap. In: Hastings A, Gross, L.J. (eds.), Encyclopedia of Theoretical Ecology. University of California Press, Berkeley, pp. 489–497.

Ebert, T., 1968. Growth rates of the Sea Urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. Ecology. 49(6), 1075-1091. https://doi.org/10.2307/1934491

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, 1883–1895. https://doi.org/10.1007/s10886-006-9116-x

Floeter, S.R., Rocha, L.A., Robertson, D.R., Joyeux, J.C., Smith-Vaniz, W.F., Wirtz, P., Edwards, A.J., Barreiros, J.P., Ferreira, C.E.L., Gasparini, J.L., Brito, A., Falcón, J.M., Bowen, B.W., Bernardi, G., 2008. Atlantic reef fish biogeography and evolution. Journal of Biogeography. 35, 22-47. https://doi.org/10.1111/j.1365-2699.2007.01790.x

Fernandez, W.S., Dias, G.M., Majer, A.P., Delboni, C.G., Denandai, M.R., Turra, A., 2017. Resource partitioning between sympatric starfish from tropical unconsolidated substrate: Implications for coexistence and top-down control on benthic prey. Estuarine, Coastal and Shelf Science. 196, 141-149. https://doi.org/10.1016/j.ecss.2017.06.039

Gil, D.G., Boraso, A.L., Lopretto, E.C., Héctor, F.Z., 2021. Depth-related plasticity in the diet composition of *Pseudechinus magellanicus* (Echinoidea, Temnopleuridae) in nearshore environments off central Patagonia, Argentina. Aquatic Ecology. 55, 589–606. https://doi.org/10.1007/s10452-021-09847-4

Gotelli, N.J., Hart, E.M., Ellison, A.M., 2015). EcoSimR: Null model analysis for ecological data. R package version 0.1.0. https://doi.org/10.5281/zenodo.16522

Gotelli, N.J., Ellison, A.M., 2013. A Primer of Ecological Statistics, second ed. Sinauer Associates, Sunderland.

Guidetti, P., Terlizzi, A., Boero, F., 2004. Effects of the edible sea urchin, *Paracentrotus lividus*, fishery along the Apulian rocky coast (SE Italy, Mediterranean Sea). Fisheries Research. 66(2-3), 287-297. https://doi.org/10.1016/S0165-7836(03)00206-6

Guillou, M., Lumingas, L. J. L., 1999. Variation in the reproductive strategy of the sea urchin *Sphaerechinus granularis* (Echinodermata: Echinoidea) related to food availability. Journal of the Marine Biological Association of the United Kingdom. 79, 131-136.

Hayden, B., Palomares, M.L.D., Smith, B.E, Poelen, J.H., 2019. Biological and environmental drivers of trophic ecology in marine fishes - a global perspective. Scientific Reports. 9, e11415. https://doi.org/10.1038/s41598-019-47618-2

Hiratsuka, Y., Uehara, T., 2007. Feeding ecology of four species of sea urchins (genus *Echinometra*) in Okinawa. Bulletin of Marine Science. 81(1), 85-100.

Horta, P.A., Amancio, E., Coimbra, C.S., Oliveira, E.C., 2001. Considerações sobre a distribuição e origem da flora de macroalgas marinhas brasileiras. Hoehnea. 28(3), 243-265.

Hughes, R.N., 1980. Optimal foraging theory in the marine context. Oceanography and Marine Biology: An Annual Review. 18, 423-481.

Johansson, C.L., Bellwood, D.R., Depczynski, M., 2010. Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia. Marine Ecology Progress Series. 414, 65-74. https://doi.org/10.3354/meps08730

Kawakami, E., Vazzoler, G., 1980. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. Boletim do Instituto Oceanográfico. 29, 205–207. https://doi.org/10.1590/S0373552419800002000043

Kent, C.M., Sherry, T.W., 2020. Behavioral niche partitioning reexamined: Do behavioral differences predict dietary differences in warblers? Ecology. 101(8), e03077 https://doi.org/10.1002/ecy.3077

Klumpp, D.W., Espinosa, J.T.S., Fortes, M.D., 1993. Feeding ecology and trophic role of sea urchins in a tropical seagrass community. Aquatic Botany. 45, 205-229. https://doi.org/10.1016/0304-3770(93)90022-O

Labbé-Bellas, R., Cordeiro, C.A.M.M., Floeter, S.R., Segal, B., 2016. Sea urchin abundance and habitat relationships in different Brazilian reef types. Regional Studies in Marine Science. 8, 33-40. https://doi.org/10.1016/j.rsma.2016.09.004

Larson, B.R., Vadas, R.L., Keser, M., 1980. Feeding and nutritional ecology of the sea urchin *Strongylocentrotus droebachiensis* in Maine, USA. Marine Biology. 59, 49–62. https://doi.org/10.1007/BF00396982

Lawlor, L.R., 1980. Overlap, similarity, and competition coefficients. Ecology Society of America. 61(2), 245-251. https://doi.org/10.2307/1935181

Lawrence, J.M, Lawrence, A.L., Watts, S.A., 2020. Chapter 9 - Ingestion, digestion, and digestibility of regular sea urchins, in: Lawrence, M.J (Ed.), Sea Urchins: Biology and Ecology. Developments in Aquaculture and Fisheries Science, Elsevier, Volume 43, pp. 165-190. https://doi.org/10.1016/B978-0-12-819570-3.00009-3

Lawrence, J.M., Sammarco, P.W., 1982. Effects of feeding on the environment: Echinoidea, in: Jangoux, M. and Lawrence J.M. (Ed.), Echinoderm nutrition. AA Balkema, Rotterdam, pp. 499-519.

Levitan, D, 1991. Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation. Marine Biology. 111(3), 431-435. https://doi.org/10.1007/BF01319415

Liedke, A.M.R., Barneche, D.R., Ferreira, C.E.L., Segal, B., Nunes, L.T., Burigo, A.P., Carvalho, J.A., Buck, S., Bonaldo, R.M., Floeter, S.R., 2016. Abundance, diet, foraging and nutritional condition of the banded butterflyfish (*Chaetodon striatus*) along the western Atlantic. Marine Biology. 163, 6. https://doi.org/10.1007/s00227-015-2788-4

Liedke, A.M.R., Bonaldo, R.M., Segal, B., Ferreira, C.E.L., Nunes, L.T., Burigo, A.P., Buck, S., Oliveira Santos, L.G.R., Floeter, S.R., 2018. Resource partitioning by two syntopic sister-species of butterflyfish (Chaetodontidae). Journal of the Marine Biological Association of the United Kingdom. 98, 1767–1773. https://doi.org/10.1017/S0025315417001321

Lindner. A., 2018. Vida Marinha de Santa Catarina, Segunda ed. Editora UFSC, Florianópolis.

Littler, D.S., Littler, M.M., 2000. Caribbean Reef Plants: An Identification Guide to the Reef Plants of Caribbean, Bahamas, Florida and Gulf of Mexico. Offshore Graphics, Washington DC.

Littler, M.M., Littler, D.S., Taylor, P.R. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. Journal of Phycology. 19, 229-237.

Longo, G.O., Morais, R.A., Martins, C.D.L., Mendes, C.T., Aued, A.W., Cândido, D.V., Oliveira, J.C., Nunes, L.T., Fontoura, L., Sissini, M.N., Teschima, M.M., Silva, M.B., Ramlov, F., Gouvea, L.P., Ferreira, C.E.L., Segal, B., Horta, P.H., Floeter, S.R., 2015. Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in South Atlantic: Rocas Atoll, NE Brazil. PLOS ONE. 10(6), e0127176. https://doi.org/10.1371/journal.pone.0127176

McClanahan, T.R., 1992. Resource utilization, competition, and predation: a model and example from coral reef grazers. Ecological Modelling. 61 (3-4), 195-215. https://doi.org/10.1016/0304-3800(92)90018-A

McClanahan, T.R., Muthiga, N.A., 2020. Chapter 28 – *Echinometra*. in: Lawrence, M.J (Ed.), Sea Urchins: Biology and Ecology. Developments in Aquaculture and Fisheries Science, Elsevier, Volume 43, pp. 497-517. https://doi.org/10.1016/B978-0-12-819570-3.00028-7

McClintock, J.B., Klinger, T.S., Lawrence, J.M., 1982. Feeding Preferences of Echinoids for Plant and Animal Food Models. Bulletin of Marine Science. 32 (1), 365-369.

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.L.T., Tavares, C.M., 2006. The relation of algal availability and food preferences in the field diet of the Equinoidae *Echinometra lucunter* on a Rocky Shore in Southeast Brazil. Journal of Coastal Research. 39, 1197-1201.

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. https://doi.org/10.12681/mms.302

Nascimento, E.F.I., Rosso, S., 2007. Fauna associada às macroalgas marinhas bentônicas (Rhodophyta e Phaeophyta) da região de São Sebastião, São Paulo. Revista Brasileira de Ecologia. 11(1-2), 38-51.

Nassar, C., 2012. Macroalgas Marinhas do Brasil – Guia de campos das principais espécies. Technical Books, Rio de Janeiro.

Navarrete, A.H., Camus, P.A., Opazo, L.P., 2008. Variación ambiental y patrones dietarios del erizo negro *Tetrapygus niger* en costas intermareales rocosas del norte de Chile. Revista Chilena de Historia Natural. 81, 305-319. http://dx.doi.org/10.4067/S0716-078X2008000300001

Oksanen, J., Blanchet, F.G., Friendly, M, Kindt., R, Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Oliveira, C.M., 1991. Survival of seaweeds ingested by three species of tropical sea urchins from Brazil. Hydrobiologia. 222, 13-17. https://doi.org/10.1007/BF00017495

Oliveira, E., Ignacio, A.R.A., Lázaro, W.L., Muniz, C.C., Campos, D.V.S., Costa, J.V.M., Ribeiro, T., 2021. Feeding aspects of *Knodus heteresthes* (Eigenmann, 1908) and *Moenkhausia lepidura* (Kner, 1858) (Characiformes, Characidae) in the Teles Pires and Juruena Rivers, southern Amazon. Brazilian Journal of Biology. 81(2), 343-350. https://doi.org/10.1590/1519-6984.226136.

Pereira, D.M., Schettini, C.A.F., Omachi, C.Y., 2009. Caracterização de feições oceanográficas na plataforma de Santa Catarina através de imagens orbitais. Revista Brasileira de Geofísica. 27, 81-93. https://doi.org/10.1590/S0102-261X2009000100007

Pianka, E.R., 1973. The structure of lizard communities. Annual Review of Ecology, Evolution, and Systematics. 4, 53–74. https://doi.org/10.1146/annurev.es.04.110173.000413

Pianka, E. R., 1974. Niche overlap and diffuse competition. PNAS. 71, 2141-2145. https://doi.org/10.1073/pnas.71.5.2141

Piola, A.R., Campos, E.J.D., Möller Jr., O.O., Charo, M., Martinez, C., 2000. Subtropical Shelf Front off eastern South America. Journal of Geophysical Research Oceans. 105, 6565-6578. https://doi.org/10.1029/1999JC000300

Piola, A.R., Matano, R.P., Palma, E.D., Möller Jr., O.O., Campos, E.J.D., 2005. The influence of the Plata River discharge on the western South Atlantic shelf. Geophysical Research Letters. 32, 1-4. https://doi.org/10.1029/2004GL021638

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. https://doi.org/10.1016/j.seares.2008.07.001

Queiroz, V., 2020. Behavioral and alimentary aspects of the sea urchin *Paracentrotus gaimardi* (Echinodermata). Research and Teaching in Exact and Natural Sciences. 4, e1482. http://dx.doi.org/10.29215/pecen.v4i0.1482

Reyes-Luján, J., Barrios, J., Arrieche, D., Zapata-ívenes, E., Salgado, W., Lodeiros, C., 2015. Dieta del erizo negro *Echinometra lucunter* (Echinometra: Echinoidea) en el Nororiente de Venezuela. Biología tropical. 63, 233-242.

R Core Team., 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ribi, G., Schärer, R., Ochsner, P., 1977. Stomach contents and size-frequency distributions of two coexisting sea star species, *Astropecten aranciacus* and *A. bispinosus*, with reference to competition. Marine Biology. 43, 181–185. https://doi.org/10.1007/BF00391266

Rodríguez-Barreras, R., Godoy-Vitorino, F., Præbel, K., Wangensteen, O.S., 2020. DNA metabarcoding unveils niche overlapping and competition among Caribbean Sea urchins. Regional Studies in Marine Science. 40. https://doi.org/10.1016/j.rsma.2020.101537.

Rodríguez-Barreras, R., Cuevas, E., Cabanillas-Terán N., Branoff, B., 2016. Understanding trophic relationships among Caribbean Sea urchins. Biologia Tropical. 64, 837-848.

Rosumek, F.B., Blüthgen, N., Brückner, A., Menzel, F., Gebauer, G., Heethoff, M., 2018. Unveiling community patterns and trophic niches of tropical and temperate ants using an integrative framework of field data, stable isotopes and fatty acids. PeerJ. 6, e5467.

Royston, J.P., 1995. Remark AS R94: A remark on algorithm AS 181: The W-test for normality. Journal of the Royal Statistical Society. 44(4), 547-551. https://doi.org/10.2307/2986146

Sammarco, P.W., 1982. Echinoid grazing as a structuring force in coral communities: Whole reef manipulations. Journal of Experimental Marine Biology and Ecology. 61(1), 31-55. https://doi.org/10.1016/0022-0981(82)90020-X

Sánchez-Jérez, P., Cesar, A., Cortez, F.S., Pereira, C.D.S., Silva, S.L.R., 2001. Distribución Espacial de las Poblaciones de Erizos Más Abundantes de la Costa Sudeste Del Litoral de São Paulo (Brasil). Ciencias Marinas. 27, 139-153.

Schoener, T. W., 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics. 2, 369–404.

Schoener, T.W., 1974. Resource Partitioning in Ecological Communities. Science. 185, 27-39.

Segal, B., Freire, A.S., Lindner, A., Krajewski, J.P., Soldateli, M. 2017. MAArE – Monitoramento Ambiental da Reserva Biológica Marinha do Arvoredo e Entorno. Universidade Federal de Santa Catarina, Florianópolis.

Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69(3), 476-498. https://doi.org/10.2307/3545860

Steneck, R.S., Graham, M., Bourque, B., Corbett, D., Erlandson, J., Estes, J., & Tegner, M., 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. Environmental Conservation. 29(4), 436-459. https://doi.org/10.1017/S0376892902000322

Steneck, R.S., 2020. Chapter 15 – Regular sea urchins as drivers of shallow benthic marine community structure in: Lawrence, M.J (Ed.), Sea Urchins: Biology and Ecology. Developments in Aquaculture and Fisheries Science, Elsevier, Volume 43, pp. 255-279. https://doi.org/10.1016/B978-0-12-819570-3.00015-9

Spitz, J., Cherel, Y., Bertin, S., Kiszka, J., Dewz, A., Ridoux, V., 2011. Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. Deep-Sea Research. 58, 273–282. https://doi.org/10.1016/j.dsr.2010.12.009

Souza, C.F., Oliveira, A.S., Perreira, R.C., 2008. Feeding preference of the sea urchin *Lytechinus variegatus* (Lamarck, 1816) on seaweeds. Brazilian Journal of Oceanography. 56(3), 239-247.

Steinberg, P., 1986. Chemical Defenses and the Susceptibility of Tropical Marine Brown Algae to Herbivores. Oecologia. 69(4), 628-630. https://doi.org/10.1007/BF00410374

Tavares, Y.A.G., 2004. Biologia reprodutiva dos equinóides *Echinometra lucunter* (Linnaeus, 1758) e *Arbacia lixula* (Linnaeus, 1758) na Ilha da Galheta, litoral paranaense, Brasil. Tese (Doutorado) - Universidade Federal do Paraná, Curitiba

Tavares, Y.A.G., Semanovschi, N.P., Camargo, J.C.M., Pellizzari, F., 2020. Feeding habits of the sea urchin *Echinometra lucunter* L. (Echinoidea) in a remote Southwestern Atlantic island, Trindade, Brazil. Pan-American Journal of Aquatic Sciences. 15, 303-319.

Trygonis, V., Sini, M., 2012. *photoQuad*: A dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. Journal of Experimental Marine Biology and Ecology. 424-425, 99-180. https://doi.org/10.1016/j.jembe.2012.04.018

Tukey, J.W., 1977. Exploratory Data Analysis, first ed. Pearson.

Vanderklift, M.A., Kendrick, G.A., 2004. Variation in abundances of herbivorous invertebrates in temperate subtidal rocky reef habitats. Marine and Freshwater Research. 55(1), 93-103. https://doi.org/10.1071/MF03057

Vanderklift, M.A., Kendrick, G.A., Smith, A.J., 2006. Differences in trophic position among sympatric sea urchin species. Estuarine, Coastal and Shelf Science. 66, 291–297. https://doi.org/10.1016/j.ecss.2005.09.004

Vásquez, J., Castilla, J., & Santelices, B., 1984. Distributional patterns and diets of four species of sea urchins in giant kelp forest (*Macrocystis pyrifera*) of Puerto Toro, Navarino Island, Chile. Marine Ecology Progress Series. 19(1-2), 55-63.

Vergés, A., Alcoverro, T., Romero, J., 2011. Plant defences and the role of epibiosis in mediating within-plant feeding choices of seagrass consumers. Oecologia. 166, 381-390. https://doi.org/10.1007/s00442-010-1830-y

Villaça, R.C., 1988. Le Phytobenthos Infralittoral des Biotopes Sciaphiles dans la Région d'Upwelling de Cabo Frio(Brésil). Thèse Doct. Univ. Aix-Marseille II.

Wangensteen, O.S., 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. https://doi.org/10.3354/meps09359

Wickham, H., 2007. Reshaping data with the reshape package. Journal of Statistical Software. 21(12), 1-20. https://doi.org/10.18637/jss.v021.i12

Wickham, H., 2011. The split-apply-combine strategy for data analysis. Journal of Statistical Software. 40(1), 1-29. https://doi.org/10.18637/jss.v040.i01

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Winemiller, K.O., Pianka, E.R., 1990. Organization in natural assemblages of desert lizards and tropical fishes. Ecological Monographs. 60, 27-55. https://doi.org/10.2307/1943025

Wing, S.R., McLeod, R.J., Clark, K.L., Frew, R.D., 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. https://doi.org/10.3354/meps07434

2.7 Supplementary Material

S1 Table

List of taxa found in benthic cover analysis in two shallow rocky shores (Gravatá and Matadeiro) in Santa Catarina island, Brazil.

Species	Morphological Groups	Sites	
		Gravatá	Matadeiro
Algae			
Chlorophyta			
Codium spp.	Corticated	-	X
Codium intertextum	Crustose	X	X
Ulva spp.	Foliose	X	X
Phaeophyceae			
Colpomenia sinuosa	Crustose	X	X
Canistrocarpus cervicornis	Foliose	X	X
Sargassum spp.	Leathery	X	X
Rhodophyceae			
Amphiroa spp.	ACA	X	X
Arthrocardia variabilis	ACA	X	X
Asparagopsis sp.	Corticated	X	-
Centroceras clavulatum	Filamentous	X	X
Jania spp	ACA	X	X
Corallinales algae	Crustose	X	X
Chondracanthus acicularis	Corticated	X	X
Hypnea pseudomussiforme	Corticated	X	X
Plocamium brasiliense	Corticated	X	-
Pterocladiella capillacea	Corticated	X	X
Metazoa			
Cnidaria			

Bunodosoma sp.	Cnidarian	X	X
Zoanthids	Zoanthids	X	-
Echinodermata			
Echinometra lucunter	Sea urchin	X	X
Paracentrotus gaimardi	Sea urchin	X	X
Parazoa			
Porifera			
Tedania ignis	Sponge	X	-

S2 Table
List of species present in the turf in both sites.

Species	Functional Groups	Sites	
		Gravatá	Matadeiro
Chlorophyta*			
Chaetomorpha sp.	Filamentous	X	X
Cladophora spp.	Filamentous	X	X
Cladophoropsis membranacea	Filamentous	-	X
Codium intertextum	Crustose	-	X
Derbesia marina	Filamentous	X	X
Ulva spp.	Foliose	X	X
Phaeophyceae*			
Canitrocarpus cervicornis	Foliose	X	-
Sargassum spp.	Leathery	X	X
Rhodophyceae*			
Aglaothamnion felipponei	Filamentous	X	-
Amphiroa spp.	ACA	X	X
Arthrocardia variabilis	ACA	X	X

Centroceras clavulatum	Filamentous	X	X
Ceramium sp.	Filamentous	X	X
Ceratodictyon planicaule	Corticated	X	-
Ceratodictyon variabile	Corticated	X	-
Champia sp.	Corticated	X	X
Chondracanthus Acicularis	Corticated	X	X
Chondria sp.	Corticated	-	X
Gelidium crinale	Corticated	X	X
Gelidium pusillum	Corticated	X	X
Gymnogongrus griffithsiae	Corticated	X	-
Herposhiponia tenella	Filamentous	X	X
Hypnea pseudomussiforme	Corticated	X	X
Hypnea spinella	Corticated	X	X
Jania spp.	ACA	X	X
Laurencia catarinenses	Corticated	X	X
Neosiphonia sp.	Filamentous	X	-
Polysiphonia spp.	Filamentous	X	X
Polysiphonia subtilíssima	Filamentous	X	-
Pterocladiella capillacea	Corticated	X	-
Pterosiphonia parasítica	Filamentous	X	-
Pterosiphonia sp.	Filamentous	X	X

S3 Table

Frequency of occurrence (%, FO), volume (%, V) in the diet and taxonomic feeding index (%, IAi_t) of organic dietary items of *Echinometra lucunter* and *Paracentrotus gaimardi* from populations of Matadeiro and Gravatá sites.

Food Items	Gravatá						Matadeiro					
	Echinometra lucunter			*Paracentrotus gaimardi*			*Echinometra lucunter*			*Paracentrotus gaimardi*		
	FO	V	IAi	FO	V	IAi	FO	V	IAi	FO	V	IAi
Algae												
Chlorophyta												
Chaetomorpha sp.	10	0.2	<0.1	30	0.7	0.2	-	-	-	-	-	-
Cladophora spp.	50	1.1	0.6	80	2.8	2.5	40	0.6	0.3	70	1.9	1.6
Cladophoropsis membranacea	-	-	-	-	-	-	-	-	-	20	0.3	<0.1
Codium spp.	90	13.8	**13.8**	40	1	0.4	90	11	**11.2**	50	2.8	1.7
Derbesia marina	10	0.4	<0.1	10	0.1	<0.1	10	0.1	<0.1	30	1.1	0.4
Ulva spp.	100	13.9	**15.5**	100	8.1	**9.2**	80	6.3	**5.7**	90	8.1	**9**
Phaeophyta												
Canitrocarpus cervicornis	30	0.5	0.1	50	1.1	0.6	10	0.1	<0.1	-	-	-
Hincksia sp.	-	-	-	50	2.4	1.4	-	-	-	-	-	-
Sargassum spp.	100	6.5	**7.2**	100	22.8	**25.8**	30	1.3	0.4	-	-	-
Spachelaria sp.	10	<0.1	<0.01	-	-	-	-	-	-	-	-	-
Rhodophyta												

Aglaothamnion felipponei	10	<0.1	<0.01	-	-	-	-	-	-	-	-	-
Bangia sp.	10	<0.1	<0.01	20	0.1	<0.1	-	-	-	-	-	-
Centroceras clavulatum	90	1.5	1.5	100	2.8	3.1	100	1.7	1.9	100	7.7	**9.5**
Ceradyction planicaule	10	0.3	<0.1	-	-	-	-	-	-	-	-	-
Ceramium spp.	20	<0.1	<0.1	30	0.3	0.1	10	<0.1	<0.01	10	<0.1	<0.1
Champia sp.	-	-	-	-	-	-	10	<0.1	<0.01	-	-	-
Chondracanthus acicularis	80	3.9	3.5	70	3.5	2.7	40	1.1	0.5	-	-	-
Corallinales**	100	16.4	**18.3**	100	23.6	**26.7**	70	8.3	**6.6**	50	5.6	3.4
Gracilaria sp.	20	0.4	<0.1	10	0.1	<0.1	10	0.3	<0.1	-	-	-
Gelidiales**	80	2.1	1.8	90	2.7	2.7	60	2.2	1.5	40	2	1
Herposhiponia tenella	-	-	-	-	-	-	10	<0.1	<0.01	10	<0.1	<0.1
Hypnea spp.	100	12.8	**14.3**	100	10.5	**11.9**	100	31	**35.4**	100	40.3	**49.6**
Polysiphonia spp.	80	1.4	1.2	80	2.1	1.9	20	0.1	<0.1	70	1.9	1.6
Plocamium brasiliense	20	0.5	0.1	50	1	0.5	20	0.5	0.1	20	1.4	0.3
Pterocladiella capillacea	100	15.5	**17.4**	70	5.3	4.2	100	29	**33.1**	80	13.5	**13.3**
Pterosiphonia spp.	20	0.6	0.1	60	1.2	0.8	10	0.1	<0.1	40	1	0.5
Rhodomelaceae*	60	2.2	1.4	20	0.7	0.1	60	1.9	1.3	20	1.2	0.3
Spyridia sp.	-	-	-	-	-	-	-	-	-	10	0.3	<0.1
Metazoa												
Annelida												
Polychaeta	20	0.9	0.2	-	-	-	-	-	-	-	-	-

Arthropoda: Crustacea												
Eucarida	-	-	-	20	0.3	<0.1	10	0.1	<0.1	-	-	-
Peracarida	40	0.8	0.3	70	1.6	1.3	40	0.7	0.3	80	3.2	3.1
Bryozoa												
Bugula sp.	-	-	-	20	0.1	<0.1	-	-	-	-	-	-
Cnidaria												
Hydrozoa	50	1	0.5	60	1.4	0.9	30	0.4	0.1	60	3.5	2.6
Mollusca												
Bivalvia	30	0.5	0.1	70	1.9	1.5	50	0.7	0.4	20	0.5	0.1
Gastropoda	10	<0.1	<0.01	10	<0.1	<0.01	20	<0.1	<0.01	20	0.1	<0.1
Eggs												
Undetermined	10	<0.1	<0.01	-	-	-	10	<0.1	<0.01	10	<0.1	<0.1
Parazoa												
Porifera	50	1.3	0.7	20	0.5	0.1	30	0.8	0.2	40	2	1
Vascular Plant												
Seeds	10	<0.1	<0.01	-	-	-	10	0.1	<0.1	20	0.3	<0.1

**Family /* Order / Bold numbers highlight IAi higher than 5.

S4 Table

Frequency of occurrence (%, FO), volume (%, V) in the diet and feeding index (%, IAi_m) of morphological dietary items of *Echinometra lucunter* and *Paracentrotus gaimardi* from populations of Matadeiro and Gravatá sites.

Food Items	Gravatá						Matadeiro					
	Echinometra lucunter			*Paracentrotus gaimardi*			*Echinometra lucunter*			*Paracentrotus gaimardi*		
	FO	V	IAi	FO	V	IAi	FO	V	IAi	FO	V	IAi
Algae												
ACA	100	16.4	**17.1**	100	23.6	**24.2**	70	8.3	**6.3**	50	5.6	3
Corticated	100	38	**39.7**	100	24.1	**24.7**	100	66.3	**72**	100	58.6	**64.5**
*Codium**	90	13.8	**13**	40	1	0.4	90	11	**10.7**	50	2.8	1.5
Filamentous	100	5.8	**6.1**	100	12.9	**13.2**	100	3	3.2	100	14.7	**16.1**
Foliose	100	14.4	**15.1**	100	9.2	**9.5**	80	6.5	**5.6**	90	8.1	**8**
Leathery	100	6.5	**6.8**	100	22.8	**23.4**	30	1.3	0.4	-	-	-
Metazoa												
Annelida	20	0.9	0.2	-	-	-	-	-	-	-	-	-
Arthropoda: Crustacea	40	0.8	0.3	80	2	1.6	40	0.9	0.4	80	3.2	2.8
Bryozoa	-	-	-	20	0.5	0.1	-	-	-	-	-	-
Cnidaria	50	1	0.5	60	1.4	0.9	30	0.4	0.1	60	3.5	2.3
Mollusca	30	0.5	0.1	80	1.9	1.6	60	0.8	0.5	40	0.6	0.2
Eggs	10	<0.1	<0.01	-	-	-	10	<0.1	<0.01	10	<0.1	<0.01
Parazoa												

Porifera	50	1.3	0.6	20	0.1	<0.1	30	0.8	0.2	40	2	0.8
Vascular plant												
Seeds	10	<0.1	<0.01	-	-	-	10	0.1	<0.01	20	0.3	<0.1

* Genus/ Numbers in bold indicate IAi higher than 5.

3.0 CONSIDERAÇÕES FINAIS

Poucos trabalhos vêm sendo realizados com as assembleias de ouriços-do-mar em Santa Catarina. Quando existem, os focos principais são sobre a distribuição e abundância das espécies (e.g. XAVIER, 2010; LABBÉ-BELLAS et al., 2016, MARTINS, 2016). Sendo a ecologia trófica tão importante para se ter uma melhor compreensão da estruturação das comunidades e um melhor entendimento das relações entre os organismos (ROSUMEK et al., 2018), nosso trabalho se propôs a suprir essa lacuna de informação, identificando o hábito alimentar de duas das espécies mais abundantes nos costões rochosos rasos do estado: *Echinometra lucunter* e *Paracentrotus gaimardi*.

Através dos nossos resultados foi possível verificar uma alta sobreposição de nicho trófico entre as espécies, com a disponibilidade de recursos sendo o principal fator de influência na dieta de *E. lucunter* e *P. gaimardi,* sendo o hábito herbívoro dominante em ambas. A alta sobreposição de nicho trófico fez com que a nossa hipótese de diferenciação alimentar entre as espécies para evitar a competição fosse rejeitada. Entretanto, a disponibilidade de recursos atuando como moduladora na dieta das espécies corroborou nossa segunda hipótese, sendo possível identificar um padrão alimentar herbívoro generalista para ambas.

A alta sobreposição trófica parece decorrer principalmente desse comportamento alimentar generalista, que tende a se adaptar à oferta de recursos disponíveis no ambiente (VANDERKLIFT et al., 2006; OLIVEIRA et al., 2021). O comportamento generalista tende a reduzir o potencial competitivo entre espécies e, ao mesmo tempo, aumentar a sobreposição de nicho trófico (SCHOENER, 1971). Do mesmo modo que diminui processos competitivos, o hábito herbívoro generalista, leva à uma alta plasticidade alimentar, fazendo com que espécies de ouriços-do-mar consigam se adaptar a diferentes ambientes, ajudando a explicar a alta variação de habitats ocupados por espécies com esse padrão (COBB & LAWRENCE, 2005; GIL et al., 2021).

Porém, mesmo com o padrão generalista evidente, o baixo consumo de algas com metabólitos secundários (que repelem a herbivoria) indica, em algum grau, seletividade alimentar. Somado a isso, a baixa taxa de ingestão de material animal corrobora o apontamento de falta de processo competitivo por recursos tróficos entre as espécies, já que somente em situações extremas, onde a disponibilidade de material vegetal é baixa, as espécies de ouriços-do-mar tendem a ingerir grandes quantidades de itens animais e algas pouco palatáveis (COBB & LAWRENCE, 2005).

Entretanto, vale ressaltar que estudos mais amplos que avaliem a forma preferencial de captação de alimento (CONTRERAS & CASTILLA, 1987) e ocupação de micro-habitats devem ser realizados com o intuito de verificar outros aspectos e dimensões do nicho de ambas as espécies (VÁSQUEZ et al., 1984), possibilitando assim, uma melhor compreensão de como elas utilizam, exploram e compartilham recursos.

3.0.1 REFÊRENCIAS BIBLIOGRÁFICAS

COBB, J; LAWRENCE, J.M. Diets and coexistence of the sea urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) along the central Florida gulf coast. **Marine Ecology Progress Series**, v. 295, p. 171-182, 2005.

CONTRERAS, S; CASTILLA, J.C. Feeding behavior and morphological adaptations in two sympatric sea urchin species in central Chile. **Marine Ecology Progress Series**, v. 38, p. 217-224, 1987.

GIL, G.D; BORASO, A.L; LOPRETTO, E.C; ZAIXSO, H.E. Depth-related plasticity in the diet composition of *Pseudechinus magellanicus* (Echinoidea, Temnopleuridae) in nearshore environments off central Patagonia, Argentina. **Aquatic Ecology**, v. 55, p. 589-606, 2021.

LABBÉ-BELLAS, R; CORDEIRO, C.A.M.M; FLOETER, S.R; SEGAL, B. Sea urchin abundance and habitat relationships in different Brazilian reef types. **Regional Studies in Marine Science**, v. 8, p. 33-40, 2016.

MARTINS, L.F. **Abundância de ouriços-do-mar em costões rochosos rasos de Santa Catarina**. Monografia (bacharelado em Oceanografia) - Universidade Federal de Santa Catarina. Florianópolis, 37. p. 2016.

OLIVEIRA, E; IGNACIO, A.R.A; LÁZARO, W.L; MUNIZ, C.C; CAMPOS, D.V.S; COSTA, J.V.M; RIBEIRO, T. Feeding aspects of *Knodus heteresthe*s (Eigenmann, 1908) and *Moenkhausia lepidura* (Kner, 1858) (Characiformes, Characidae) in the Teles Pires and Juruena Rivers, southern Amazon. **Brazilian Journal of Biology**, v. 81, p. 343-350, 2021.

ROSUMEK, F.B; BLÜTHGEN, N; BRÜCKNER, A; MENZEL, F.; GEBAUER, G; HEETHOFF, M. Unveiling community patterns and trophic niches of tropical and temperate ants using an integrative framework of field data, stable isotopes and fatty acids. **PeerJ**, 6 e5467, p. 1-31, 2018.

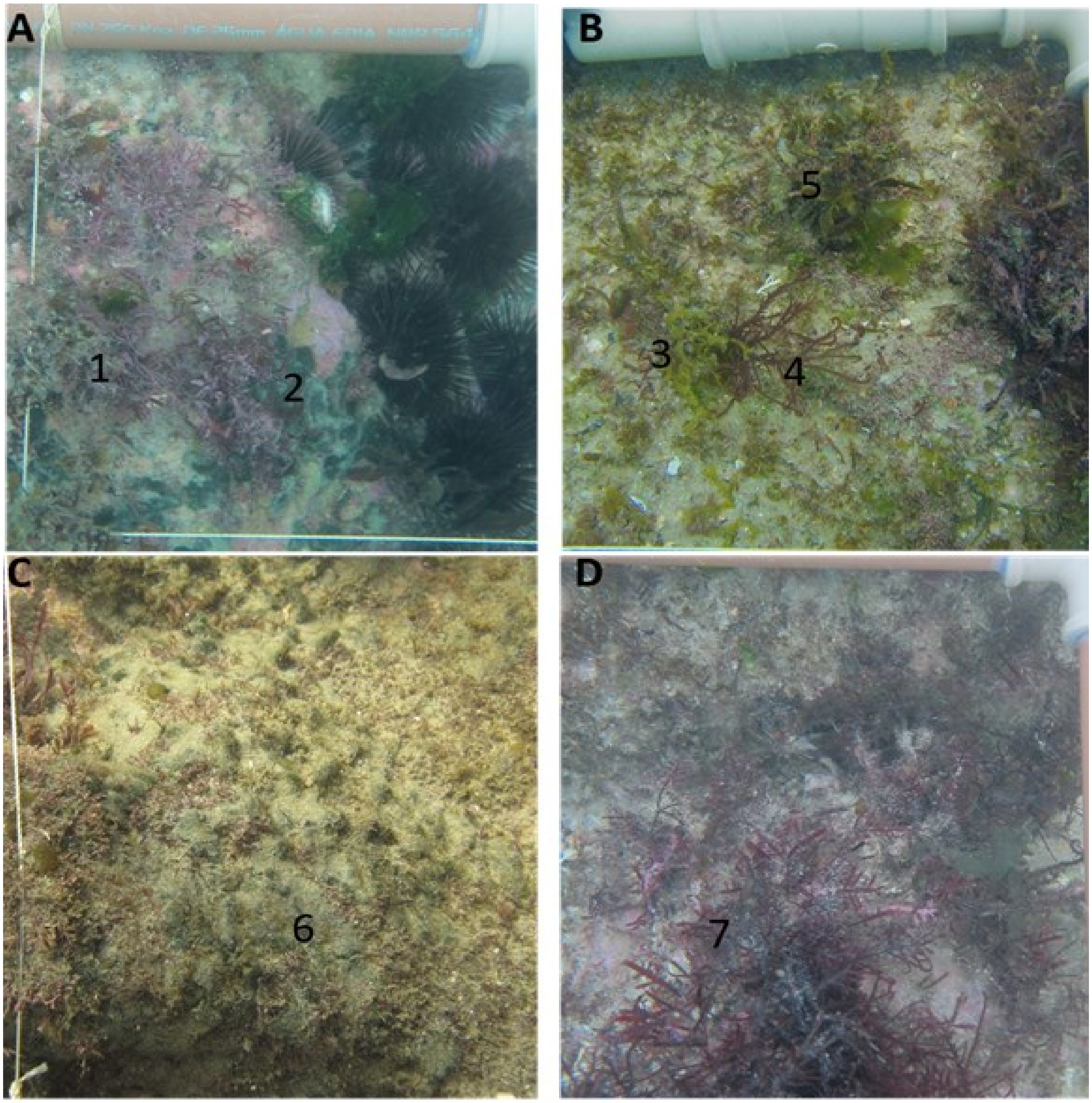
SCHOENER, T. W. Theory of feeding strategies. **Annual Review of Ecology and Systematics**, v. 2, p. 369–404, 1971.

VANDERKLIFT, M.A; KENDRICK, G.A; SMITH, A.J. Differences in trophic position among sympatric sea urchin species. **Estuarine, Coastal and Shelf Science**, v. 66, p.291–297, 2006.

VÁSQUEZ, J CASTILLA, J; SANTELICES, B. Distributional patterns and diets of four species of sea urchins in giant kelp forest (*Macrocystis pyrifera*) of Puerto Toro, Navarino Island, Chile. **Marine Ecology Progress Series**, v. 19, p. 55-63, 1984.

XAVIER, L.A.R. Inventário dos equinodermos do estado de Santa Catarina, Brasil. **Brazilian Journal of Aquatic Science and Technology**. v. 14, p.73-78, 2010.

4.0 APÊNDICES



Apêndice 1: Imagens A e B são referentes ao costão do Gravatá e C e D ao costão do Matadeiro. Números sinalizam a espécie de alga/ grupo identificado no *PhotoQuad*. N°1: *Jania* spp., N°2: *Codium intertextum*, N°3: *Canistrocarpus cervicornis*, N° 4: *Hypnea pseudomusciformis*, N°5: *Sargassum* spp., N°6: Matriz de alga epilítica (*turf*), N°7: *Pterocladiella capillacea*. Câmera: G12

Apêndice 2: Prancha de identificação das algas mais comuns encontradas no ambiente e no conteúdo estomacal dos ouriços-do-mar. A) *Amphiroa* spp. (calcária articulada), B) *Centroceras clavulatum* (filamentosa), C) *Canistrocarpus cervicornis* (folhosa), D) *Hypnea pseudomusciformis* (corticada), E) *Cladophora* spp. (filamentosa), F) *Sargassum* spp. (coriácea), G) *Pterocladiella capillacea* (corticada), H) *Pterosiphonia* spp. (filamentosa), *Ulva* spp. (folhosa). Câmera: Carl Zeiss AxioCam MRc.

TABELAS ESTATÍSTICAS COMPLEMENTARES

Shapiro-Wilk: teste de normalidade para comparar tamanho dos ouriços usando teste-t

Site	*Echinometra lucunter*		*Paracentrotus gaimardi*	
	W	p-value	W	p-value
Gravatá	0.95	0.68	0.94	0.57
Matadeiro	0.91	0.30	0.94	0.61

Shapiro-Wilk: teste de normalidade para índice de repleção (RI)

Site	*Echinometra lucunter*		*Paracentrotus gaimardi*	
	W	p-value	W	p-value
Gravatá	0.93	0.49	0.96	0.81
Matadeiro	0.90	0.25	0.83	0.04

Shapiro-Wilk: teste de normalidade para Índice de Repleção de Matéria orgânica (IRMO)

Site	*Echinometra lucunter*		*Paracentrotus gaimardi*	
	W	p-value	W	p-value
Gravatá	0.93	0.44	0.93	0.55
Matadeiro	0.96	0.83	0.91	0.30

Resultado do teste-t do IRMO do Matadeiro *(*Comparação interespecífica)

T	df	p-value
0.27	17.58	0.78

Resultado do teste-t do IRMO do Gravatá (Comparação interespecífica)

T	df	p-value
1.44	15.34	0.16

Shapiro-Wilk: teste para comparação de diversidade do conteúdo estomacal entre espécies e sites para validar uso da ANOVA

Espécie	Site	p-value
Echinometra	Gravatá	0.44
Paracentrotus	Gravatá	0.43
Echinometra	Matadeiro	0.26
Paracentrotus	Matadeiro	0.12

Resultado do *Bartlett 's test* do conteúdo estomacal para validar a ANOVA

K-squared	df	p-value
4.41	3	0.22

BETADISPER para validar a utilização da PERMANOVA para verificar diferenças na composição bentônica

FN	Perm	Pr(>F)
1.41	999	0.25

SIMPER com dados de cobertura relativa analisados no *PhotoQuad*

	Ava	Avb	Cs	p
Turf	39.48	42.66	0.22	0.31
SED	7.89	28.43	0.42	0.001***
Crustose	18.66	2.45	0.58	0.004**
Sea urchin	13.55	3.77	0.70	0.08
Corticated	10.58	6.99	0.80	0.37
Leathery	0.54	6.69	0.85	0.003**
ACA	0.83	3.94	0.89	0.06

Rock	3.20	0.27	0.92	0.046*
Foliose	0.82	2.88	0.95	0.06
Filamentous	2.61	0.40	0.97	0.12
Cnidarian	1.78	0.81	0.99	0.54
Zoanthids	0.00	0.40	0.99	1.00
Sponge	0.00	0.26	1.00	0.48

SIMPER com dados de grupos funcionais (Gravatá)

	Ava	Avb	Cs	p
Leathery	7.96	23.12	0.19	0.001***
Corticated	34.86	24.05	0.37	0.06
Crustose	13.75	1.12	0.54	0.003**
ACA	19.03	23.34	0.68	0.30
Foliose	13.76	9.00	0.79	0.16
Filamentous	5.43	13.19	0.90	0.001*
Mollusca	0.79	2.05	0.92	0.050*
Crustaceae	0.73	1.95	0.94	0.08
Sponge	1.66	0.55	0.96	0.12
Cnidarian	0.98	1.45	0.98	0.77
Annelida	0.90	0.00	0.99	0.25
Bryozoan	0.00	0.13	0.99	0.47
Seed	0.05	0.00	0.99	0.69
Egg	0.04	0.00	1.00	0.65

SIMPER com dados de grupos funcionais (Matadeiro)

	ava	Avb	Cs	p
Corticated	66.87	57.10	0.24	0.12
Filamentous	2.87	15.14	0.43	0.001***
ACA	9.59	6.44	0.58	0.62
Crustose	9.78	2.67	0.70	0.012*
Foliose	5.74	7.92	0.80	0.72
Cnidarian	0.56	4.13	0.86	0.035*
Crustaceae	0.72	3.25	0.90	0.011*
Sponge	1.01	2.13	0.94	0.40
Leathery	1.77	0.00	0.97	0.20
Mollusca	0.96	0.83	0.99	0.72
Seed	0.11	0.30	0.99	0.49
Egg	0.02	0.05	1.00	1.00