UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO"

INSTITUTO DE BIOCIÊNCIAS – CAMPUS DE BOTUCATU

PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

ÁREA DE CONCENTRAÇÃO – ZOOLOGIA

DISSERTAÇÃO DE MESTRADO

MUDANÇAS NOS PADRÕES DE DIVERSIDADE DE CARANGUEJOS ERMITÕES COSTEIROS: ALTERAÇÕES APÓS 20 ANOS

GABRIEL FELLIPE BARROS RODRIGUES

ORIENTADOR: PROF. DR. ADILSON FRANSOZO

BOTUCATU – SÃO PAULO

2019

MUDANÇAS NOS PADRÕES DE DIVERSIDADE DE CARANGUEJOS ERMITÕES COSTEIROS: ALTERAÇÕES APÓS 20 ANOS

Gabriel Fellipe Barros Rodrigues

Orientador: Prof. Dr. Adilson Fransozo

Dissertação apresentada ao curso de pós-graduação em Ciências Biológicas – Zoologia, do Instituto de Biociências (IBB), Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), *campus* de Botucatu, como parte dos requisitos para obtenção do título de Mestre em Ciências Biológicas – Área de Zoologia

BOTUCATU - SP

2019

FICHA CATALOGRÁFICA ELABORADA PELA SEÇÃO TÉC. AQUIS. TRATAMENTO DA INFORM.
DIVISÃO TÉCNICA DE BIBLIOTECA E DOCUMENTAÇÃO - CÂMPUS DE BOTUCATU - UNESP
BIBLIOTECÁRIA RESPONSÁVEL: LUCIANA PIZZANI-CRB 8/6772

Barros Rodrigues, Gabriel Fellipe.
Mudanças nos padrões de diversidade de caranguejos ermitões costeiros : alterações após 20 anos / Gabriel Fellipe Barros Rodrigues. - Botucatu, 2019

Dissertação (mestrado) - Universidade Estadual Paulista "Júlio de Mesquita Filho", Instituto de Biociências de Botucatu
Orientador: Adilson Fransozo
Capes: 20400004

1. Caranguejo. 2. Biodiversidade marinha. 3. Gastrópodes. 4. Biodiversidade - Conservação.

Palavras-chave: Diversidade beta particionada; Mudanças ambientais ; Padrões de abundância; Paguroidea; Redes de interação.

“O que você faz, faz a diferença, e você tem que decidir que tipo de diferença você quer fazer.”

Dra. Jane Goodall

NEBECC
Núcleo de Estudos em Biologia,
Ecologia e Cultivo de Crustáceos

‘

Agradecimentos

Eu gostaria de começar por reconhecer a riqueza de conselhos, sugestões e principalmente críticas que recebi durante todo o período que envolveu a pós-graduação do **Prof. Dr. Adilson Fransozo**, propiciando todo suporte para realização e financiamento desse projeto. Espero ter atingido meu objetivo inicial de fornecer um trabalho que expanda o conhecimento atual.

Agradeço à **Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES),** pela concessão da bolsa de estudos ao nível de Mestrado Acadêmico, à FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo), pelo financiamento do projeto nos anos de 1995-1996 (proc. 95/2833-0) e referente a obtenção de um veículo para transporte, ao **Núcleo de Estudos de Biologia, Ecologia e Cultivo de Crustáceos (NEBECC),** pela infraestrutura dos laboratórios e materiais disponíveis, ao **IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais)** e à Polícia Federal, por concederem a licença para a coleta do material nas áreas estudadas.

Agradeço também ao **Prof. Dr. Fernando Luis Medina Mantelatto (coordenador do projeto), Prof. Dra. Giovana Bertini Profa.**, **Profa. Dra. Lissandra, Dr. Rogério Caetano da Costa** pelos dados já levantados do projeto pertencente aos anos de 1995 e 1996 na Enseada de Ubatuba-SP.

Agradeço a todos os colegas do **Núcleo de Estudos de Biologia, Ecologia e Cultivo de Crustáceos (NEBECC)**, pelo apoio nas diferentes etapas do projeto.

Agradeço aos pescadores **Luciano** pelas coletas em 1995-1996 e **Djalma Rosa (Passarinho)** comandante da embarcação “Primavera” e seus auxiliares, pela competência e auxílio durante as coletas.

Agradeço à minha família, principalmente a meus pais **Osni Rodrigues** e **Elizabete da Silva Barros Rodrigues**, por todo apoio dado durante os anos da graduação e pós-graduação.

Aos técnicos, funcionários e colegas do departamento que me auxiliaram e me ajudam de diversas formas.

À minha namorada, **Danielle Hamae Yamauchi,** por estar comigo em todos os momentos e me ajudar a passar pelas situações adversas.

‘

Permaneço em débito com os professores: **Dra. Maria Lúcia Negreiros-Fransozo** e **Dr. Fernando Luis Medina Mantelatto** pelos comentários dos capítulos que compõem essa dissertação.

‘

Sumário

‘

Considerações iniciais

O termo "biodiversidade" foi cunhado em 1985, sendo uma contração de "diversidade biológica". Pode-se dizer que biodiversidade é toda a variedade da vida na Terra, em todas suas formas e interações. Toda essa complexidade gerada por milhões de anos de evolução é responsável por tornar o planeta habitável, provendo serviços de extremo valor para a manutenção da vida na Terra. Sabe-se que a diversidade biológica não está distribuída de forma homogênea na superfície da Terra, ou seja, existem áreas que abrigam uma enorme e fantástica riqueza de espécies, muitas das quais nunca foram sequer documentadas (Magurran, 2004). Pesquisadores buscam entender como e por que as espécies estão distribuídas do jeito que estão, para uma melhor compreensão do funcionamento da vida em nosso planeta (Schemske et al., 2009).

Há muito tempo naturalistas buscam entender padrões da distribuição de espécies ao redor do globo. Por exemplo, o gradiente latitudinal de riqueza percebido por Humboldt (1808), que escreveu: *"Quanto mais perto chegamos dos trópicos, maior o aumento na variedade das estruturas, na beleza das formas e na mistura das cores, assim como na juventude perpétua e no vigor da vida orgânica"*, pode ser considerado o mais antigo padrão ecológico (Hawkins, 2001). Dessa forma a região tropical é vista como o coração da biodiversidade na Terra. Embora que muitas teorias elaboradas com intuito de investigar a enorme biodiversidade presente nos trópicos (teoria da heterogeneidade ambiental, teoria

da competição, teoria da estabilidade climática, teoria da competição e predação) (Pianka, 1966; Schemske & Mittelbach, 2017), pouco se sabe sobre a real riqueza de espécies dos trópicos. A complexidade dos ecossistemas tropicais possibilita a coexistência de um enorme número de espécies originando uma miríade de relações entre elas. Um único ecossistema florestal na mata atlântica pode ter uma configuração de vários "andares", desde comunidades biológicas próximas ao solo até aquelas nos dosséis das árvores, cada uma com suas peculiaridades e ao mesmo tempo inter-relacionadas entre si (Yoshimura & Yamashita, 2012). Da mesma forma, recifes de corais das regiões tropicais possuem uma estrutura bastante complexa, servindo como substrato para muitas espécies sésseis e bentônicas e como refúgio para organismos de vida livre, este tipo de ecossistema possibilita nichos novos como os "limpadores", animais que se alimentam de ectoparasitas ou tecidos injuriados da superfície corpórea de outros animais (clientes) (Guimarães et al., 2007b). A dimensão da riqueza de espécies encontradas nos trópicos é completamente diferente das demais regiões (Magurran, 2004).

A ecologia de comunidades é o estudo de organismos de múltiplas espécies que interagem entre si em um determinado lugar e tempo, cujo o foco é os padrões de diversidade, abundância, composição e os processos que estão por trás desses padrões. Existem diversas abordagens para a compreensão da estrutura das comunidades. A abordagem espacial busca entender como as espécies estão distribuídas em uma determinada escala espacial. A escala delimitada para o estudo depende fundamentalmente do organismo a ser estudado, podendo variar de cm^2 para nematódeos presentes no solo, m^2 para invertebrados terrestres, e até

km² para a megafauna (> 40 kg). Outra abordagem é a temporal, também conhecida como "dinâmica das comunidades", cujo o foco são as mudanças da abundância relativa das espécies de uma especificada área, incluindo extinções e adição de espécies, via competição, dispersão ou especiação (Vellend, 2010). Independentemente de quais forem as abordagens utilizadas, os padrões na composição e diversidade de espécies podem ser sumarizados em apenas quatro classes de processos: (1) seleção, (2) deriva, (3) especiação e (4) dispersão (Vellend, 2010). A seleção ocorre quando indivíduos da mesma população variam em alguma característica, e quando essas variantes se reproduzem em taxas diferentes. Assim a seleção pode favorecer a espécie A sobre a espécie B em uma dada comunidade, sendo que a espécie com maior *fitness* (sucesso reprodutivo diferenciado) tende a excluir as outras. O processo de deriva refere-se a mudanças aleatórias na abundância relativa das espécies dentro de uma escala de espaço ou tempo. Assim como a mutação é a principal fonte de variação genética, a especiação pode ser entendida como uma fonte de variação dentro de comunidades ecológicas (Vellend, 2010). Por fim, a dispersão, ou seja, o movimento dos organismos em uma determinada área influencia toda a comunidade biológica, assim como determina a resiliência de uma espécie frente a distúrbios ambientais.

Ameaças à biodiversidade no ambiente marinho

Entender as ameaças que provocam perdas na biodiversidade é o primeiro passo para reverter a situação. As principais ameaças a biodiversidade são a sobre-exploração, espécies invasoras e degradação e perda de habitat (Worm et al., 2006). No entanto, para qualquer caso particular são múltiplos tipos de ameaças

que contribuem para o declínio e extinção de um táxon. Atualmente a taxa de extinção de espécies é cerca de 1,000 vezes maior do que antes da dominação humana do planeta (Aldhous, 2014). A "sexta extinção em massa já começou", e não há dúvidas que nós, seres humanos, somos os grandes responsáveis (Kolbert, 2014). O ambiente marinho cobre 2/3 da superfície terrestre e definitivamente não está isento da massiva perda da biodiversidade. Embora acreditava-se que as espécies marinhas eram mais resistentes a extinção devido à grande capacidade de dispersão, atualmente sabe-se que esses organismos são bastante impactados (Kaiser et al., 2006). Os mares e oceanos provêm uma indispensável fonte de proteínas para mais de 2.5 milhões de pessoas (Carrington, 2016) e atualmente mais da metade da área dos oceanos é pescada industrialmente (Jowit, 2018). A sobrepesca é reconhecida como uma das atividades que mais contribuem para a perda da biodiversidade. Os arrastões comerciais acabam capturando muitas espécies sem interesse econômico (*bycatch*) e muitas vezes de proeminente interesse para a conservação, como mamíferos marinhos, tartarugas e aves marinhas. Além disso, a pesca de arrasto tem afetado espécies bentônicas como corais e esponjas, e assim degradando o habitat de muitas outras espécies marinhas. Outro fato que ameaça a biodiversidade marinha é recorrente homogeneização taxonômica, que embora aconteça em vários habitats, é bastante perceptível nos ambientes costeiros (Thrush et al., 2016), na medida que seleciona grupos específicos capazes de suportar tal regime de distúrbios.

Ao longo do último século a população humana está percorrendo enormes distâncias em um tempo cada vez mais curto, carregando consigo organismos e

aumentando as taxas de introduções de novas espécies em todas as partes do globo (Bax et al., 2003; Stuer-lauridsen et al., 2018). Essas espécies invasoras acabam causando o declínio de espécies nativas (principalmente as especialistas) pela perda de hábitat, competição e predação (Olden et al., 2004). Á agua de lastro presente em grandes embarcações comerciais são muitas vezes responsáveis por trazer espécies invasoras de diversas regiões do planeta (Bax et al., 2003). As biotas das ilhas são particularmente mais vulneráveis à introdução de espécies cosmopolitas, frequentemente levando a extinção de espécies endêmicas. Suspeita-se ainda que essa "homogeneização" possa estar acontecendo no nível de funcionamento do ecossistema, com menor diversidade e maior preponderância de generalistas, diminuindo o número de grupos funcionais em comunidades naturais (Olden et al., 2004; Martello et al., 2018).

Percebemos, cada vez mais, que o estudo da biodiversidade é o primeiro passo para conservação e uso sustentável do meio ambiente em que estamos inseridos. Do mesmo modo, a biodiversidade é uma singular "biblioteca genética" e temos o dever moral de proteger os até então únicos seres viventes com os quais compartilhamos o universo (Ehrlich & Wilson, 1991).

Infra-ordem Anomura MacLeay, 1838

A infraordem Anomura (do grego "cauda irregular") representa um grupo altamente diversificado de crustáceos decápodes sendo representados principalmente pelos caranguejos ermitões (Paguroidea), caranguejo-topeira (Hippoidea), caranguejo-rei (Lithodidae) e porcelanídeos (Galatheoidea) (Mclaughlin et al., 2010). O registro fóssil contém representantes de quase todas

os grupos atuais e datam do Triássico superior (Chablais et al., 2011). Esse grupo tem cativado biólogos evolucionistas devido a impressionante diversidade morfológica e adaptações ecológicas. A diversidade de arranjos corpóreos desse grupo inclui quatro configurações: 1) formas tipo-caranguejo, 2) formas de lagosta com achatamento dorso-ventral, 3) forma de caranguejo ermitão com abdome simétrico (presente em apenas uma família) e 4) formas de caranguejo ermitão com abdome assimétrico (presente em 4 famílias) (Lemaitre & McLaughlin, 2009). Os anomúros são constituídos por 17 famílias, 222 gêneros, e cerca de 2500 espécies, dos quais 54% dos gêneros e 43 % das espécies pertencem a família Paguridae (Mclaughlin et al., 2007). Esse táxon tem como clado irmão os braquiúros (Brachyura Latreille, 1802), que dominam a diversidade de crustáceos decápodes com mais 6500 espécies descritas (De Grave et al., 2009). Devido à grande complexidade morfológica e ecológica do táxon, inúmeros debates acerca da taxonomia e filogenia foram realizados nas últimas décadas. Podemos citar mudanças significativas, como por exemplo a inclusão dos caranguejos-rei (Lithodidae) na superfamília Paguroidea, devido a morfologia assimétrica de seu abdome, sendo um resquício evolutivo presente em animais com simetria bilateral (Cunningham et al., 1992) e mais recentemente foi proposto a inclusão desses organismos na família Paguridae (Tsang et al., 2011). Estudos com base genética indicam que Anomura é um grupo natural (monofilético), no entanto as superfamílias Paguroidea e Galatheoidea são polifiléticas (Tsang et al., 2011). Toda essa diversidade morfológica e debates acerca das relações de parentesco evidenciam o peculiar interesse científico presente nesse grupo.

Superfamília Paguroidea Latreille, 1802

Esse táxon é representado por sete famílias e 122 gêneros (McLaughlin, 2003), composto por caranguejo ermitões e caranguejo rei (Lithodidae). Os caranguejos ermitões, cujo abdome é mole e geralmente torcido, necessita estar protegido por alguma estrutura, sendo na maioria das vezes conchas de moluscos gastrópodes. A íntima relação entre ermitões e conchas de gastrópodes permite com que esses organismos realizem precisas distinções entre a qualidade das conchas encontradas no habitat, até mesmo aquelas ocupadas por outros ermitões, e a sua atual concha (Kellogg, 1976; Hazlett, 1981; Tricarico & Gherardi, 2007), visto que a sobrevivência, reprodução e crescimento dos ermitões dependem estritamente da ocupação de conchas com tamanho e forma apropriada (Hazlett, 1981). A maioria das espécies de ermitão necessitam de conchas adequadas durante toda sua ontogenia, no entanto, a espécie semi-terrestre *Birgus latro* (Linnaeus, 1767) (Anomura: Coenobitidae) ao atingir determinado tamanho abandona a concha, devido a adaptações morfológicas, fisiológicas e comportamentais que permitem esse evento (Greenaway, 2003). Ainda em relação às conchas alguns estudos sugerem que a assimetria do abdome (característica que possibilitou a ocupação de conchas) dos ermitões tem origem parafilética no grupo e evoluiu independentemente possivelmente até três vezes (Ahyong, 2009), no entanto descobertas mais recentes indicam que essa característica evoluiu apenas duas vezes, uma na família Parapaguridae e outra para ancestral comum de todos os outros ermitões assimétricos, indicando que a assimetria do pléon e sua descalcificação evoluiu independentemente em duas linhagens diferentes,

possibilitando a exploração de conchas de moluscos amonites e gastrópodes (Tsang et al., 2011). Os ermitões tornam-se organismos modelos para estudos ecológicos sobre partição de nicho, compartilhamento e avaliação do recurso (Kellogg, 1977; Laidre, 2012; Tran, 2014) devido a intrínseca relação com seu principal recurso para a sobrevivência.

Em relação a importância ecológica desse grupo, embora que a maioria das espécies possuam habito detritívoro, contribuindo para a ciclagem de nutrientes nos ciclos biogeoquímicos (Duineveld et al., 1997), os ermitões podem ocupar diversas posições numa teia trófica. Desde espécies com adaptações para o habito filtrador, como o ermitão *Loxopagurus loxochelis* (Moreira, 1901) (Mantelatto et al., 2004; Ayres-Peres & Mantelatto, 2008), até espécie carnívoras como *Petrochirus diogenes* (Linnaeus, 1758) (Caine, 1975). Essas espécies compõem a fauna bentônica de ecossistemas marinhos, responsáveis por serviços ecossistêmicos indispensáveis como: estabilidade do sedimento, redução da turbidez da coluna d'água, processamento de nutrientes e carbono, e sequestro de contaminantes (Thrush & Dayton, 2002).

Os ermitões estão agrupados em seis famílias: Coenobitidae Dana, 1851; Parapaguridae Smith, 1882; Pylochelidae Spence Bate, 1888; Pylojacquesidae McLaughlin e Lemaitre, 2001; Paguridae Latreille, 1802; e Diogenidae Ortmann, 1892 (Mclaughlin et al., 2007, 2010). No litoral brasileiro há registro de aproximadamente 62 espécies descritas de ermitões, pertencendo às famílias Pylochelidae (1), Diogenidae (27), Paguridae (28), e Parapaguridae (6) (Lemaitre & Tavares, 2015).

Considerando a crescente necessidade da preservação da fauna local de ambientes impactados pela ação antrópica e de estudos ecológicos com o foco na comunidade, o presente estudo busca uma melhor compreensão da estrutura da comunidade de ermitões na Enseada de Ubatuba, litoral norte do Estado de São Paulo. Para tanto, foi abordado no primeiro capítulo padrões de abundância, riqueza e composição de espécies capturadas na região com intervalo de 20 anos. No segundo capítulo foi investigada a variação da diversidade espacial de ermitões em uma escala temporal, buscando entender como a assembleia de ermitões se modificou após 20 anos. No terceiro capítulo as interações entre ermitões e seus indispensáveis recursos (conchas) foram analisadas a nível de comunidade.

Referências

Ahyong, S., 2009. Anomuran Phylogeny: New Insights from Molecular Data Decapod crustacean phylogenetics. CRC Press, Boca Raton, FL: 399–414.

Aldhous, P., 2014. We are killing species at 1000 times the natural rate. NewScientist. https://www.newscientist.com/article/dn25645-we-are-killing-species-at-1000-times-the-natural-rate/.

Ayres-Peres, L., & F. L. Mantelatto, 2008. Patterns of distribution of the hermit crab *Loxopagurus loxochelis* (Moreira, 1901) (Decapoda, Diogenidae) in two coastal areas of southern Brazil. Revista De Biologia Marina Y Oceanografia 43: 399–411.

Bax, N., A. Williamson, M. Aguero, E. Gonzalez, & W. Geeves, 2003. Marine invasive alien species: A threat to global biodiversity. Marine Policy 27: 313–323.

Caine, E. A., 1975. Feeding and masticatory structures of selected Anomura (Crustacea). Journal experimental marine biology and ecology 18: 277–301.

Carrington, D., 2016. Overfishing causing global catches to fall three times faster than estimated. The Guardian. https://www.theguardian.com/environment/2016/jan/19/overfishing-causing-global-catches-to-fall-three-times-faster-than-estimated.

Chablais, J., R. M. Feldmann, & C. E. Schweitzer, 2011. A new Triassic decapod, *Platykotta akaina*, from the Arabian shelf of the northern United Arab Emirates: earliest occurrence of the Anomura. Paläontologische Zeitschrift Springer 85: 93–102.

Cunningham, C., N. W. Blackstone, & L. W. Buss, 1992. Evolution of kings crabs from hermit crab ancestors. Nature 355: 539–542.

Ehrlich, P. R., & E. 0. Wilson, 1991. Biodiversity Studies: Science and Policy. Science.

Greenaway, P., 2003. Terrestrial adaptations in the Anomura (Crustacea : Decapoda). Memoirs of Museum Victoria 60: 13–26.

Hawkins, B. A., 2001. Ecology's oldest pattern? Trends in Ecology & Evolution 16: 470.

Hazlett, B., 1981. The behavioral ecology of hermit crabs. Annual Review of Ecology and Systematics 12: 1–22.

Humboldt, A. Von, 1808. Ansichten der natur. JG Cotta.

Jowit, J., 2018. Half of world's oceans now fished industrially, maps reveal. The Guardian. https://www.theguardian.com/environment/2018/feb/22/half-of-worlds-oceans-now-fished-industrially-maps-reveal.

Kaiser, M. J., K. R. Clarke, H. Hinz, M. C. V. Austen, P. J. Somerfield, & I. Karakassis, 2006. Global analysis of response and recovery of benthic biota to fishing. Marine Ecology Progress Series 311: 1–14.

Kolbert, E., 2014. The sixth extinction: An unnatural history. A&C Black.

Laidre, M. E., 2012. Niche construction drives social dependence in hermit crabs. Current Biology Elsevier 22: R861–R863, http://dx.doi.org/10.1016/j.cub.2012.08.056.

Mantelatto, F. L. M., J. M. Martinelli, & A. Fransozo, 2004. Temporal-spatial distribution of the hermit crab Loxopagurus loxochelis (Decapoda : Diogenidae) from Ubatuba Bay, São Paulo State, Brazil. Revista De Biologia Tropical 52: 47–55.

McLaughlin, P. A., 2003. Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. Memoirs of Museum Victoria 60: 111–144.

Mclaughlin, P. a., T. Komai, R. Lemaitre, & D. L. Rahayu, 2010. Annotated checklist of anomuran decapod crustaceans of the world. PART I: Lithodoidea, Lomisoidea and Paguroidea. The raffles bulletin of zoology 5–107.

Mclaughlin, P. A., R. Lemaitre, & U. Sorhannus, 2007. Hermit crab phylogeny: a reappraisal and its "fall-out". 27: 97–115.

Melo, G. A. S., 1999. Manual de identificação dos Crustacea Decapoda do litoral Brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea. Editora Plêiade. São Paulo. 551pp

Olden, J. D., N. L. R. Poff, M. R. Douglas, M. E. Douglas, & K. D. Fausch, 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19: 18–24.

Pianka, E. R., 1966. Latitudinal Gradients in Species Diversity: A Review of Concepts. The American Naturalist 100: 33–46, http://www.journals.uchicago.edu/doi/10.1086/282398.

Schemske, D. W., & G. G. Mittelbach, 2017. "Latitudinal Gradients in Species Diversity": Reflections on Pianka's 1966 Article and a Look Forward. The American Naturalist 000–000, http://www.journals.uchicago.edu/doi/10.1086/691719.

Thrush, S. F., & P. K. Dayton, 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annual Review of Ecology and Systematics 33: 449–473.

Thrush, S. F., K. E. Ellingsen, & K. Davis, 2016. Implications of fisheries impacts to seabed biodiversity and ecosystem-based management. Ices Journal of Marine Science 73: 144–150.

Tricarico, E., & F. Gherardi, 2007. Resource assessment in hermit crabs: The worth of their own shell. Behavioral Ecology 18: 615–620.

Tsang, L. M., T. Y. Chan, S. T. Ahyong, & K. H. Chu, 2011. Hermit to king, or hermit to all: Multiple transitions to crab-like forms from hermit crab ancestors. Systematic Biology 60: 616–629.

Vellend, M., 2010. Conceptual Synthesis in Community Ecology. The Quarterly Review of Biology 85: 183–206, http://www.journals.uchicago.edu/doi/10.1086/652373.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, & K. A. Selkoe, 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science 314: 787–791.

How hermit crab assemblages structure changed after 20 years in the northern coast of São Paulo state, Brazil

ABSTRACT

Examination of spatial patterns of organisms in coastal regions is critical and necessary to understand which factors control and maintain the diversity of species. Patterns of abundance and richness of hermit crabs inhabiting Ubatuba bay were investigated in two periods separated by 20 years: 1995-1996 (P1) and 2016-2017 (P2), and the influence of environmental factors on the assemblages. We hypothesized that sites with a high degree of heterogeneity will have a higher richness when compared to homogeneous sites. In a complete randomized block design (CRBD), samples were taken monthly in five sites with trawl nets. Additionally, we collected data from environmental variables: bottom water temperature and salinity, organic matter and sediment texture. Overall, 2,165 hermit crabs were over 24 months of study (12 months for both periods), representing a total of 11 species. We obtained 419 (10 species) and 1,746 hermit crabs (7 species) in P1 and P2, respectively. We found differences among the hermit crab assemblages on sites in both periods, and also differences between the P1 and P2. The abundance and richness were inversely correlated with bottom water temperature and sediment texture. Our results show that hermit crab fauna can change considerably in a small-scale landscape. Homogenization of the substratum may have increased hermit crab abundance and reduced species

richness. In short, the hermit crab assemblage changed in 20 years, that could be caused by some environmental features and/or anthropic pressure.

Keywords: Richness patterns; spatial patterns; environmental change; Paguroidea; Coastal hermit crabs

1. Introduction

The knowledge of biodiversity in coastal regions is of peculiar importance considering that nowadays is where the majority of the human population lives (Small & Nicholas, 2003). Evaluating patterns of diversity over space and time, and the factors and dynamics creating and maintaining those patterns are critical for understanding the ecology of biodiversity, guiding management and conservation efforts (Zajac et al., 2013). There still many gaps in our knowledge of spatial and temporal patterns of diversity and abundance of many marine organisms, which hinder out our ability to understand ocean systems and to detect human impacts on them (Hunt et al., 2017).

Seabed fauna is essential for the functioning of marine ecosystems. Bottom invertebrates (benthos) help oxygenation of the sea floor, breaking down organic material, providing habitat structure and food sources for other organisms (Tagliapietra & Sigovini, 2010). Many benthic species are sensitive to disturbance; thus, the extent and intensity of human activity in marine ecosystems can ultimately disrupt the services that benthos provide (Thrush & Dayton, 2002). Environmental drivers may act like filters that select benthic species due their

capability to tolerate the abiotic stress, some characteristics can modulate the whole benthic community and their interactions (Alsaffar et al., 2017). A clear understanding on how the composition of species and their abundance change along spatial and across environmental gradients will provide data necessary to comprehend how communities will respond to environmental change, fundamental for conservation efforts (Sommer et al., 2014).

Hermit crabs are decapod crustaceans which constitute an important parcel of macrobenthic fauna. Most of the hermit crabs are omnivorous and detritivorous which contribute to biogeochemical processes in ecosystems, recycling nutrients due to its ability to obtain food from several trophic levels (Nagabhushanam & Sarojini, 1968; McNatty et al., 2009; Selin et al., 2016). Some studies found that environmental variables like water temperature (Fransozo et al., 2008; Frameschi et al., 2013; Stanski et al., 2016), organic matter and sediment (Negreiros-Fransozo et al., 1997; Frameschi et al., 2013) influence the abundance of hermit crabs. Another particular feature modulates the hermit crab diversity, gastropod shells are an important and limiting factor that plays a crucial role in the interaction with the environment (Hazlett, 1981). Due their naked and no calcified abdomens, hermit crabs must find and occupy empties gastropod shells or other materials such as bivalve and scaphopod shells, polychaete tubes, sponge, corals, wood or even hollowed-out fragments of stones to protect themselves (Lancaster, 1986; Williams & McDermott, 2004). Such use makes them a hard mobile substrate provider, several animals inhabit the surface and interior of those shells, contributing to the diversity of many others invertebrate taxon. There are almost

550 invertebrate species associated with over 180 species of hermit crab species worldwide (McDermott et al., 2010). However, patterns and processes that control the richness and abundance of hermit crabs within coastal areas still are not clear.

The niche diversification hypotheses proposed by Connell (1978), pointed that niche sub-divisions are a consequence of some degree of habitat heterogeneity. Different species need different aspects of habitat like food, space habitat and time of activity (called "niche space"). High biotic diversities occur in sites with a broad range of biotic and abiotic characteristics, maintaining specialist species and preventing generalist species dominance (Miserendino et al., 2018). Heterogenic substrates could permit that species occupy narrower niches, because of the effective partitioning of resources allowing the coexistence of several species.

Long-term studies would significantly increase our understanding of the relative importance of abundance and richness spatial patterns, since different processes may be acting in particular sites, altering local assemblages (Vellend, 2010; Anderson et al., 2011). These singularities point towards different management and conservation options, especially if these changes are studied in relation to environmental change in coastal ecosystems (Gray, 2001).

This study focuses on how hermit crab abundance and richness change over [1] a 20 years' time-break and [2] across distinct environmental sites in a bay system, understanding the effects of environmental variables in the assemblage structure. Our hypothesis is that sites with a high degree of heterogeneity will have a higher richness when compared to homogeneous sites, according to "niche

diversification hypothesis", which explains diversity in terms of specialization to sub-division of a habitat.

2. Material and methods

2.1 Study Area

Ubatuba Bay (23°26' S and 45°02' W) is located along the northern coast of São Paulo State, Brazil, facing to the east and presents a constriction in its coastline, which induces wave diffraction (Mahiques et al., 1998). The proximity of the coastal range (Serra do Mar) results in small bays and headland-embayed beaches with variable orientation. This causes incident waves to approach the coastline at different angles, resulting in locally specific sediment transport patterns (Mahiques et al., 2016). In most of the area, the sediments contain mainly silt and very fine sand and few samples show coarse sand or clay modal distribution. This region presents a mixed fauna, that includes tropical, temperate and sub-Antarctic species, which are explained by the thermal regime of the coastal water (Coelho & Ramos, 1972). In 2008, a Marine Protection Area (Cunhambebe sector) was created with the intent to protect biodiversity in the north coast of São Paulo State (Proclamation No. 53525, October 8, 2008) forbidding pair trawl (a technique in which a bottom trawl is towed simultaneously by two boats). However, local fisheries are permitted and well-established, generating damages on soft-bottom communities. Also, in 2008, a closed season shrimp-fishing (IBAMA, 2008) was established, comprehending the period from march 1st to may 31th, forbidden any type of trawl fishing procedures.

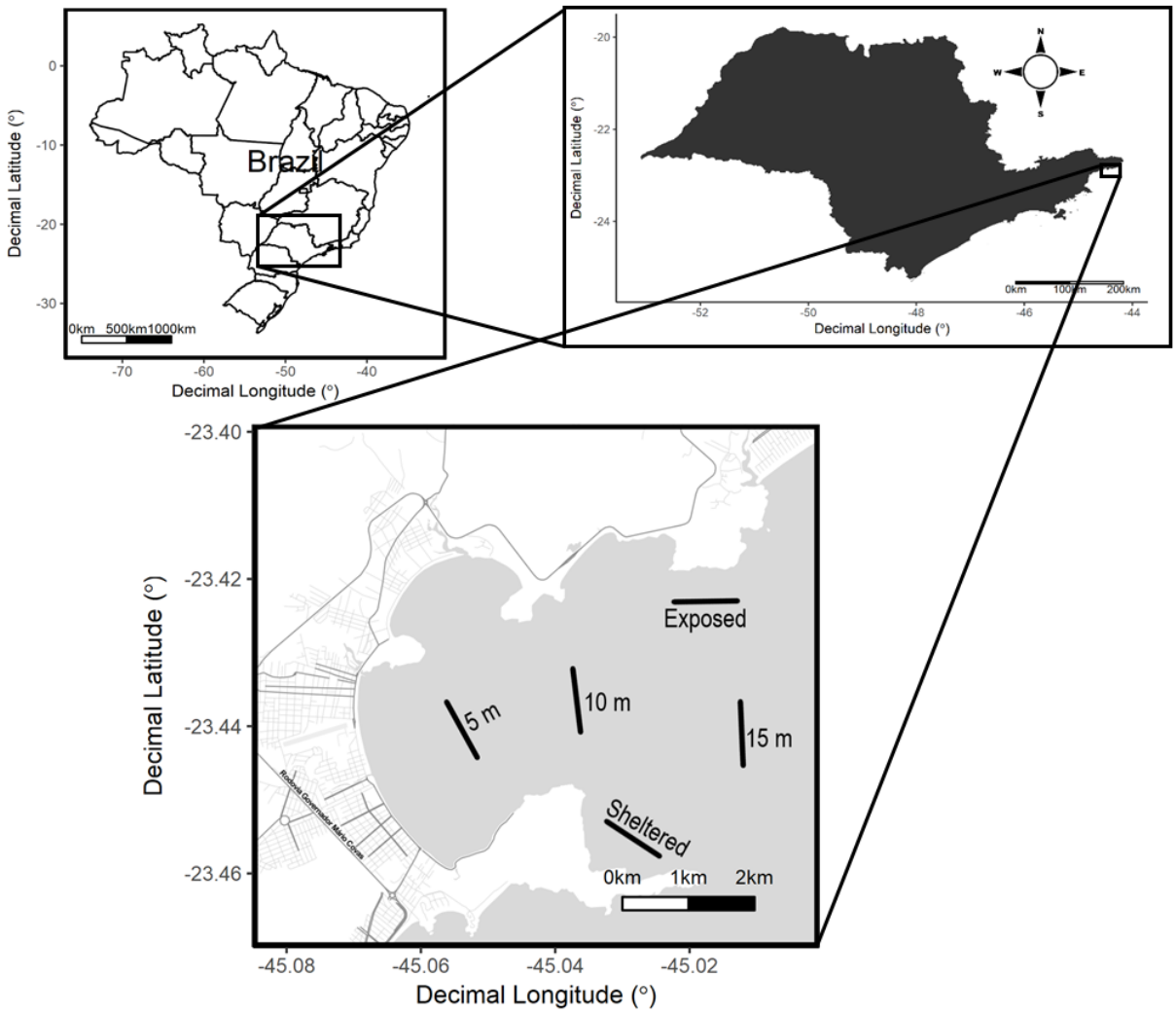


Fig. 1 Location of sampling sites on Ubatuba bay. Ubatuba, São Paulo, Brazil. Black lines indicate the area surveyed.

2.2 Biotic and environmental data collection

The hermit crabs were collected (trawled) utilizing a fishing boat equipped with double-rig nets (4.5 m wide at the mouth, 25 mm of body mesh size, and 15 mm of cod end mesh size). Each trawl lasted 30 minutes, covering an estimated swept area of 18.000 m². The samples were performed in same locations for both periods (1995-1996 and 2016-2017). Samples were taken, monthly, in three consecutive days, during both periods. The Ubatuba Bay was classified into five

sampling sites differing in terms of their location in relation to the bay mouth, the presence of a rock wall or a beach along the boundaries, the inflow of fresh water, the proximity of an offshore area, depth and sediment composition (Fransozo et al., 1998). A global positioning system (GPS) was used to record the location at the sampling sites, ensuring the sampling in the same sites for all months surveyed. Thus, we selected five available sites to this sampling period as follows: three sites plotted at depths of 5, 10, and 15 meters; and two sites defined perpendicular to the beach line - one localized in a sheltered area, and other, in an exposed area to wave action (Mahiques et al., 1998) (Figure. 1). The individuals were kept in plastic bags, properly marked, in thermal boxes containing crushed ice. In the lab, the hermit crabs (Paguroidea) were removed from their shells, and identified, according to Melo (1999).

Additionally, and based on previous evidences (Mantelatto & Franzoso, 1999; Fransozo et al., 2011) we selected four environmental variables to evaluate their probable action on the hermit crab fauna as follows: water temperature, water salinity, organic matter and sediment texture (phi). Details on methodology are available at Mantelatto & Fransozo (1999). Water samples were obtained with a Nansen bottle, from which we measured temperature (ºC) and salinity. Sediment samples were collected with a 0.06 m² van Veen grab to measure the organic matter content and sediment texture. All environmental data were collected simultaneously with biotic data in central point of each site sampled (Mantelatto and Franzoso 1999).

For sediment analysis procedures, two 50 g subsamples were taken, to which we added 250 ml of a NaOH (0.2 N) solution, aiming to lift up the silt + clay (Tucker, 1988). Afterward, we washed the subsamples using a sieve (mesh= 0.063 mm), washing away the silt + clay. The remaining sediment was dried and then submitted to a differential sieving, classifying the sediment grains according to the Wentworth (1922) scale.

Phi values were calculated based on the equation $phi = -log_2 d$, where d= grain diameter (mm). Based on the obtained values, we calculated the central trend measurements, determining the most frequent grain fractions in the sediment. We calculated these values based on data graphically taken from cumulative sediment samples frequency distribution curves. We used values corresponding to the 16^{th}, 50^{th} and 84^{th} percentages to determine the mean diameter (*MD*), using the equation $MD= (\varphi_{16} + \varphi_{50} + \varphi_{84}/3)$ (Suguio, 1973).

Organic matter content was determined by loss on ignition (LOI). We put the subsamples (10g each) in porcelain containers, previously labelled and weighed. After that, we put them into an oven (500ºC for 3 hours) and weighed them again. The LOI is then calculated using the following equation: LOI = (Wi –Wf)/Wi * 100, where: LOI = organic matter content (%), Wi = initial weight of the sediment subsample; Wf = final weight after ignition (Hieri et al., 2001).

2.3 Statistical analysis

We utilized a randomized complete block design (RCBD) to reduce temporal sources of variation (Halpern and McKenzie 2001), with ten sites (five for each period) randomly assigned to 12 months (blocks) at each studied period.

Species richness and abundance of all hermit crabs were compared among each site using a repeated measures nonparametric Friedman ANOVA by ranks, where the abundance and richness of each site were a repeated measure. Post hoc pairwise comparisons were then made with Conover matched-pairs tests. These procedures were adequate because no temporal autocorrelation, assessed through the Durbin–Watson statistic (p-value < 0.05), was detected. Exploratory multivariate analyses were applied to abundance data transformed and using Bray-Curtis dissimilarity coefficient to construct resemblance matrices to compare sites. These dissimilarities were represented in two dimensions using non-metric multidimensional scaling (nMDS) representing the samples as points in a two-dimensional space. A cluster analysis was utilized to describe sites based on the mean value of the abundance of each taxon per sampling site. A Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was used to compare the hermit crab assemblages between years and sites. To verify the species-environment relationship in the separation of sample sites, we performed a Redundancy Analysis (RDA) (Gotelli & Ellison, 2016). Collinearity among environmental variables were assessed through variance inflation factors (VIF), since no collinearity was detected, all variable remains in the RDA. The statistical significance of eigenvalues of the RDA axis was evaluated by randomization (Monte Carlo) tests, using 9,999 randomized runs for each analysis. All analyses were carried out in R statistical program (R Core Team, 2019), using package "stats" for Friedman ANOVA test (R Core Team, 2019), "PMCMR" for Post hoc comparisons (Pohlert, 2014), "lmtest" to detect temporal autocorrelation (Zeileis

& Hothorn, 2002), "vegan" for multivariate analysis (Oksanen et al., 2015) and "PerformanceAnalytics" to detect collinearity (Peterson & Carl, 2018).

3. Results

Across all sites, 2,165 hermit crabs were collected from 360 samples over 24 months of study (12 months in first period and 12 months in second period), representing a total of 11 species. During the first period (P1) 419 organisms were captured (Table 2) while in the second period (P2) we captured 1.746 paguroideans (Table 3). In general, hermit crab richness was 2.2 species per site, ranging from zero to five species. The hermit crab *Dardanus insignis* (de Saussure, 1858) (To pictures see supplementary material) was the most widely distributed, being found in almost all sites sampled.

Table 2. Abundance of hermit crab species (family) sampled in Ubatuba Bay, from September 1995 to August 1996.

Species/site	5 m	10 m	15 m	Exposed	Sheltered	Total
Family Diogenidae Ortmann, 1892						
Dardanus insignis (de Saussure, 1858)	11	0	22	5	83	121
Isocheles sawayai Forest & de Saint Laurent, 1968	2	0	1	0	1	4
Loxopagurus loxochelis (Moreira, 1901)	4	5	158	5	0	172
Pseudopaguristes calliopsis (Forest and Saint Laurent,1968)	1	0	0	0	1	2
Petrochirus diogenes (Linnaeus, 1798)	35	1	4	0	57	97
Paguristes erythrops Holthuis, 1959	2	0	0	0	1	3
Paguristes tortugae Schmitt, 1933	1	0	0	0	3	4
Family Paguridae Latreille 1802						
Pagurus criniticornis (Dana, 1852)	0	0	0	0	3	3

Pagurus exilis (Benedict, 1892)	0	0	4	0	3	7
Pagurus leptonyx Forest and Saint Laurent, 1967	2	2	1	0	1	6
Total	58	8	190	10	153	419

Table 3. Abundance of hermit crab species (family) sampled in Ubatuba Bay, from September 2016 to August 2017.

Species/Sites	5 m	10 m	15 m	Exposed	Sheltered	Total
Family Diogenidae Ortmann 1892						
Dardanus insignis (de Saussure, 1858)	140	38	38	2	746	964
Isocheles sawayai Forest & de Saint Laurent 1968	0	2	0	0	8	10
Loxopagurus loxochelis (Moreira, 1901)	136	20	162	28	70	416
Petrochirus diogenes (Linnaeus, 1798)	12	4	2	0	26	44
Paguristes sp.	0	0	0	2	0	2
Family Paguridae Latreille 1802						
Pagurus exilis (Benedict, 1892)	52	12	26	2	208	300
Pagurus criniticornis (Dana, 1852)	10	0	0	0	0	10
Total	350	76	228	34	1058	1746

3.1 Spatio-temporal trends

When the same sites sampled in both P1 and P2 were compared (Pairwise comparisons), sites “5m”, “10m” and “Sheltered” had differences in total abundance of hermit crabs (Friedman chi-squared $_{(9, 120)} = 60.34$, $p < 0.001$), having the second period greater abundance of these organisms (Figure 2). The same

procedure was applied to richness (Figure 3), and only site "10m" had difference when comparing the richness of same sites sampled in both P1 and P2 (Friedman chi-squared $_{(9, 120)} = 49.43$, $p < 0.001$).

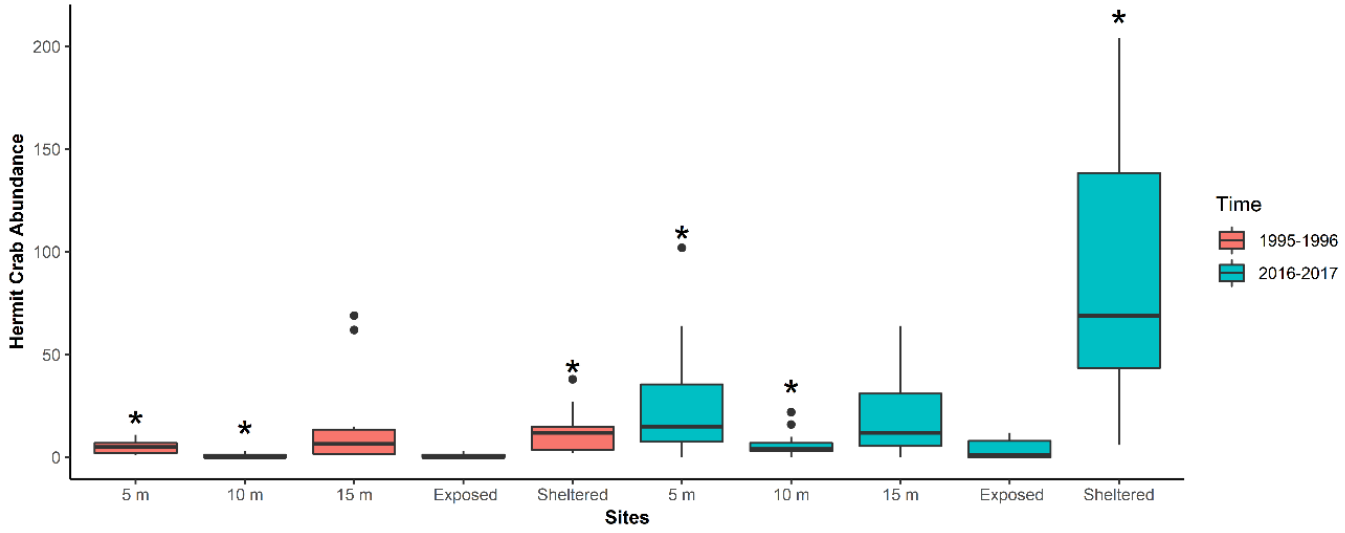


Fig. 2 Boxplots summarizing abundance of hermit crabs in all sites selected, comprehending both periods. Asterisks (*) indicate difference between same sites through periods, assessed by Conover's Post-hoc analysis. Black dots indicate outliers.

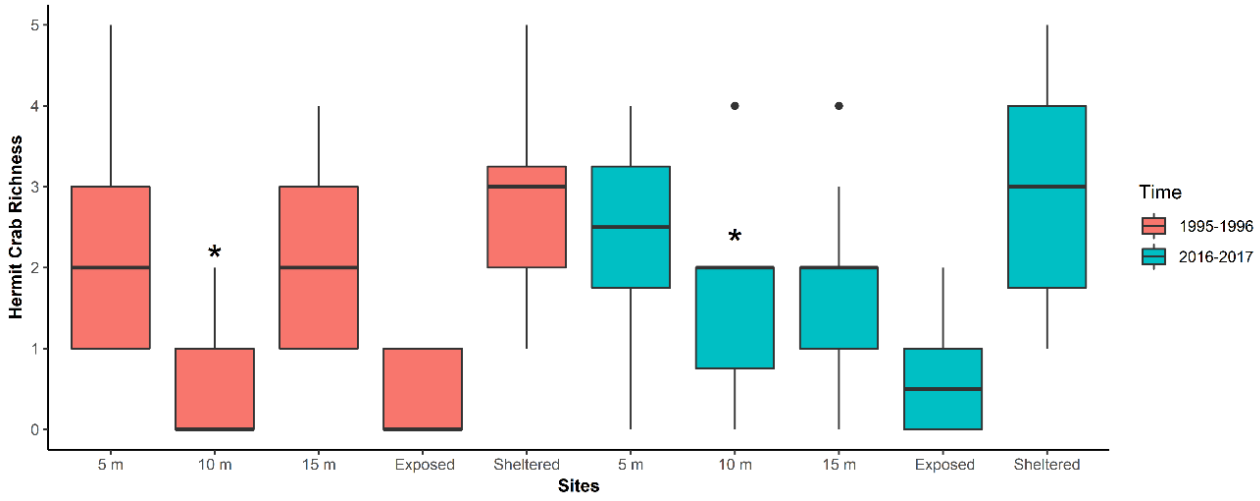


Fig. 3 Boxplots summarizing richness of hermit crabs in all sites selected, comprehending both periods. Asterisks (*) indicate difference between same sites through periods, assessed by Conover's Post-hoc analysis. Black dots indicate outliers

None single species was found in all sites, the most abundant species found in the first period was *Loxopagurus loxochelis* (41%) (To pictures see supplementary material), while in the second period was *D. insignis* (55%), also being the most abundant species overall.

Multivariate analysis (PERMANOVA) revealed significant differences among the hermit crab assemblages on sites in P1 (PERMANOVA, Pseudo-$F_{(4,120)}$ = 6.631, p < 0.005) and P2 (PERMANOVA, Pseudo-$F_{(4,120)}$ = 7.961, p < 0.005). These differences are shown graphically in a nMDS plot (Figure 4). Also, PERMANOVA analysis revealed significant differences between P1 and P2 (PERMANOVA, Pseudo-$F_{(1,120)}$ = 8.297, p < 0.005) (Figure 5).

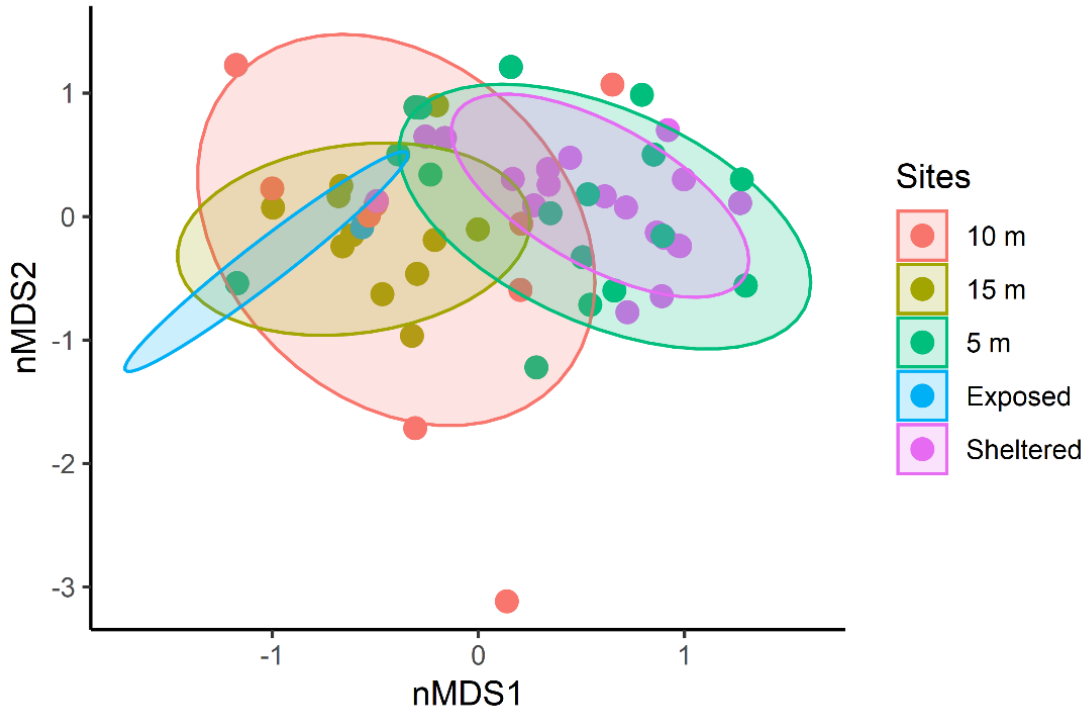


Fig. 4 Multivariate analysis nMDS plot of hermit crab assemblage structure from Ubatuba bay. Based on species abundance data and Bray-Curtis similarity measure; individual sites are displayed, ellipses = 0.75% of similarity.

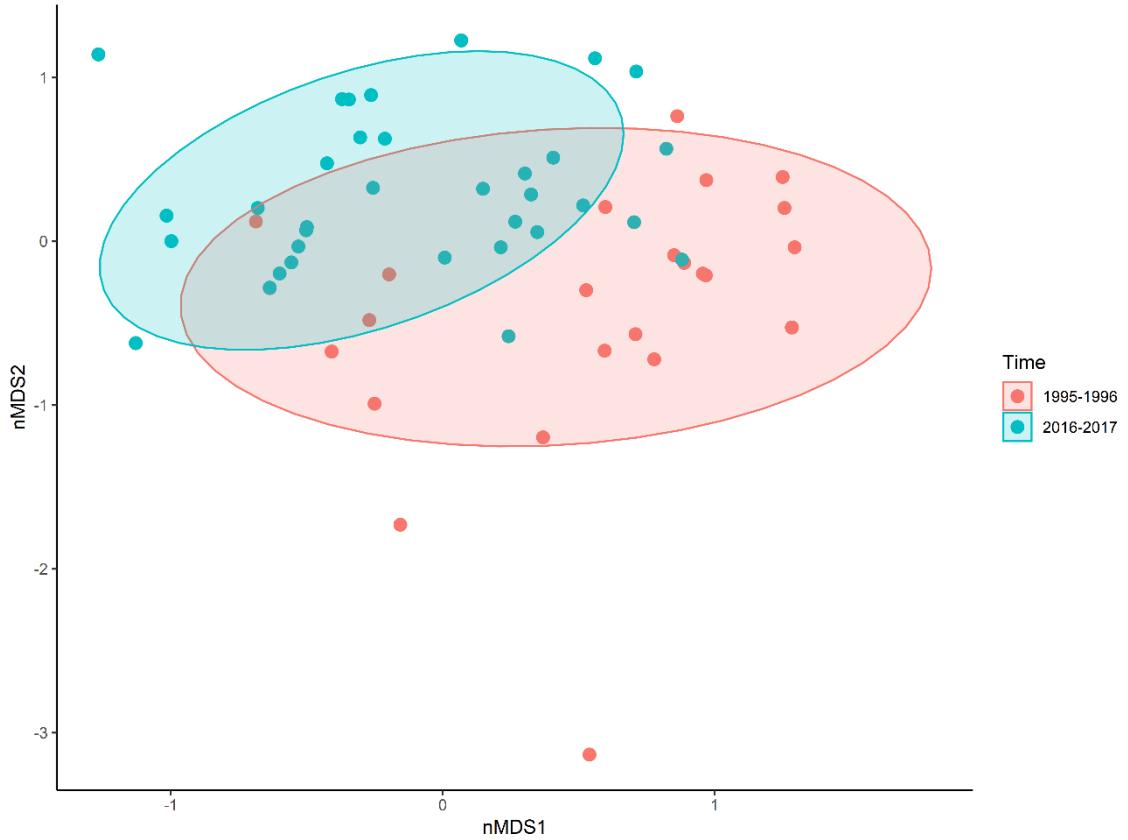


Fig. 5 Multivariate analysis nMDS plot of hermit crab assemblage structure from Ubatuba bay**.** Based on species abundance data and Bray-Curtis similarity measure; comparison of individual sites from both periods, ellipses = 0.75% of similarity.

We used the clusters analysis to compare the abundance of all sites; the Exposed and Sheltered sites showed lower similarity in both periods. In first period, sites 15 m, Exposed and Sheltered showed higher similarity while in the second period 5m and 10 m showed presented greater similarity (Figure 6).

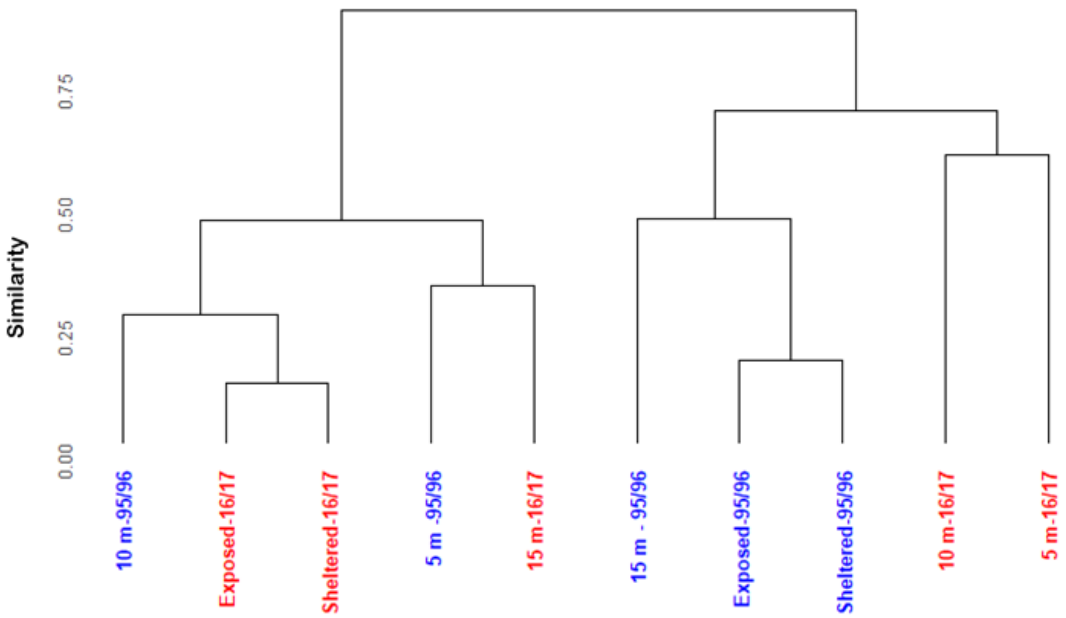


Fig. 6 Results of hierarchical clusters analysis applied to the abundance of hermit crabs in 10 sites of Ubatuba bay, representing both periods (1995-1996 & 2016-2017).

3.2 Correlation with environmental variables

The relationship between hermit crab (abundance and richness) and environmental variables shown by RDA is represented by two axes (Figure 7). The first axis explained 96.38 % of the variance. The Monte Carlo test indicated that only first axis ($p < 0.05$) was significant. This test also indicated that bottom temperature and phi were significantly correlated. Based on this analysis, we may attest that the bottom water temperature and sediment grain size (phi) is inversely proportional to the hermit crab abundance and richness. It characterizes a preference for low water temperature and for heterogeneous sediment, mainly

composed by granulometric classes such as gravel, very coarse sand, coarse sand and medium sand (Table 4).

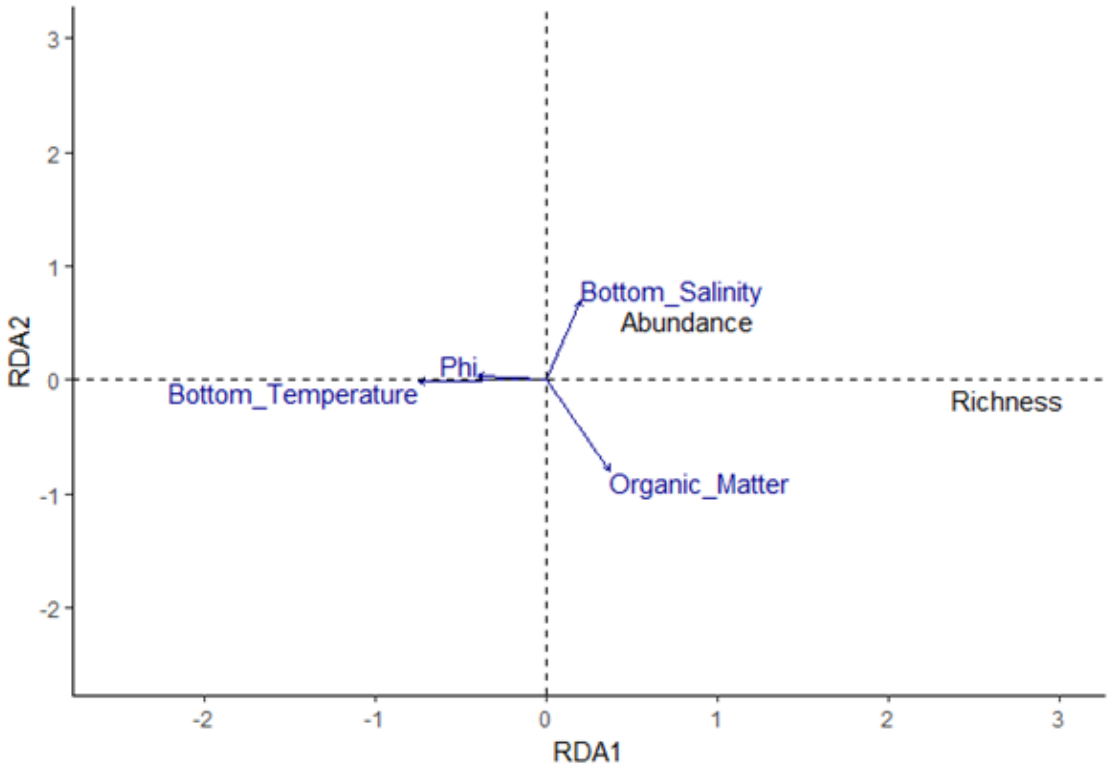


Fig. 7 RDA plot. Visualizes the position of the biotic variables (Abundance and Richness) fitted to the environmental variables (bottom water temperature, bottom water salinity, organic matter and phi) affecting the entire hermit crab community (see Table 4 for statistical results).

Table 4. Redundancy Analysis (RDA). Summary results of hermit crabs and environmental variables. Asterisks (*) indicate statistical significance. Significance was inferred using α ($p < 0.05$): *p*-value based on 9,999 permutations.

	Axis		Monte Carlo test	
	RDA1	RDA2	F	*p*
Proportion Explained	0.963	0.036	3.598	0.011
Bottom Temperature	-0.747	-0.008	7.746	0.007*
Bottom Salinity	0.201	0.693	0.942	0.350
Organic Matter	0.368	-0.796	2.428	0.109
Phi	-0.398	0.040	3.275	0.05*

4. Discussion

Patterns of abundance and richness

Several studies achieved in São Paulo State focusing on hermit crab fauna registered a richness, that ranged from six to eleven species, and evidenced *Dardanus insignis* as the species most found in almost all studies (Hebling et al., 1994; Fransozo et al., 1998, 2011; Mantelatto & Garcia, 2002). Other studies also investigated hermit crab communities near islands in Ubatuba region (Frameschi et al., 2013) and in south Brazilian Coast (Stanski et al., 2016) found eight and six species, respectively. The hermit crabs *D. insignis* and *Isocheles sawayai* Forest & de Saint Laurent, 1968 were the most abundant species in each area, respectively.

The results presented here pointed that hermit crab fauna can change considerably in a small-scale landscape and that these changes could be caused by some specific environmental features. The abundance of hermit crabs in the sampled sites showed a clear spatial configuration, with greater abundance in the Sheltered one (P2), probably because environmental characteristics – like soft substrate grain composition – in this site were more heterogenic (Mantelatto & Franzoso, 1999). Different habitats allow the establishment of various species, allowing an increase in local abundance. The complexity of benthic landscapes displays spatial heterogeneity with potential implications related to trophic interactions and larval recruitment (Johnson, 2015), complexes benthic structure provides a greater diversity of food resources (preys, decomposing matter, suspensive particles) and several refuges and settlement sites for multiple species (Thrush et al., 2016). Also, small environmental differences, both temporal and spatial, that would be insignificant at high population densities, may provide sufficient complexity to avoid competition at low densities (Huston, 1979).

One of the main questions to be answered is "why the abundance of hermit crabs was higher in the second period of time?". Several studies show that trawling disturbance caused by fishery activities could change the community structures of marine organisms (Mazor et al., 2017; Ramalho et al., 2017). Since 1970, the fisheries industries established in Ubatuba city, boosted by tax breaks policies and tourism, became one of the main economic activity (Vianna & Valentini, 2004). Non-selective fishery devices (trawls) are designed to penetrate the surface of the

sediment, disturbing and damaging benthic and infaunal animals (Watling & Norse, 1998).

When comparing the number of fishing boats in Ubatuba between these two periods, we noted an increase of 35% (162 to 219 fishing boats) (Vianna & Valentini, 2004; Ávila-da-Silva et al., 2017). Fishery activities provide an amount of organic matter (by-catch) released near inshore sites which predators and scavenger animals may consume. Some studies found that hermit crabs are attracted to areas disturbed by trawling, rapidly migrating onto a trawled way line to increase their food intake (Kaiser & Spencer, 1996; Ramsay et al., 1996). These fisheries discards may improve the food intake by hermit crabs, increasing the abundance of these crustaceans. The hermit crabs *Pagurus bernhardus* (Linnaeus, 1758) populations at the northeast coast of Anglesey, Irish Sea, respond strongly to trawling disturbance, rapidly migrating onto a trawled sites (Ramsay et al., 1997). Also, the shells that hermit crabs dwells help to reduce mechanic damage occurring during trawls, leading to a low mortality rate (Kaiser & Spencer, 1995). However, fisheries disturbances could affect sensitive hermit crab species, which explain the lower richness found in the second period of time. A repeated intense disturbance will select for species with appropriate facultative responses, and communities are likely to become dominated by juvenile stages, mobile species, and rapid colonists (Thrush & Dayton, 2002).

Homogenization of the substratum (indicated by higher values of phi, see Figure 8) is one of the most conspicuous long-term physical effects of bottom fishing. Loss of small-scale heterogeneity is caused by the removal of sessile organisms

capable of forming biogenic substrata (Veale et al., 2000) leading to a simpler abiotic structure, without biological structures like burrow walls, tubes, and galleries of the infauna (Schwinghamer et al., 1996). The removal of small-scale heterogeneity associated with the homogenization of habitats is, by definition, loss of biodiversity (Thrush & Dayton, 2002).

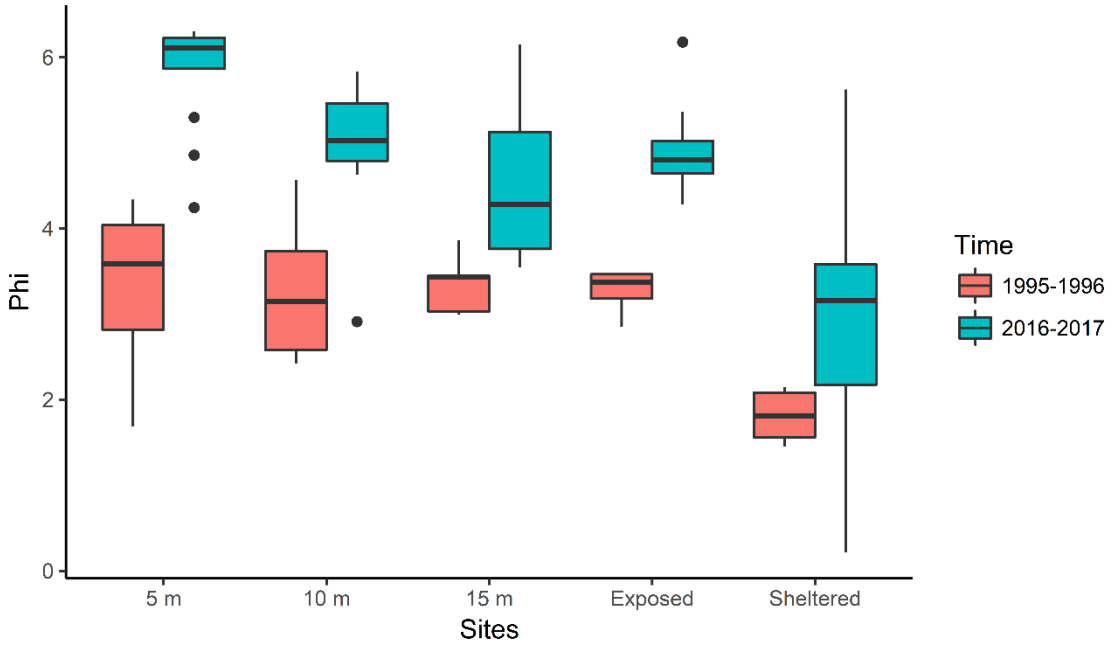


Fig 8. Boxplots summarizing sediment texture (phi values) in all sampled sites, comprehending both periods. Black dots indicate outliers.

In addition, multivariate analysis indicated a change in community structure, with significant differences between the first and the second period. The most abundant species changed when comparing the two periods of time (*L. loxochelis* in the first period to *D. insignis* in the second one). Generalist species tend to be less affected by fragmentation and disturbance than most of the species, some generalist species can even be benefited in these conditions (Devictor et al., 2008). The hermit crab *D. insignis* present some generalist characteristics like brief embryonic development, a high number of eggs produced per ovigerous female and reduced

size of the eggs (Miranda et al., 2006), which can explains the higher abundance in disturbed sites. The hermit crab *L. loxochelis* also increased abundance in second period, this species obtain food from suspended particles (suspension-feeder organism) (Biagi et al., 2006; Ayres-Peres & Mantelatto, 2008). Fisheries activities cause resuspension of organic matter in soft-substrates, facilitating suspensive species and resistant to trawl disturbance (*L. loxochelis* characteristics) (Van Denderen et al., 2015).

Hermit crab fauna was dissimilar in Exposed and Sheltered sites (in both periods). This pattern can be consequence to the distinct hydrodynamics features, related to different energy levels acting distinctly over each site. The site Sheltered has more influence of marine biogenic constituents (shell, ophiuroid, echinoderm and other marine animals fragments) than others sites in the studied bay (Mahiques et al., 1998). Shell's fragments indicate the presence of living snails which can provide shells availability to hermit crabs.

Environmental variables

Results in our study indicate that bottom temperature has been correlated inversely with hermit crab abundance. In Ubatuba the intrusion of the South Atlantic Central Water (SACW) toward the coast in the bottom layer of the continental shelf results in the movement of the Coastal Water (CW), rich in suspended matter from the continent (Castro Filho et al., 1987; Mahiques et al., 1998), which increases the amount of food for larvae because of the increase in primary productivity (De Léo & Pires-Vanin, 2006). SACW is a water mass characterized by low temperatures

(Castro Filho et al., 1987) which can explain the inverse correlation between bottom temperature and hermit crab abundance.

Local sediments attributes may be responsible for differences in both the fauna and the overall densities in macrobenthic communities (Johnson, 2015). Sediment properties (sand, mud, gravel) is one of the most important predictors among benthos models (Mazor et al., 2017). Greater values of phi indicate the presence of finest sediment, decreasing soft-bottom sediment texture heterogeneity. Our results showed an inverse correlation between phi values and hermit crab richness. Spatial heterogeneity has long been considered to promote overall species diversity in ecosystems (Huston, 1979; Rodrigues et al., 2017). A gradient of decreasing species diversity with decreasing soft-bottom heterogeneity is well-established in some benthos communities (Mcclain & Barry, 2010; Cardone et al., 2014; Alsaffar et al., 2017). Based on our results, sediment texture must be a key factor that maintains hermit crab richness in those sites.

5. Conclusion

Our investigation highlights the study of biodiversity to understand long-term changes in a well-established hermit crab assembly. It is clear the existence of small-scale variance in species composition, this shifts may be caused by some environmental features. However, we can't minimize the anthropic effects, like trawling, in these populations. Future studies should expand our analysis comparing distinct periods of time on a large scale, possibly quantifying the trawling to determine whether benthos are sustainable under the current regimes

of exposure and protection. The results can help managers achieve balance between conservation and sustainable industries in these bay ecosystems.

References

Alsaffar, Z., J. Cúrdia, A. Borja, X. Irigoien, & S. Carvalho, 2017. Consistent variability in beta-diversity patterns contrasts with changes in alpha-diversity along an onshore to offshore environmental gradient: the case of Red Sea soft-bottom macrobenthos. Marine Biodiversity 1–16.

Anderson, M. J., 2001. A new method for non parametric multivariate analysis of variance. Austral ecology 26: 32–46.

Ávila-da-Silva, A. O., M. H. Carneiro, J. T. Mendonça, G. C. C. Bastos, L. V. de Miranda, W. do R. Ribeiro, & S. dos Santos, 2017. Produção Pesqueira Marinha e Estuarina no Estado de São Paulo Setembro de 2017. Informe Pesqueiro de São Paulo São Paulo 89: 1–4.

Cardone, F., G. Corriero, A. Fianchini, M. F. Gravina, & C. Nonnis Marzano, 2014. Biodiversity of transitional waters: Species composition and comparative analysis of hard bottom communities from the south-eastern Italian coast. Journal of the Marine Biological Association of the United Kingdom 94: 25–34.

Castro Filho, B. M. de, L. B. de Miranda, & S. Y. Miyao, 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. Boletim do Instituto Oceanográfico 35: 135–151.

Coelho, P. A., & M. de A. Ramos, 1972. A constituição e a distribuição da fauna de decapodos do litoral leste da América do Sul entre as latitudes 5 N e 30 S. Trabalhos Oceanograficos da Universidade Federal de Pernambuco. Recife, 133–236.

Connell, J. H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science 199: 1302–1310.

De Léo, F. C., & A. M. S. Pires-Vanin, 2006. Benthic megafauna communities under the influence of the South Atlantic Central Water intrusion onto the Brazilian SE shelf: A comparison between an upwelling and a non-upwelling ecosystem. Journal of Marine Systems 60: 268–284.

Devictor, V., R. Julliard, & F. Jiguet, 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117: 507–514.

Frameschi, I. F., L. S. De Andrade, F. G. Taddei, V. Fransozo, & L. C. Fernandes-Goés, 2013. Assemblage of hermit crabs near coastal islands in southeastern Brazil. Neotropical Biology and Conservation 9: 9–19.

Fransozo, A., L. Fernandes-Góes, V. Fransozo, J. Góes, V. Cobo, G. Teixeira, & R. Gregati, 2011. Marine anomurans (Decapoda) from the non-consolidated sublittoral bottom at the southeastern coast of Brazil. Crustaceana 84: 435–450.

Fransozo, A., F. L. M. Mantelatto, G. Bertini, L. C. Fernandez-Góes, & J. M. Martinelli, 1998. Distribution and assemblages of anomuran crustaceans in Ubatuba bay, north coast of São Paulo state, Brazil. Acta Biológica Venezuelana 18: 17–25.

Gotelli, N. J., & A. M. Ellison, 2016. Princípios de estatística em ecologia. Artmed Editora, Porto Alegre.

Hazlett, B., 1981. The behavioral ecology of hermit crabs. Annual Review of Ecology and Systematics 12: 1–22.

Hebling, N. J., F. L. Mantelatto, M. L. Negreiros-Fransozo, & A. Fransozo, 1994. Levantamento e distribuição de braquiúros e anomuros (Crustacea, Decapoda) dos sedimentos sublitorais da região da Ilha Anchieta, Ubatuba (SP). Boletim Do Instituto De Pesca 21: 1–9.

Hunt, H. L., R. A. Wahle, J. Tremblay, M. Comeau, A. Silva, & R. Rochette, 2017. Spatial patterns of richness and abundance of benthic decapod crustaceans and fishes in the North-west Atlantic as measured by cobble-filled bio-collectors. Marine Biology Research 1000: 1–19.

Huston, M., 1979. A General Hypothesis of Species Diversity. The American Naturalist 113: 81–101.

IBAMA, 2008. Normative Instruction No. 189, 23th September, 2008. .

Johnson, W. S., 2015. Suprabenthic species distributions relative to small-scale bathymetric features along the Virginia coast, USA. Marine Biology Research 11: 1009–1020.

Kaiser, M. J., & B. E. Spencer, 1995. Survival of by-catch from a beam trawl. Marine Ecology Progress Series 126: 31–38.

Kaiser, M. J., & B. E. Spencer, 1996. Behavioural responses of scavengers to beam trawl disturbance. Aquatic predators and their prey Blackwell Scientific Publications Oxford 116: 123.

Lancaster, I., 1986. Pagurus bernhardus (L.)–an introduction to the natural history of hermit crabs. Field studies 7: 189–238.

Mahiques, M. M. de, E. Siegle, J. Alcántara-Carrió, F. G. Silva, P. H. G. de Sousa, & C. C. Martins, 2016. The Beaches of the State of São Paulo In Short, A. D., & A. H. da F. Klein (eds), Brazilian Beach Systems. Springer: 397–418.

Mahiques, M. M., M. G. Tessler, & V. V. Furtado, 1998. Characterization of energy gradient in enclosed bays of Ubatuba region, south-eastern Brazil. Estuarine, Coastal and Shelf Science 47: 431–446.

Mantelatto, F. L. M., & A. Franzoso, 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, Northern coast of São Paulo State, Brazil. Revista Brasileira de Biologia 59: 23–31.

Mantelatto, F. L. M., & R. B. Garcia, 2002. Hermit crab fauna from the infralittoral zone of Anchieta Island (Ubatuba, Brazil) In Escoba-Briones, E., & F. Alvarez (eds), Modern approaches to the study of Crustacea. : 137–143.

Mazor, T. K., C. R. Pitcher, N. Ellis, W. Rochester, S. Jennings, J. G. Hiddink, R. A. McConnaughey, M. J. Kaiser, A. M. Parma, P. Suuronen, M. Kangas, & R. Hilborn, 2017. Trawl exposure and protection of seabed fauna at large spatial scales. Diversity and Distributions 23: 1280–1291.

Mcclain, C. R., & J. P. Barry, 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. Ecological Society of America 91: 964–976.

McDermott, J. J., J. D. Williams, & C. B. Boyko, 2010. The unwanted guests of hermits: A global review of the diversity and natural history of hermit crab parasites. Journal of Experimental Marine Biology and Ecology 394: 2–44.

Melo, G. A. S., 1999. Manual de identificação dos Crustacea Decapoda do litoral Brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea. Editora Plêiade. São Paulo.

Miranda, I., A. L. Meireles, R. Biagi, & F. L. Mantelatto, 2006. Is the abundance of the red brocade hermit crab *Dardanus insignis* (Decapoda: Anomura: Diogenidae) in the infralittoral region of southern Brazil determined by reproductive potential? Crustacean Research 6: 45–55.

Miserendino, M. L., C. Brand, L. B. Epele, C. Y. Di, G. H. Omad, M. Archangelsky, O. Martínez, & A. M. Kutschker, 2018. Environment Biotic diversity of benthic macroinvertebrates at contrasting glacier-fed systems in Patagonia Mountains: The role of environmental heterogeneity facing global warming. Science of the Total Environment 622–623: 152–163.

Negreiros-Fransozo, M. L., A. Fransozo, F. L. M. Mantelatto, M. A. Pinheiro, & S. Santos, 1997. Anomuran species (Crustacea, Decapoda) and their ecological distribution at Fortaleza Bay sublittoral, Ubatuba, São Paulo, Brazil. Iheringia Série Zoologia 194: 187–194.

Oksanen, A. J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O. Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2015. Package ‘ vegan .’ .

Peterson, B. G., & P. Carl, 2018. PerformanceAnalytics: Econometric Tools for Performance and Risk Analysis. , https://cran.r-project.org/package=PerformanceAnalytics.

Pohlert, T., 2014. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). , https://cran.r-project.org/package=PMCMR.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria, https://www.r-project.org/.

Ramalho, S. P., L. Lins, J. Bueno-Pardo, E. A. Cordova, J. M. Amisi, N. Lampadariou, A. Vanreusel, & M. R. Cunha, 2017. Deep-Sea Mega-Epibenthic Assemblages from the SW Portuguese Margin (NE Atlantic) Subjected to Bottom-Trawling Fisheries. Frontiers in Marine Science 4: 1–16.

Ramsay, K., M. J. Kaiser, & R. N. Hughes, 1996. Changes in hermit crab feeding patterns in response to trawling disturbance. Marine Ecology Progress Series 144: 63–72.

Ramsay, K., M. J. Kaiser, & R. N. Hughes, 1997. A Field Study of Intraspecific Competition for Food in Hermit Crabs (Pagurus bernhardus). Estuarine, Coastal and Shelf Science 44: 213–220.

Rodrigues, L. C., B. M. Pivato, L. C. G. Vieira, V. M. Bovo-Scomparin, J. C. Bortolini, A. Pineda, & S. Train, 2017. Use of phytoplankton functional groups as a model of spatial and temporal patterns in reservoirs: a case study in a reservoir of central Brazil. Hydrobiologia 805: 147–161.

Schwinghamer, P., J. Y. Guigné, & W. C. Siu, 1996. Quantifying the impact of trawling on benthic habitat structure using high resolution acoustics and chaos theory. Canadian Journal of Fisheries and Aquatic Sciences 53: 288–296.

Selin, N. I., E. S. Kornienko, & O. M. Korn, 2016. The species composition and pattern of distribution of hermit crabs (Decapoda: Paguroidea) in Vostok Bay, Sea of Japan. Russian Journal of Marine Biology 42: 481–488.

Small, C., & R. J. Nicholas, 2003. A global analysis of human settlement in coastal zones. Journal of coastal research 19: 584–599.

Sommer, B. R., P. L. Harrison, Ma. Beger, & J. M. Pandolfi, 2014. Trait-mediated environmental filtering drives assembly at biogeographic transition zones. Ecology 95: 1000–1009.

Stanski, G., F. L. Mantelatto, & A. Leão-Castilho, 2016. Hermit crab bycatch fauna (Decapoda, Anomura) off the coast of Santa Catarina State, Brazil: diversity and spatial-temporal distribution. Latin American Journal of Aquatic Research 44: 546–556.

Tagliapietra, D., & M. Sigovini, 2010. Benthic fauna : collection and identification of macrobenthic invertebrates. Terre et Environnement 88: 253–261.

Thrush, S. F., & P. K. Dayton, 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annual Review of Ecology and Systematics 33: 449–473.

Thrush, S. F., K. E. Ellingsen, & K. Davis, 2016. Implications of fisheries impacts to seabed biodiversity and ecosystem-based management. Ices Journal of Marine Science 73: 144–150.

Tucker, M. E., 1988. Techniques in sedimentology. Blackwell Scientific Publications, Oxford – UK.

Van Denderen, P. D., S. G. Bolam, J. G. Hiddink, S. Jennings, A. Kenny, A. D. Rijnsdorp, & T. Van Kooten, 2015. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Marine Ecology Progress Series 541: 31–43.

Veale, L. O., A. S. Hill, S. J. Hawkins, A. R. Brand, & S. A. Hill, 2000. Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats. Marine Biology 137: 325–337.

Vianna, M., & H. Valentini, 2004. Observações Sobre a Frota Pesqueira Em Ubatuba , Litoral norte Do Estado De São Paulo, Entre 1995 E 1996. Boletim Do Instituto De Pesca 30: 171–176.

Watling, L., & E. A. Norse, 1998. Disturbance of the Seabed by Mobile Fishing Gear: A comparison to Forest Clearcutting. Conservation Biology 12: 1180–1197.

Williams, J. D., & J. J. McDermott, 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. Journal of Experimental Marine Biology and Ecology 305: 1–128.

Zajac, R. N., J. M. Vozarik, & B. R. Gibbons, 2013. Spatial and temporal patterns in macrofaunal diversity components relative to sea floor landscape Structure. PloS ONE 8: 1–11.

Zeileis, A., & T. Hothorn, 2002. Diagnostic Checking in Regression Relationships. R News 2: 7–10, https://cran.r-project.org/doc/Rnews/.

Changes in coastal hermit crab biodiversity patterns: partitioning beta diversity with an interval of 20 years

Abstract

Changes in diversity, density, and community structure of soft-bottom hermit crab assemblages were investigated in different areas of a bay system in the southeastern Brazilian coast in two periods with an interval of 20 years. Density of several hermit crab species increased in second period. Most of the alpha diversity index did not change, when comparing the sampling periods. Partitioned beta diversity indicated that dissimilarities between the two periods (1995-1996 and 2016-2017) were higher in sites close to the coastline, and the relative importance of nestedness and turnover component were distinct among the sites. Also, the hermit crab assemblage composition was distinct between the periods. The first period assemblage was inversely correlated with sediment texture (Phi), while the second one the opposite was observed. Despite the similarities observed for alpha-diversity across the five sites, beta-diversity measures indicated consistently changes. The sedimentation change (probably due higher erosive processes) may be one of the factors that have altered the marine environment, causing notable changes in the hermit crab community structure after 20 years. Even being difficult with this data set to precise the anthropic influence on hermit crab assemblages, these results are useful to guide conservation efforts in this bay system and also to predict the premises on biodiversity changes along the time.

Key-words: Anomura; Temporal changes; Coastal environment; Paguroidea; Nestedness component; Turnover component.

3. Introduction

Patterns of biodiversity provide insights into the organization of metacommunities and their responses to the local and regional footprints of human-induced environmental change (Zajac et al., 2013; Mantelatto et al., 2016; Hunt et al., 2017; Chatzinikolaou et al., 2018). Regional long-term studies would significantly increase our understanding of how local communities respond to environmental changes caused by both natural and anthropic processes (Angeler, 2013).

Knowledge of the processes that govern the structure of communities across space and time is the key for conserving regional biodiversity (Tylianakis et al., 2005; Leprieur et al., 2009; Angeler, 2013; Chatzinikolaou et al., 2018). Several studies focused on local scales (alpha diversity), while efforts to characterize the spatial variability in species composition across sites (beta diversity) increased recently (Anderson et al., 2011). An advantageous approach to understand the changes in biodiversity across space and time is partition of beta diversity. The beta diversity is partitioned resulting in two antithetic components: nestedness that occurs when biotas of sites with smaller numbers of species are subsets of biotas at richer sites and replacement (turnover) component that implies in the replacement of some species by others in different sites (Baselga, 2010). This approach allows the implementation of different conservation guidelines. Dominating nestedness suggests the necessity of prioritizing a few high-diversity sites in conservation

planning, while dominating turnover requires a regional approach focusing on multiple sites (Wright & Reeves, 1992).

Benthic fauna is often used as indicators for assessing the status and health of marine ecosystems (Rosenberg et al., 2004). Previous studies have found benthic communities with reduced richness and diversity in sites with human-induced disturbances like trawl fishery (Mazor et al., 2017) and contamination by pollutants (Chatzinikolaou et al., 2018).

The hermit crabs are decapod crustaceans that compose an important piece of benthic fauna. These crustaceans are unique for their dependency on gastropod shells as a 'mobile home' to protect them from predators (Childress, 1972) which make them extremely dependent of shell supply, provided by gastropod and other mollusks communities (Hazlett, 1981). Despite its omnivorous and detritivore feeding behavior them are a key element in the trophic chain, obtaining food from several trophic levels (Selin et al., 2016). Some studies aiming to understand the biodiversity of hermit crabs and environmental variables, which modulate this patterns have been published for the Brazilian coast, being most of them in the Southern and Southeast region (Hebling et al., 1994; Negreiros-Fransozo et al., 1997; Fransozo et al., 1998, 2011; Mantelatto & Garcia, 2002; Meireles et al., 2012; Frameschi et al., 2013; Stanski et al., 2016; Fernandes & Alves, 2018). Nevertheless, an information lack still remains on how hermit crab assemblages changed over a time gap, and how the assemblage responds to environmental changes.

Here, we used a unique data set of coastal hermit crabs, that have been sampled in five sites in Ubatuba Bay during two periods (comprising 12 sampling months, each period) to (1) compare density, richness and alpha diversity indices between these periods, (2) investigate the influence of environmental factors in hermit crab assemblage and (3) evaluate the relative importance of turnover and nestedness components in sites, temporally. Such approach considers that temporal beta diversity can be understood as temporal variability of spatial beta diversity; that is, comparing the spatial beta diversity over time (Angeler, 2013).

2. Material and Methods

2.1 Study Area

The coast of the State of São Paulo is, probably, one of the most affected by anthropogenic activities from the whole Brazilian coastline (Mahiques et al., 2016). For the northern beaches, from Ubatuba to São Sebastião municipalities, the proximity of the coastal range (Serra do Mar) results in small bays and headland-embayed beaches with variable orientation (Mahiques et al., 1998, 2016). Ubatuba Bay faces to the east and presents a constriction in its coastline, which induces wave diffraction (Mahiques et al., 1998). The artisanal fishery in the Ubatuba Bay is well-established, being an important economic source for human populations, boosted by tourism in the region. These activities result in severe impacts to the coastal environments. The Ubatuba bay is important for conservation efforts, sheltering several species from tropical, temperate and sub-

Antarctic faunas (Amaral & Nallin, 2017), and considered a hotspot for decapod crustaceans (Mantelatto et al., 2018). Some efforts intending to preserve local marine biodiversity includes the establishment of a Marine Protection Area (Cunhambebe sector), in 2008, and a closed season shrimp-fishing (IBAMA, 2008) that forbid any type of trawl fishing procedures from march 1st to may 31th, each year.

2.2 Data Collection

The hermit crabs were collected (trawled) utilizing a fishing boat equipped with double-rig nets (4.5 m wide at the mouth, 25 mm of body mesh size, and 15 mm of cod end mesh size). Each trawl lasted 30 minutes, covering an estimated swept area of 18.000 m². Samples were taken, monthly, in three consecutive days, during two periods. The samples were performed in same locations for both periods (1995-1996 and 2016-2017). The Ubatuba Bay was classified into five sampling sites differing in terms of their location in relation to the bay mouth, the presence of a rock wall or a beach along the boundaries, the inflow of fresh water, the proximity of an offshore area, depth and sediment composition (Fransozo et al., 1998). A global positioning system (GPS) was used to record the location at the sampling sites, ensuring the sampling in the same sites for all months surveyed. Thus, we selected five available sites to this sampling period as follows: three sites plotted at depths of 5, 10, and 15 meters; and two sites defined perpendicular to the beach line - one localized in a sheltered area, and other, in an exposed area to wave action (Figure 1). The individuals were kept in plastic bags, properly marked,

in thermal boxes containing crushed ice. In the lab, the hermit crabs (Paguroidea) were removed from their shells, and identified, according to Melo (1998).

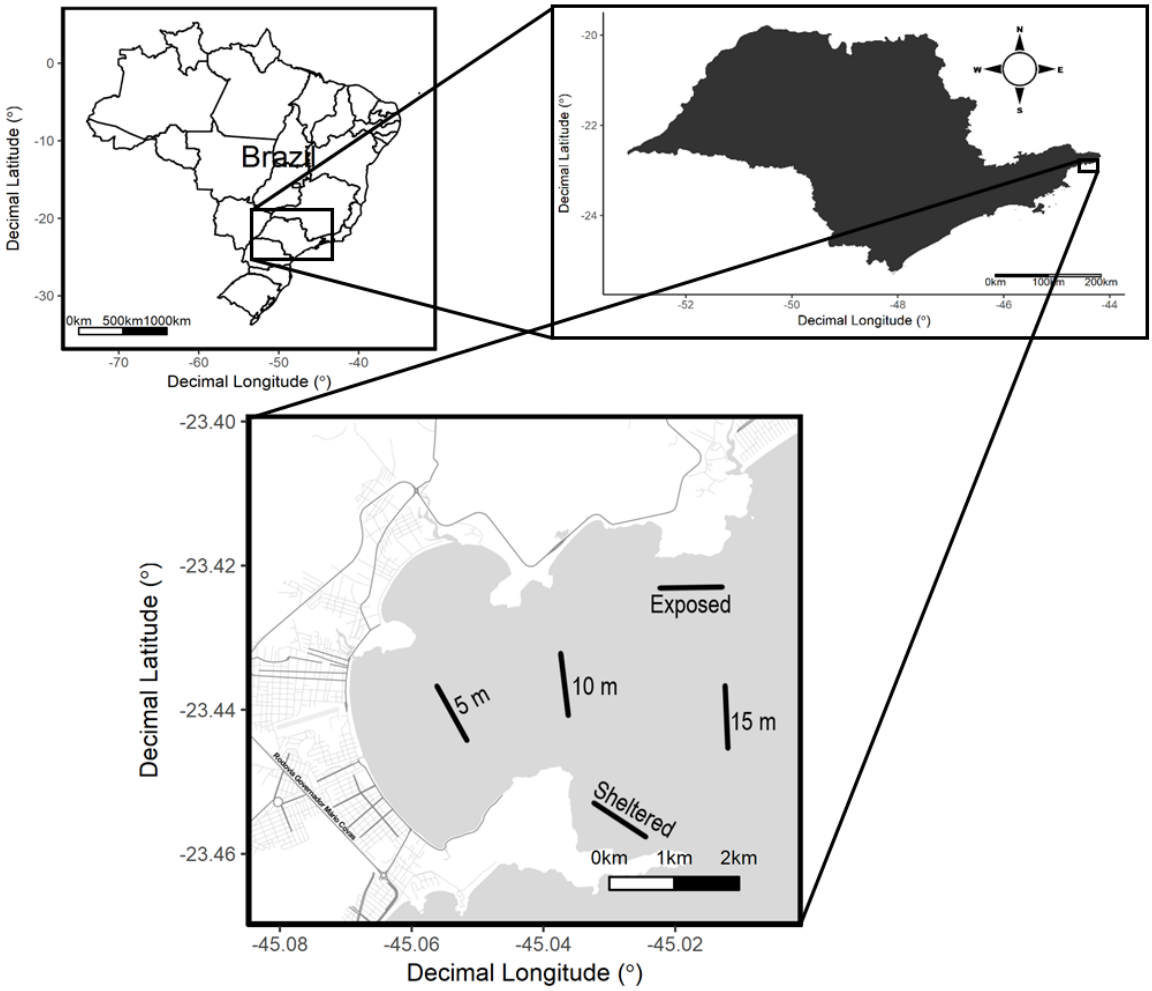


Fig. 1 Location of sampling sites on Ubatuba bay. Ubatuba, São Paulo, Brazil. Black lines indicate the area surveyed.

Additionally, and based on previous evidences (Mantelatto & Franzoso, 1999; Fransozo et al., 2011) we selected four environmental variables to evaluate their probable action on the hermit crab fauna as follows: water temperature, water salinity, organic matter and sediment texture (phi). Details on methodology are

available at Mantelatto & Fransozo (1999). Water samples were obtained with a Nansen bottle, from which we measured temperature (ºC) and salinity. Sediment samples were collected with a 0.06 m² van Veen grab to measure the organic matter content and sediment texture. All environmental data were collected simultaneously with biotic data in central point of each site sampled (Mantelatto and Franzoso 1999).

For sediment analysis procedures, two 50 g subsamples were taken, to which we added 250 ml of a NaOH (0.2 N) solution, aiming to lift up the silt + clay (Tucker, 1988). Afterward, we washed the subsamples using a sieve (mesh= 0.063 mm), washing away the silt + clay. The remaining sediment was dried and then submitted to a differential sieving, classifying the sediment grains according to the Wentworth (1922) scale.

Phi values were calculated based on the equation $phi = -log_2 d$, where d= grain diameter (mm). Based on the obtained values, we calculated the central trend measurements, determining the most frequent grain fractions in the sediment. We calculated these values based on data graphically taken from cumulative sediment samples frequency distribution curves. We used values corresponding to the 16^{th}, 50^{th} and 84^{th} percentages to determine the mean diameter (*MD*), using the equation $MD= (\varphi_{16} + \varphi_{50} + \varphi_{84}/3)$ (Suguio, 1973).

Organic matter (OM) content was determined by loss on ignition (LOI). We put the subsamples (10 g each) in porcelain containers, previously labelled and weighed. After that, we put them into an oven (500ºC for 3 hours) and weighed them again. The LOI is then calculated using the following equation: LOI = (W_i –

$W_f)/W_i$ * 100, where: LOI = organic matter content (%), W_i = initial weight of the sediment subsample; W_f = final weight after ignition (Hieri et al., 2001).

2.3 Data Analysis

Tests for homoscedasticity (Levene tests) and normality (Shapiro–Wilk tests) were first performed as pre-requisites for the statistical test (α = 0.05). Temporal changes in in total density (ind/km²), richness (S) and alpha diversity indexes (described below) were assessed using Student's t-test for paired samples (Zar, 1999). Total density comparisons of each hermit crab was assessed using Wilcoxon test (nonparametric data) for pairwise comparisons between both periods (Hollander & Wolfe, 1999).

2.3.1 Ecological indexes

Alpha diversity was estimated for hermit crabs at all sites at Ubatuba bay. The alpha diversity indexes included: Shannon index (*H'*), Simpson index (*D'*), taxonomic diversity (Δ) (Clarke & Warwick, 1998) and taxonomic distinctness (Δ^+) (Clarke & Warwick, 2001). The lasts two indexes incorporate phylogenetic information. A composite phylogeny of hermit crabs in the Southeastern Brazilian Coast classification scheme was compiled from Lemaitre & Tavares (2015). Four levels of classification (Superfamily, Family, Genus and Species) were used for the measurement of taxonomic distance between species in the study region. The taxonomic diversity (Δ) measured as: $\Delta = \sum\sum_{i>j} \omega_{ij} x_i x_j / \frac{\sum\sum_{i>j} x_i x_j + \sum_i n(n-1)}{2}$

where x_i denotes the abundance of the *i*th species, *n* is the total number of

individuals in the sample and w_{ij} is the "distinctness weight" given to the path length linking species I and *j* in the hierarchical classification. The Taxonomic distinctness (Δ^+) based on presence/absence of species in study sites is given by the equation $\Delta^+ = \frac{\sum\sum_{i>j}\omega_{ij}}{S(S-1)/2}$, where s denotes the number of species observed and ω_{ij} is the weight given to the path length linking species I and j in the taxonomy.

2.3.2. Partitioning beta diversity

Overall beta diversity can be partitioned into two additive components: (1) turnover (β_{sim} *sensu* Baselga, 2010), which is conceptually associated with species replacement; and (2) nestedness (β_{nes} *sensu* Baselga, 2010), akin to species addition. These two components of overall beta diversity are opposing factors which represent either compositional distinctness (β_{sim}), or the degree to which a site species pool is determined by, or nested within, a neighbouring species pools (β_{nes}). Both spatial turnover and nestedness contribute to overall compositional difference between assemblages ($\beta_{sor} = \beta_{sim} + \beta_{nes}$). To assess overall partitioned beta diversity, we used package "betapart" (Baselga & Orme, 2012). Using species presence–absence data, we calculated total species beta diversity (βsor) and its two additive components: turnover (βsim) and nestedness (βnes). Partitioned beta diversity coefficients were calculated separately for each sites comparing P1(*n* = 12) vs. P2 (*n* = 12).

2.3.3. Correlation between environmental variables

Distance-based redundancy analysis (dbRDA) was applied to visualize the position of the periods fitted to the significant environmental predictor variables affecting the biological assemblage data by analyzing marginal and sequential

tests. The analysis included bottom water temperature, bottom water salinity, sediment texture (phi), and OM (%). The direction and magnitude of the relationships between environmental variables and biological assemblages were visually presented in a dbRDA biplot. The statistical significance of eigenvalues of the dbRDA axis was evaluated by randomization (Monte Carlo) tests, using 9,999 randomized runs for each analysis. To understand the effect of natural or human induced sedimentation we compared the phi values of each site between the first and second period. Sediment grain size was evaluated following the Suguio (1973) approach, were higher values of phi indicate finer sediments.

All analyses were carried out in R statistical program (R Core Team, 2019), using package "stats" for Wilcoxon test (R Core Team, 2019), "vegan" to calculate alpha diversity indexes and for multivariate analysis (Oksanen et al., 2015) and "betapart" to assess beta diversity components.

3. Results

Descriptive statistics of the biological data and environmental factors measured at each sampling site are shown in Table I. Hermit crab assemblage sampled across the Ubatuba Bay yielded 11 species belonging to 2 families, six of which were common for both periods. Table II lists the hermit crab fauna present at each location and indicates the dominant species on each sampled site for both periods. We found a density (ind x km^{-2}) of 387.96 in the first period and 1616.67 in second one (Table III). The hermit crabs *Dardanus insignis* (de Saussure, 1858), *Loxopagurus loxochelis* (Moreira, 1901) and *Pagurus exilis* (Benedict, 1892) were the species most frequent during the overall periods surveyed. Clear changes in

species compositions were detect comparing the periods. The hermit crabs *Pseudopaguristes calliopsis* (Forest & de Saint Laurent, 1968), *Paguristes erythrops* Holthuis, 1959, *Paguristes tortugae* Schmitt, 1933 and *Pagurus leptonyx* Forest & de Saint Laurent, 1968 were found exclusively in the first period. Six species were shared between first and second period communities, whereas the three most abundant species contributed more to the hermit crab assemblage composition, representing a 91.45% of total density.

Table I. Biological and environmental characterization of the identified hermit crab assemblages in each sampled site at the coast of Ubatuba, State of São Paulo, Brazil, and in each period (1995-1996 and 2016-2017).

1995-1996	5 m	10 m	15 m	Exposed	Sheltered
Depth (m)	5	10	15	7.5	10
Latitudinal (decimal º)	-23.437	-23.435	-23.435	-23.424	-23.452
Longitudinal (decimal º)	-45.044	-45.031	-45.015	-45.016	-45.026
Water column					
Bottom temperature (ºC)	23.96 ± 2.6	23.4 ± 2.7	22.55 ± 2.8	23.40 ± 2.8	23.74 ± 2.7
Salinity	33.15 ± 1.8	33.4 ± 1.7	33.75 ± 1.5	33.33 ± 1.7	33.25 ± 1.8
Sediment properties					
Sediment texture (Phi)	3.34 ± 0.8	3.24 ± 0.7	3.32 ± 0.2	3.29 ± 0.2	1.81 ± 0.2
Organic matter (%)	14.55 ± 2.2	13.22 ± 1.5	5.52 ± 5.1	5.35 ± 3.0	18.54 ± 9.6
Biological variables					
Richness (S)	2.08 ± 1.3	1.5 ± 0.5	2.08 ± 1.0	1.00 ± 0.0	2.66 ± 1.07
Total no. Ind.	58.00	8.00	190.00	10.00	153.00
Density (ind/km²)	26.38 ± 18.3	8.33 ± 2.7	87.96 ± 131.8	9.25 ± 4.5	69.44 ± 59.7
H'	0.48 ± 0.5	0.33 ± 0.3	0.33 ± 0.3	0.00 ± 0	0.69 ± 0.25
Simpson	0.37 ± 0.39	0.34 ± 0.39	0.32 ± 0.31	0 ± 0.00	0.62 ± 0.20
2016 – 2017	5 m	10 m	15 m	Exposed	Sheltered
Depth (m)	5	10	15	7.5	10
Latitudinal (decimal º)	-23.437	-23.435	-23.435	-23.424	-23.452
Longitudinal (decimal º)	-45.044	-45.031	-45.015	-45.016	-45.026
Water column					
Bottom temperature (ºC)	24.08 ± 2.4	23.87 ± 1.8	23.37 ± 1.7	23.91 ± 2.2	23.46 ± 2.0
Salinity	35.25 ± 1.2	34.91 ± 1.9	34.83 ± 2.12	34.83 ± 1.94	35.33 ± 1.7

Sediment properties					
Sediment texture (Phi)	5.83 ± 0.6	4.9 ± 0.7	4.50 ± 0.9	4.90 ± 0.4	3.00 ± 1.6
Organic matter (%)	9.5 ± 2.85	6.57 ± 2.96	4.75 3.53	6.09 ± 2.21	6.22 ± 3.12
Biological variables					
Richness (S)	2.63 ± 1.1	2.11 ± 0.7	2.00 ± 0.9	1.40 ± 0.8	2.83 ± 1.4
Total no. Ind.	350.00	76.00	228.00	34.00	1058.00
Density (ind/km²)	215.74 ± 17.05	53.7 ± 3.79	194.44 ± 17.80	31.48 ± 2.80	896.29 ± 63.72
H'	0.56 ± 0.5	0.67 ± 0.3	0.47 ± 0.5	0.15 ± 0.3	0.33 ± 0.31
Simpson	0.59 ± 0.30	0.59 ± 0.24	0.43 ± 0.32	0.14 ± 0.33	0.46 ± 0.30

Table II. Hermit crab species present at each site Ubatuba Bay surveyed in both periods. 'X' indicates presence; 'D' indicates a dominant species on that particular site; dash (–) indicates absence.

	1995-1996					**2016-2017**				
Species	**5 m**	**10 m**	**15 m**	**Exposed**	**Sheltered**	**5 m**	**10 m**	**15 m**	**Exposed**	**Sheltered**
Family Diogenidae Ortmann 1892										
Dardanus insignis (de Saussure, 1858)	X	-	X	D	D	D	D	D	X	D
Isocheles sawayai Forest & de Saint Laurent 1968	X	-	X	-	X	-	X	-	-	X
Loxopagurus loxochelis (Moreira, 1901)	X	D	D	D	-	X	X	D	D	X
Pseudopaguristes calliopsis (Forest and Saint Laurent, 1968)	X	-	-	-	X	-	-	-	-	-
Petrochirus diogenes (Linnaeus, 1798)	D	X	X	-	X	X	X	X	-	X
Paguristes erythrops Holthuis, 1959	X	-	-	-	X	-	-	-	-	-
Paguristes tortugae Schmitt, 1933	X	-	-	-	X	-	-	-	-	-
Paguristes sp.	-	-	-	-	-	-	-	-	-	X
Family Paguridae Latreille 1802										
Pagurus criniticornis (Dana, 1852)	-	-	-	-	X	X	-	-	-	-

Pagurus exilis (Benedict, 1892)	-	-	X	-	X	X	X	X	X	X
Pagurus leptonyx Forest and Saint Laurent, 1968	X	X	X	-	X	-	-	-	-	-

The density of the three dominant species was higher in second period (Wilcoxon test, *p-value* < 0.05). Only hermit crab *Petrochirus diogenes* (Linnaeus, 1758) had lower abundance in second period (Mann-Whitney, *p-value* < 0.05). Overall, some ecological indexes (*H'*, Simpson, Δ) did not differ between the two surveyed periods. Only taxonomic distinctness (Δ+) values were different (Mann-Whitney; *p-value* < 0.05), reaching higher values in the second period (Figure 2). However, we found lower number of species in the second period (10 species in the first and 7 in second periods).

Table III. Hermit crabs' density (ind/km²) sampled by trawl at the coast of Ubatuba, State of São Paulo, Brazil, and in each period (1995-1996 and 2016-2017). Bold values indicate statistical differences in density between periods (Wilcoxon test; *p-value* < 0.05)

Species	P_1 (1995-1996)	P_2 (2016-2017)	*p-value*
Family Diogenidae Ortmann 1892			
Dardanus insignis (de Saussure, 1858)	**112.04**	**892.59**	**0.0002**
Isocheles sawayai Forest & de Saint Laurent 1968	3.70	9.26	0.6683
Loxopagurus loxochelis (Moreira, 1901)	**159.26**	**385.19**	**0.0004**
Pseudopaguristes calliopsis (Forest and Saint Laurent, 1968)	1.85	0.00	-
Petrochirus diogenes (Linnaeus, 1798)	**89.81**	**40.74**	**0.0004**
Paguristes erythrops Holthuis, 1959	2.78	0.00	-

Paguristes tortugae Schmitt, 1933	3.70	0.00	-
Paguristes sp.	0.00	1.85	-
Family Paguridae Latreille 1802			
Pagurus criniticornis (Dana, 1852)	2.78	9.26	0.9670
Pagurus exilis (Benedict, 1892)	**6.48**	**277.78**	**0.0001**
Pagurus leptonyx Forest and Saint Laurent, 1968	**5.56**	**0.00**	-
Total	387.96	1616.67	**0.0001**

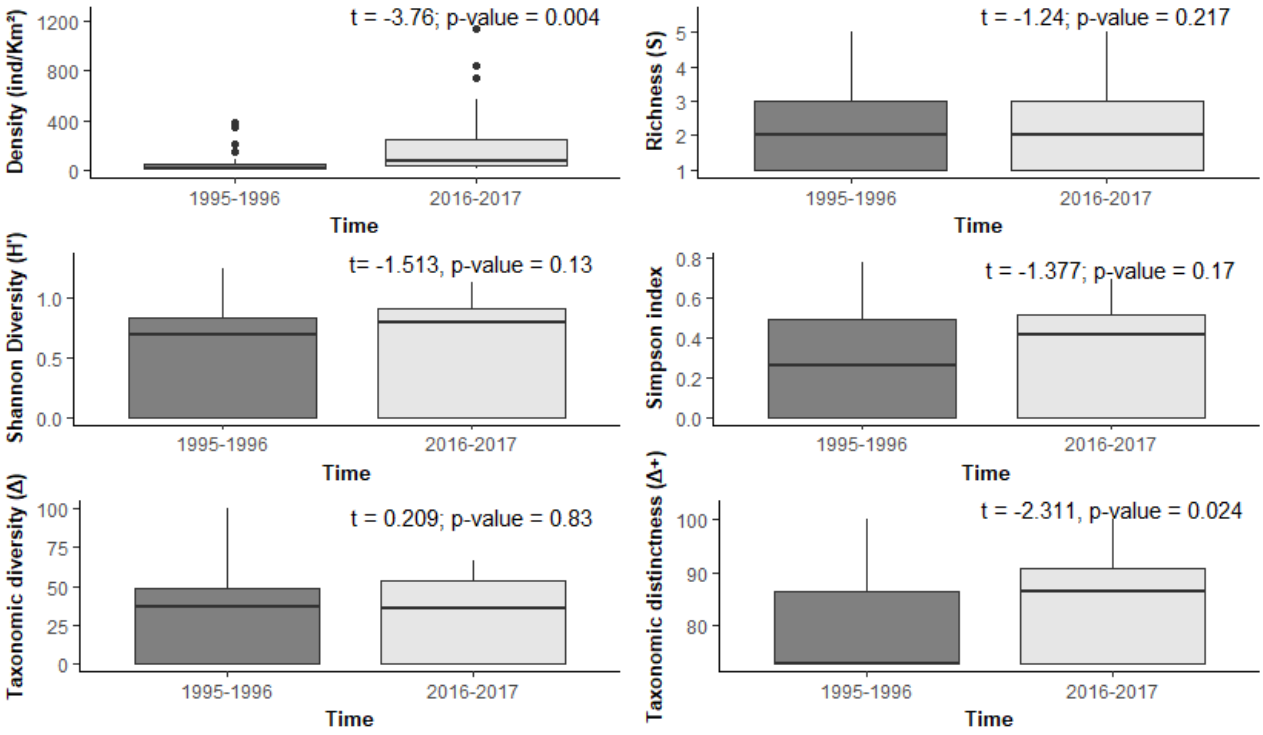


Figure 2. Density (ind/ km²), Richness, Shannon index (H'), Simpson index, Taxonomic diversity (Δ) and Taxonomic distinctness (Δ^+) of hermit crab assemblages sampled by trawl at the coast of Ubatuba, State of São Paulo, Brazil, and in each period (1995-1996 and 2016-2017).

Pairwise-sites measures of Sørensen (βsør) presented dissimilarity; their turnover and nestedness components were calculated comparing the same sites for both

periods (Figure 3). Total Sørensen dissimilarity were higher in the sites "5 m" and "10 m", composed mainly by turnover component (βsim), indicating that the variation in species composition is mainly due to gain and loss of species. The relative importance of nestedness (βnes) component was higher in "15 m", "Exposed" and "Sheltered". It was clear that dissimilarities values increase in regions near to mainland and decrease in higher depths.

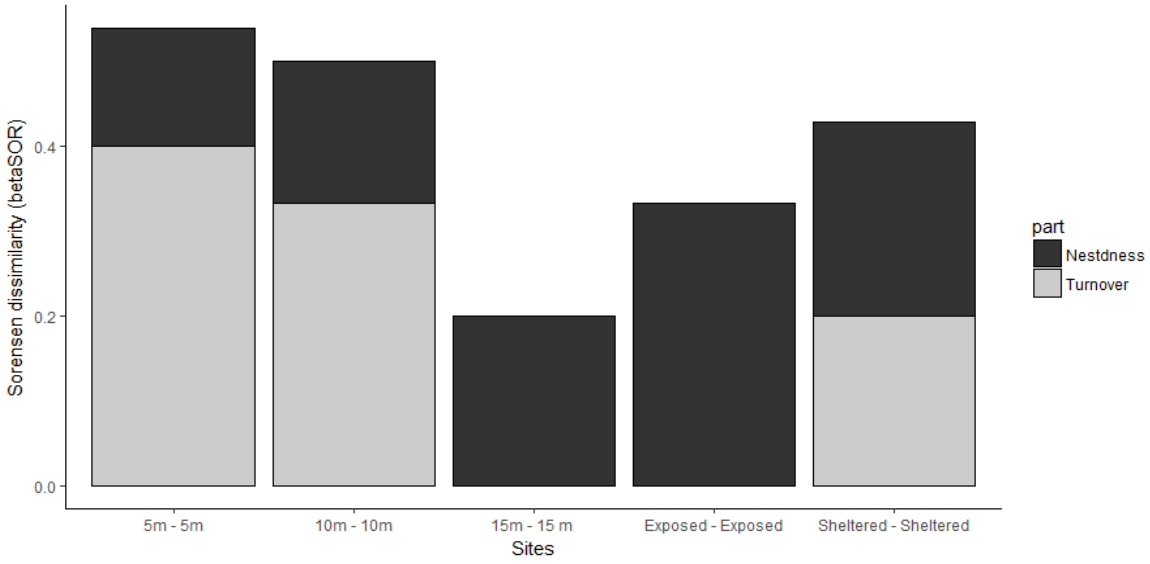


Figure 3. Overall of β diversity and the nestedness and turnover components in each sampled site at the coast of Ubatuba, State of São Paulo, Brazil, and in each period (1995-1996 and 2016-2017).

Distance-based redundancy analysis (dbRDA) showed that only sediment texture (phi) was significant (F = 5.11; p=0.001) for explaining the biological patterns (Figure 4). The first axis explained 80.91% of total variation (F_{dbRDA1} = 5.24, p = 0.001; F_{dbRDA2} = 1.49, p = 0.213). This procedure confirmed the separation of the two distinct hermit crab assemblages, being the community of the first period correlated inversely with phi values, while in second period the community was correlated directly with phi values. We found higher phi values in the second

period (for all sites), indicating a substrate with finer grains, composed mainly by silt and clay (Figure 5).

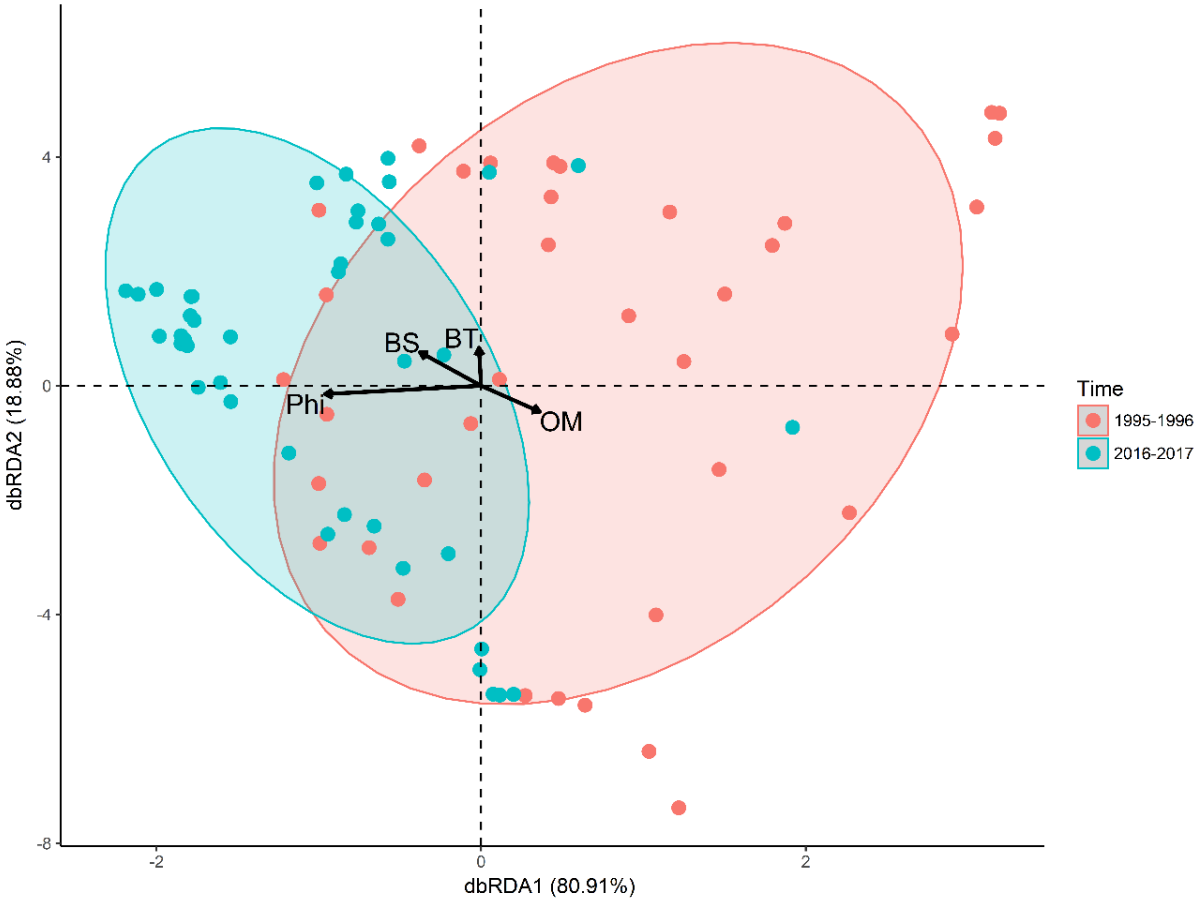


Figure 4. Distance-based redundancy analysis (dbRDA), ordination plot based on a set of environmental variables (BT = Bottom water temperature, BS = Bottom water salinity, OM = Organic matter content (%), Phi = sediment texture) and hermit crabs' data, which were sampled by trawl at the coast of Ubatuba, State of São Paulo, Brazil, and in each period (1995-1996 and 2016-2017).

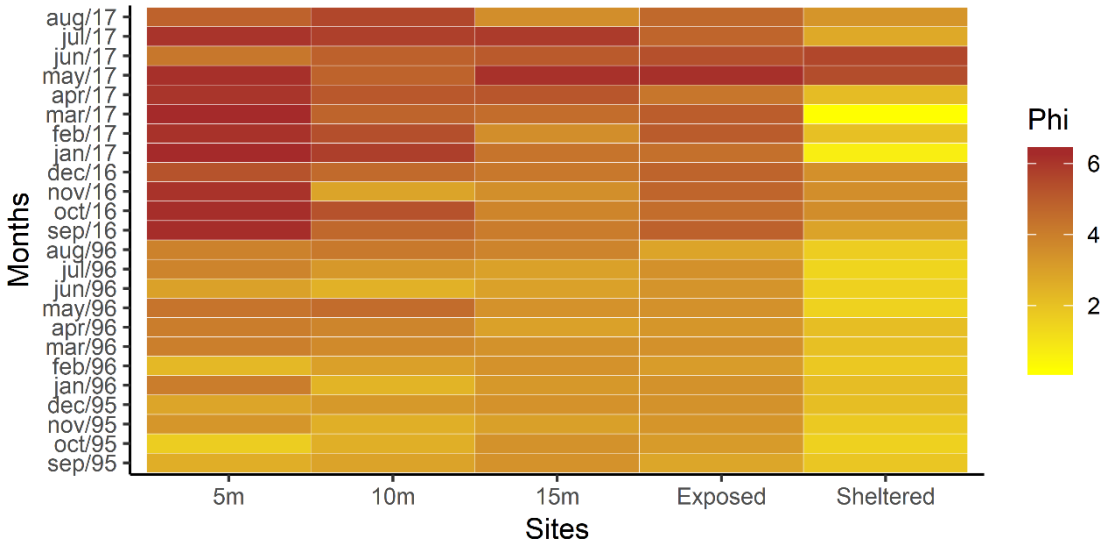


Figure 5. Spatial configuration of sediment texture (Phi) values across each sampled site in the study region.

4. Discussion

A major challenge in community ecology studies has been to detect the variation in species abundance. In a given site certain populations could increase, decrease or remains the same. Understanding the factors and processes that lead these variations is a central theme for management actions (Angeler, 2013; Laity et al., 2015; Mellin et al., 2016). The hermit crabs *Dardanus insignis*, *Loxopagurus loxochelis* and *Pagurus exilis*) (To pictures see supplementary material) had their densities increased in the second period. It has been postulated that generalist species tend to increase their abundances in disturbed sites, while sensible species many times are competitive excluded in soft benthic communities (Thrush & Dayton, 2002). The hermit crab *D. insignis* present some generalist characteristics like brief embryonic development, a high number of eggs produced per ovigerous female and reduced size of the eggs (Miranda et al., 2006), which could explain the higher density in the second period. *L. loxochelis* are known to occur in soft

sediments with finer grains due to their burrowing and filtering behavior, which is facilitated in those features already mentioned (Bertini et al., 2004; Mantelatto et al., 2004). Finer sediments (higher values of phi) were predominant in second period, thus enabling the greatest density of *L. loxochelis* in the second period. It was surprising the increase of *P. exilis* density in the second period, the above mentioned species reach smaller sizes (Mantelatto et al., 2007b; Terossi et al., 2010; Rodrigues et al., 2016) and probably become sexually mature quicker than others hermit crab species. Species with rapid development (small body size) and early reproduction faces the challenges of disturbed sites better than large bodied species with late reproduction (Pianka, 1970, 1972), contrasting to the large bodied hermit crab *Petrochirus diogenes*) (To pictures see supplementary material), whose density decreased in the second period. The preference of *P. diogenes* for sediments with coarser grains (lowest values of phi) (Bertini & Fransozo, 1999) could substantially explain the density decrease in the second period.

The general results indicate that in terms of alpha diversity hermit crab assemblage from both periods were quite similar. Most of the alpha diversity values did not change after 20 years of the first survey. Only taxonomic distinctness (Δ^+) has changed, probably because in second period Paguridae (family) hermit crabs were found often, contrasting to what occur in the first period, when these species constituted only 3.81% of the total density. The hermit crab *Pagurus exilis* was the third most found species in the second period.

However, partitioned beta diversity data measures revealed different processes structuring hermit crab communities, even in a small-scale habitat. Also, these data

measures revealed patterns that were not clear using traditionally alpha diversity indexes. The relative importance of turnover and nestedness component varied among distinct sites, indicating that processes underlying these beta diversity values are quite different: in “5 m” and “10 m” sites, beta diversity is caused mainly by species turnover component, while in sites “15 m” and “Exposed” only nestedness component composed the dissimilarity observed. Site “Sheltered” were partially caused by nestedness, but also by turnover component. It is noted that beta diversity increased in sites close to the coastline and decreased as depth increase. Higher values of phi were recorded in all sites after 20 years, indicating a decrease in the mean grain size of substratum, being composed by silt and clay particles. Changes in the sediment alter the whole benthic community (Thrush & Dayton, 2002) that explains the greater values turnover component appearance in sites near to the coastline. Replacement of some species by others are common in sites, where environmental variables have changed (Legendre, 2014).

In sites “15 m” and “Exposed”, communities are structured by nestedness component, which mean that no replacement of species occurred in those sites, even with the increasing of phi values. Based in our dataset, in site “15m” the second period hermit crab assemblage is a subset of first one that explains nestedness as responsible for overall dissimilarity. Several, but non-exclusive hypotheses on biological and abiotic context may explain this scenario. Possibly the higher wave energy levels in those sites (Mahiques et al., 2016) which would reduce the set of species that can survive in those sites, promoting the dominance of some organisms. Sites with powerfully wave action, causes stress in benthic

community and may inhibit the recolonization of some species, acting as a barrier to be surpass in dispersal events. Variation in wave exposure regimes appears to affect benthic communities, selecting species which have some physiological, behavioral and morphological traits to tolerate wave induced stress (Underwood, 1979; Wells et al., 1998). Hermit crabs are directly affected by hydrodynamic stress that is an important factor determining shell use and preference (Scully, 1979; Hahn, 1998), which are the most important resource for this group of decapods; besides this, wave action are important determinants of gastropods community structure (hermit crab shells providers) (Underwood, 1979). Populations of sea snails (Gastropoda) from areas exposed to wave-action have thinner shells and wider apertures than those in sheltered areas (Underwood, 1979). However, in second period *P. exilis* colonized the site "Exposed", becoming the first period assemblage a subset of the second one.

Several studies have highlighted the significant role of environmental variables in macroinvertebrates community structure (Alsaffar et al., 2017; Chatzinikolaou et al., 2018; Miserendino et al., 2018) and for decapod crustaceans (Negreiros-Fransozo et al., 1997; Fransozo et al., 2011; Furlan et al., 2013; Hunt et al., 2017). Our study highlights the sediment texture (phi measure) as an environmental variable explaining biological pattern. In the first period, hermit crab assemblage was associated with low values of phi, while in second period it was associated with higher values of phi. Higher phi values indicate a substratum composed mainly by silt and clay; our data revealed an increase in phi values in all sites surveyed. Anthropic effects, like erosive processes (leaching) in Ubatuba city

(mainly in Serra do Mar mountain range), promoted by real estate expansion in the lasts years (Burone & Pires-Vanin, 2006), could have changed sediment features in the Ubatuba bay, bearing in mind that rains carry allochthone sediment to the sea. Studies found that benthic communities were less rich and present lower values of diversity in sites influenced by human activities, such as water contamination (Chatzinikolaou et al., 2018) and land use (Seitz et al., 2017). Some studies showed that hermit crab richness and diversity were higher in sites with heterogeneous sediment, which provide a wide variety of microhabitats (Teoh et al., 2014).

This study supports the premise that hermit crab communities changed over the observed period. It was clear that many hermit crab species had their abundances altered after 20 years. However, it is difficult to precise with this data set if these changing conditions are caused by natural variability of environmental features or if it reflects a human-induced directional change (as the establishment of a Marine Protection Area in 2008, closed season shrimp-fishing along Ubatuba region or even increasing in fishery activities) in the shorter term that deviates from patterns of natural variability. Thus, hermit crab community most probably was benefited from these conditions and being as one the representative member of decapod biota in the region, we recommend that conservation efforts should not be focused solely on protecting habitats with the highest diversity, but should instead consider the characteristics of distinct sites across a region if the goal is to maintain regional diversity.

References

Alsaffar, Z., J. Cúrdia, A. Borja, X. Irigoien, & S. Carvalho, 2017. Consistent variability in beta-diversity patterns contrasts with changes in alpha-diversity along an onshore to offshore environmental gradient: the case of Red Sea soft-bottom macrobenthos. Marine Biodiversity 1–16.

Amaral, A. C. Z., & S. A. H. Nallin, 2017. Marine benthic biodiversity and ecosystems from the Northern coast of the State of São. UNICAMP/IB, Campinas – SP.

Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, & N. G. Swenson, 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters 14: 19–28.

Angeler, D. G., 2013. Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake metacommunities. Diversity and Distributions 19: 772–781.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134–143.

Baselga, A., & C. D. L. Orme, 2012. Betapart: An R package for the study of beta diversity. Methods in Ecology and Evolution 3: 808–812.

Bertini, G., & A. Fransozo, 1999. Spatial and seasonal distribution of *Petrochirus diogenes* (Anomura, Diogenidae) in the Ubatuba Bay, Sao Paulo, Brazil. Iheringia Serie Zoologia 86: 145–150, http://biostor.org/reference/80049.

Bertini, G., A. Fransozo, & A. A. Braga, 2004. Ecological distribution and reproductive period of the hermit crab Loxopagurus loxochelis (Anomura, Diogenidae) on the northern coast of Sao Paulo State, Brazil. Journal of Natural History 38: 2331–2344.

Burone, L., & A. M. S. Pires-Vanin, 2006. Foraminiferal assemblages in Ubatuba Bay, South – Eastern Brazilian coast. Scientia Marina 70: 203–217.

Chatzinikolaou, E., M. Mandalakis, P. Damianidis, T. Dailianis, S. Gambineri, C. Rossano, F. Scapini, A. Carucci, & C. Arvanitidis, 2018. Spatio-temporal benthic biodiversity patterns and pollution pressure in three Mediterranean touristic ports. Science of the Total Environment 624: 648–660.

Childress, J. R., 1972. Behavioral ecology and fitness theory in a tropical hermit crab. Ecology 53: 960–964.

Clarke, K. R., & R. M. Warwick, 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35: 523–531.

Clarke, K. R., & R. M. Warwick, 2001. A further biodiversity index applicable to species lists: Variation in taxonomic distinctness. Marine Ecology Progress Series 216: 265–278.

Fernandes, D., & R. Alves, 2018. Composition, density, and shell use of hermit crabs (Crustacea : Paguroidea) from subtidal boulder fields in southeastern Brazil. Latin American Journal of Aquatic Research 46: 72–82.

Frameschi, I. F., L. S. De Andrade, F. G. Taddei, V. Fransozo, & L. C. Fernandes-Goés, 2013. Assemblage of hermit crabs near coastal islands in southeastern Brazil. Neotropical Biology and Conservation 9: 9–19.

Fransozo, A., L. Fernandes-Góes, V. Fransozo, J. Góes, V. Cobo, G. Teixeira, & R. Gregati, 2011. Marine anomurans (Decapoda) from the non-consolidated sublittoral bottom at the southeastern coast of Brazil. Crustaceana 84: 435–450.

Fransozo, A., F. L. M. Mantelatto, G. Bertini, L. C. Fernandez-Góes, & J. M. Martinelli, 1998. Distribution and assemblages of anomuran crustaceans in Ubatuba bay, north coast of São Paulo state, Brazil. Acta Biológica Venezuelana 18: 17–25.

Furlan, M., A. L. Castilho, L. C. Fernandes-Goes, V. Fransozo, G. Bertini, & R. C. da Costa, 2013. Effect of environmental factors on the abundance of decapod crustaceans from soft bottoms off southeastern Brazil. Anais Da Academia Brasileira De Ciencias 85: 1345–1356.

Hahn, D. R., 1998. Hermit crab shell use patterns: response to previous shell experience and to water flow. Journal of Experimental Marine Biology and Ecology 228: 35–51.

Hazlett, B., 1981. The behavioral ecology of hermit crabs. Annual Review of Ecology and Systematics 12: 1–22.

Hebling, N. J., F. L. Mantelatto, M. L. Negreiros-Fransozo, & A. Fransozo, 1994. Levantamento e distribuição de braquiúros e anomuros (Crustacea, Decapoda) dos sedimentos sublitorais da região da Ilha Anchieta, Ubatuba (SP). Boletim Do Instituto De Pesca 21: 1–9.

Hieri, O., A. F. Lotter, & G. Lemcke, 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25: 101–110.

Hollander, M., & D. A. Wolfe, 1999. Nonparametric statistical methods. Wiley-Interscience.

Hunt, H. L., R. A. Wahle, J. Tremblay, M. Comeau, A. Silva, & R. Rochette, 2017. Spatial patterns of richness and abundance of benthic decapod crustaceans and fishes in the North-west Atlantic as measured by cobble-filled bio-collectors. Marine Biology Research 1000: 1–19.

IBAMA, 2008. Normative Instruction No. 189, 23th September, 2008. .

Laity, T., S. W. Laffan, C. E. González-Orozco, D. P. Faith, D. F. Rosauer, M. Byrne, J. T. Miller, D. Crayn, C. Costion, C. C. Moritz, & K. Newport, 2015. Phylodiversity to inform conservation policy: An Australian example. Science of the Total Environment Elsevier B.V. 534: 131–143.

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23: 1324–1334.

Leprieur, F., J. D. Olden, S. Lek, & S. Brosse, 2009. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. Journal of Biogeography 36: 1899–1912.

Mahiques, M. M. de, E. Siegle, J. Alcántara-Carrió, F. G. Silva, P. H. G. de Sousa, & C. C. Martins, 2016. The Beaches of the State of São Paulo In Short, A. D., & A. H. da F. Klein (eds), Brazilian Beach Systems. Springer: 397–418.

Mahiques, M. M., M. G. Tessler, & V. V. Furtado, 1998. Characterization of energy gradient in enclosed bays of Ubatuba region, south-eastern Brazil. Estuarine, Coastal and Shelf Science 47: 431–446.

Mantelatto, F. L., C. H. Bernardo, T. E. Silva, V. P. Bernardes, V. J. Cobo, & A. Fransozo, 2016. Composition and distribution of decapod crustaceans associated by fisheries of seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) at the northern coast of Sao Paulo. Boletim Do Instituto De Pesca 42: 307–326.

Mantelatto, F. L., D. L. a. Espósito, M. Terossi, R. Biagi, & a. L. Meireles, 2007. Population features of the Western Atlantic hermit crab *Pagurus exilis* (Anomura, Paguridae) in Brazil. Atlantica 29: 107–114.

Mantelatto, F. L. M., & A. Franzoso, 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, Northern coast of São Paulo State, Brazil. Revista Brasileira de Biologia 59: 23–31.

Mantelatto, F. L. M., & R. B. Garcia, 2002. Hermit crab fauna from the infralittoral zone of Anchieta Island (Ubatuba, Brazil) In Escoba-Briones, E., & F. Alvarez (eds), Modern approaches to the study of Crustacea. : 137–143.

Mantelatto, F. L. M., J. M. Martinelli, & A. Fransozo, 2004. Temporal-spatial distribution of the hermit crab *Loxopagurus loxochelis* (Decapoda : Diogenidae) from Ubatuba Bay, Sao Paulo State, Brazil. Revista De Biologia Tropical 52: 47–55.

Mantelatto, F. L., M. Terossi, M. Negri, R. C. Buranelli, R. Robles, T. Magalhães, A. F. Tamburus, N. Rossi, & M. J. Miyazaki, 2018. DNA sequence database as a tool to identify decapod crustaceans on the São Paulo coastline. Mitochondrial DNA Part A: DNA Mapping, Sequencing, and Analysis Informa UK Ltd. 29: 805–815, https://doi.org/10.1080/24701394.2017.1365848.

Mazor, T. K., C. R. Pitcher, N. Ellis, W. Rochester, S. Jennings, J. G. Hiddink, R. A. McConnaughey, M. J. Kaiser, A. M. Parma, P. Suuronen, M. Kangas, & R. Hilborn, 2017. Trawl exposure and protection of seabed fauna at large spatial scales. Diversity and Distributions 23: 1280–1291.

Meireles, A. de L., R. G. Biagi, A. Fransozo, & F. L. M. Mantelatto, 2012. Os Ermitões (Crustacea, Anomura) In Amaral, A. C. Z., & S. A. H. Nallin (eds), Biodiversidade e ecossistemas bentônicos marinhos do Litoral Norte de São Paulo – Sudeste do Brasil. UNICAMP/IB, Campinas – SP: 479–488.

Mellin, C., M. Aaron Macneil, A. J. Cheal, M. J. Emslie, & M. Julian Caley, 2016. Marine protected areas increase resilience among coral reef communities. Ecology Letters 19: 629–637.

Melo, G. A. S., 1999. Manual de identificação dos Crustacea Decapoda do litoral Brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea. Editora Plêiade. São Paulo.

Miranda, I., A. L. Meireles, R. Biagi, & F. L. Mantelatto, 2006. Is the abundance of the red brocade hermit crab *Dardanus insignis* (Decapoda: Anomura: Diogenidae) in the infralittoral region of southern Brazil determined by reproductive potential? Crustacean Research 6: 45–55.

Miserendino, M. L., C. Brand, L. B. Epele, C. Y. Di, G. H. Omad, M. Archangelsky, O. Martínez, & A. M. Kutschker, 2018. Environment Biotic diversity of benthic macroinvertebrates at contrasting

glacier-fed systems in Patagonia Mountains: The role of environmental heterogeneity facing global warming. Science of the Total Environment 622–623: 152–163.

Negreiros-Fransozo, M. L., A. Fransozo, F. L. M. Mantelatto, M. A. Pinheiro, & S. Santos, 1997. Anomuran species (Crustacea, Decapoda) and their ecological distribution at Fortaleza Bay sublittoral, Ubatuba, São Paulo, Brazil. Iheringia Série Zoologia 194: 187–194.

Oksanen, A. J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O. Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2015. Package ‘ vegan .’ .

Pianka, E. R., 1970. On r- and K- selection. The American Naturalist 592–597.

Pianka, E. R., 1972. R and K Selection or b and d Selection ?. The American naturalist 106: 581–588.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria, https://www.r-project.org/.

Rodrigues, G. F. B., I. F. Frameschi, V. P. Bernardes, & A. Fransozo, 2016. Dinâmica populacional do ermitão endêmico *Pagurus exilis* (Benedict , 1892) (Crustacea : Decapoda : Paguridae) na região de Ubatuba-SP. Ciência et Praxis 9: 17–24.

Rosenberg, R., M. Blomqvist, H. C. Nilsson, H. Cederwall, & A. Dimming, 2004. Marine quality assessment by use of benthic species-abundance distributions: A proposed new protocol within the European Union Water Framework Directive. Marine Pollution Bulletin 49: 728–739.

Scully, E. P., 1979. The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. Journal of Experimental Marine Biology and Ecology 37: 139–152.

Seitz, R. D., K. E. Knick, T. M. Davenport, & G. G. Saluta, 2017. Human influence at the Coast: upland and shoreline stressors affect coastal macrofauna and are mediated by salinity. Estuaries and Coasts Estuaries and Coasts 1–17.

Selin, N. I., E. S. Kornienko, & O. M. Korn, 2016. The species composition and pattern of distribution of hermit crabs (Decapoda: Paguroidea) in Vostok Bay, Sea of Japan. Russian Journal of Marine Biology 42: 481–488.

Stanski, G., F. L. Mantelatto, & A. Leão-Castilho, 2016. Hermit crab bycatch fauna (Decapoda, Anomura) off the coast of Santa Catarina State, Brazil: diversity and spatial-temporal distribution. Latin American Journal of Aquatic Research 44: 546–556.

Suguio, K., 1973. Introdução à sedimentologia. Edgard Blucher, EDUSP, São Paulo.

Teoh, H. W., M. Ali, S. Hussein, & V. C. Chong, 2014. Influence of habitat heterogeneity on the assemblages and shell use of hermit crabs (Anomura : Diogenidae). Zoological Studies 53: 1–9.

Terossi, M., L. S. Torati, I. Miranda, M. A. Scelzo, & F. L. Mantelatto, 2010. Comparative reproductive biology of two southwestern Atlantic populations of the hermit crab *Pagurus exilis* (Crustacea: Anomura: Paguridae). Marine Ecology 31: 584–591.

Thrush, S. F., & P. K. Dayton, 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annual Review of Ecology and Systematics 33: 449–473.

Tucker, M. E., 1988. Techniques in sedimentology. Blackwell Scientific Publications, Oxford – UK.

Tylianakis, J. M., A. M. Klein, & T. Tscharntke, 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. Ecology 86: 3296–3302.

Underwood, A. J., 1979. The ecology of intertidal gastropods. Advances in Marine Biology 16: 111–210.

Wells, R. M. G., P. E. McShane, N. Ling, R. J. Wong, T. O. C. Lee, & J. Baldwin, 1998. Effect of wave action on muscle composition, metabolites and growth indices in the New Zealand abalone, Paua (*Haliotis iris*), with implications for harvesting and aquaculture. Comparative Biochemistry and Physiology – B Biochemistry and Molecular Biology 119: 129–136.

Wright, David, H., & J. H. Reeves, 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia 92: 416–428.

Zajac, R. N., J. M. Vozarik, & B. R. Gibbons, 2013. Spatial and temporal patterns in macrofaunal diversity components relative to sea floor landscape Structure. PloS ONE 8: 1–11.

Zar, J. H., 1999. Biostatistical analysis. Upper Saddle River, New Jersey – NY.

The interaction network pattern of coastal hermit crab and shells: new insights from a unique relationship

Abstract

The interaction between hermit crabs and gastropods shells are known as one of the most fascinating relationship in nature. There is compelling evidence that hermit crabs' shells choice is not a random process. Here, we evaluated the pattern of interaction in a given hermit crab community at Ubatuba bay (Brazil). Data were gathered on a monthly basis over 1 year. Our results show that the hermit crab-shell network was more specialized and modular than expected by null models. Moreover, connectance, nestedness (wNODF) and niche overlap from hermit crabs had lower estimated values than expected by null models. For niche overlap from gastropods (shells) no consistent pattern was found. The network produced was modular with three highly distinguishable modules. There are consistent differences in resource utilization among hermit crab species. Also, some species present higher specialization (specialist) despite most of them present lower values (generalists). Hermit crab-shells network from the investigated tropical environment is modular and specialized, which should be taken into account in the conservation efforts, where not hermit crabs and shells species with different roles must be preserved.

Introduction

The relationship between resources and species abundances is an important feature to understand biological diversity patterns (Magurran, 2004). Resource competition generate negative interactions between individuals (intraspecific and interspecific) caused by the reduction of consumable resources that they both require (Tilman, 2004). Within ecological communities, similar animal species commonly tend to compete for the same resources which may lead to resource-use differences in a given community. (Kellogg, 1977; Alcaraz & Kruesi, 2017).

Hermit crabs may be ideal organisms to investigate resource partitioning at community level, since these crustaceans have an inmost relationship with gastropod shells (Hazlett, 1981). The shells definitely represent a "niche axis" to hermit crabs, the survival, growth, and reproduction of this taxon strictly depend on the occupancy of gastropod shells of appropriate size and shape (Kellogg, 1976). Also, hermit crabs must continually obtain new, suitable shells, either because of their growth (Hazlett & Herrnkind, 1980) or alteration in the condition of their current shell caused by sessile epibionts (Hazlett, 1981; McLean, 1983). This dependence on shells creates competition, both within and between hermit crab species, because individuals cannot obtain shells directly from living gastropods (Laidre, 2011). These crustaceans exchange shells by fighting, bargaining or by a chain reaction caused by a single empty shell (Chase et al., 1988; Rotjan et al., 2010). Previous studies have found that hermit crab developed precise mechanisms to obtain information about resource value of their own shell (Tricarico & Gherardi, 2007) and in what context the hermit crabs abandon or not

their shells (Turra & Gorman, 2014). The "shell exchange market" hypothesis—which suggests that the main function of clustering is to allow hermit crabs to acquire new shells (Gherardi & Vannini, 1993; Peres et al., 2018)—is an adaptive behavior that allows these animals to obtain new shells.

These organisms have evolved the ability to make fine distinctions between the quality of a shell found in the habitat, either empty or occupied by conspecifics or heterospecifics, and the current domicile shell (Hazlett, 1981). Thus, a given hermit crab species could better exploit determined gastropod shell species, leading to a specialization based in both hermit crab and shell morphologies. The selection or use of shells is not a random process and it is related to intra- and inter-specific competition (Vale et al., 2017). However, neutral processes (as abundance) could result in higher frequency of interactions between hermit crabs and shells but cannot explain completely all the complex questions of shell choice (Benvenuto & Gherardi, 2001). Abundance can influence network structure and the interactions between species, as the chance of links in ecological networks is higher when both consumer and resource have higher abundance (Jordano, 1987; Bascompte et al., 2003). Therefore, intrinsic characteristics (i.e. morphology, sex, etc.) and extrinsic (i.e. abundance, environment, competition, shell availability) might influence the shell choice by hermit crabs (Dowds & Elwood, 1985; Barnes, 1999; Oba & Goshima, 2004; Hazlett et al., 2005).

The interaction network approach helps to uncover community-level patterns of ecological specialization in different types of interspecific interactions (Vázquez et al., 2009). The existence of clearly defined groups of species (compartments or

modules) with many intragroup links and few intergroup links is the main characteristic of a modular network which may reflect some degree of specialization (Fortuna et al., 2010). Contrasting to the modular network, some interspecific networks is characterized by a nested pattern wherein specialists interact with proper subsets of the species interacting with generalists (Bascompte et al. 2003).

Despite several studies have been performed focusing in patterns of shells selection and utilization at population level (Scully, 1979; Bertini & Fransozo, 2000; Mantelatto et al., 2007a; Vale et al., 2017; Oliveira et al., 2018), there is a lack of investigations in the structure of interactions between hermit crabs and gastropod shells at community level. In this sense, the study of ecological interaction networks may be an interesting approach to understand which hermit crabs interact with which gastropod shells in the ecological context in which they occur.

Our goal is to detect any pattern of interaction in a given hermit crab community; does hermit crab community mold clear subsets of interactions (modular network) or no clear preference for shells species are detected (nestedness network)? Also, we may find an intermediate level between the nested and modular patterns.

2. Material and Methods

2.1 Study Area

Ubatuba Bay (23°26’ S and 45°02’ W) is located along the northern coast of São Paulo State, Brazil, facing to the east and presents a constriction in its coastline,

which induces wave diffraction (Mahiques et al., 1998). The proximity of the coastal range (Serra do Mar) results in small bays and headland-embayed beaches with variable orientation. This region presents a mixed fauna, that includes tropical, temperate and sub-Antarctic species, which are explained by the thermal regime of the coastal water (Coelho & Ramos, 1972).

2.2 Sampling

The animals were collected (trawled) utilizing a fishing boat equipped with double-rig nets (4.5 m wide at the mouth, 25 mm mesh size, and a cod end mesh diameter of 15 mm). Each trawl lasted 30 minutes, covering an estimated swept area of 18,000 m^2. Samples were taken monthly on three consecutive days from September 2016 to August 2017 (Figure 1). A global positioning system (GPS) was used to record the location at the sampling sites, ensuring the sampling in the same sites for all months surveyed. In the boat, the hermit crabs were kept in plastic bags, properly marked, in coolers with crushed ice. In the lab, the hermit crabs (Paguroidea) were removed from their shells, and identified, according to Melo (1998) , while the gastropod shells were identified according to Rios (1994)

2.3 Network analysis

Network-level indexes

Interactions between a shell and a hermit crab were compiled into quantitative interaction matrices. For this, we considered each hermit crab species and each

shell species as one interactive node, and each interaction between these groups as one link, that were visualized and analyzed using the package bipartite (Dormann et al., 2008, 2009) for R (R Core Team, 2019). Further, to illustrate structurally the interactions between these organisms, we calculated five network metrics, giving priory for the quantitative indices, that shows less influence of the sampling effort (Fründ et al., 2016; Vizentin-Bugoni et al., 2016). Connectance I, that calculates the proportion between realized and all possible links within the network. Low values of connectance (closer to zero) means that realized links are outlying to the total number of possible links. Niche overlap (R_0), which measures the degree of interaction superposition between species from the same level, calculated by the Horn's index (Horn 1966). Lower values of Niche Overlap indicate that species are partitioning one or more of their niche's axis (Hutchinson, 1957), meaning that realized links between species of the same level are drastically different. We performed niche overlap for both interacting groups – hermit crabs and shells – since these index calculates one value for each level of interacting species (for both hermit crabs and gastropod species); Network specialization (H_2'), which measures how much species from the same level interact with their available partners. Low values of H_2'indicates that species within the community are more generalists, that is, they interact with a large assembly of partners, not depending on a specific pairwise interaction. Weighted nestedness, that quantifies whether specialized pairwise interactions express subsets of those generealists pairwise interactions ones, calculated by the wNODF index (Almeida-Neto & Ulrich, 2011). High values of wNODF demonstrate that the cores species of the network,

represent species with generalist habits, establish interactions with more partners (Almeida-Neto & Ulrich, 2011). And modularity (Q'), that calculates whether species from the same subset interact more with each other than with species composing other subsets. Higher values of Q' demonstrate the existence of compartmentalization within the community. So a particular subset of hermit crab exhibits a preference to interact with one singular subset of shell. We estimated the modularity of the networks using the QuanBiMo algorithm (Dormann & Strauss, 2014)), which calculate modularity in an iterative approach, thus, the value of Q' might have a slight variation between the algorithm runs, therefore we ran the algorithm 10 times to find the optimal module conformation with the highest value of Q, and the number of Markov Chain Monte Carlo (MCMC) moves was set to 10^9 steps (Dormann & Strauss, 2014; Maruyama et al., 2014, 2015). We used bipartite in R to calculate all network-level metrics.

To gauge the significance of network metrics we tested whether the observed network level descriptors differ from randomness generated networks, utilizing Patefield algorithm (Patefield, 1981) through r2dtable (Dormann et al., 2008, 2009) to check if the observed descriptors lay outside the respective 95% confidence intervals obtained (Sazatornil et al., 2016).

Species role

Also, to highlight species role within the interaction network we calculated three species-level indexes: Species strength (ss'), that express the sum of the interactions' ratio that a given species performs with all of your partners. High

values demonstrated how an interacting agent depends heavily on its partner (Bascompte et al., 2006). Species-level specialization (*d'*), that indicate how the distribution of interactions of a given species occurs in relation to interactions available with all possible partners. Thus, higher values denote high specialization, that is, from all possible interactions, a given species interacts just with few partners (Blüthgen et al., 2006). Partner diversity (Shannon diversity applied to species interactions). To understand the local species role for a given hermit crab and gastropod shell we calculated the within-module degree (*z*) which indicates the number of connections a species has within its own module relative to other species in that module, and the among-module connectivity I that informs about how well a given species is connected to species from other modules (Olesen et al., 2007). According to their *c* and *z*-values, species were classified as: peripherals (low values of both *c* and *z*), connectors (high *c* and low *z*- values), module hubs (high *z* and low *c* values) or network hubs (high values of both *c* and *z*). We defined the threshold utilizing the standard deviation of the range of both *c* and *z* scores in order to preserve an equiprobability of species to rely on these four categories.

3. Results

A total of 625 hermit crabs (six species) were recorded occupying 15 gastropod shells species. The hermit crab *Dardanus insignis* (de Saussure, 1858) occupied 13 shells species (59% of all interactions), followed by *Pagurus exilis* (Benedict, 1892) which occupied 8 shells species (20.8%). The most frequent occupied shell was *Buccinanops cochlidium* (Dillwyn, 1817), protecting all hermit crab species found (33%), followed by *Olivancillaria urceus* (Röding, 1798) protecting four

hermit crab species (21.92%). Each hermit crab occupied only one shell. Hermit crabs without shells or within deteriorated gastropods shells (enabling species-level identification) were excluded from the analysis.

3.1. Network-level metrics

The hermit crab-shell network was more specialized and modular than expected by null models (Figure 1). Moreover, connectance, nestedness (wNODF) and niche overlap from hermit crabs had lower estimated values than expected by null models. For niche overlap from gastropods (shells) no consistent pattern was found (Table 1, also supplementary material).

3.2. Species-level metrics and species roles

The species-level descriptors are summarized in table 2. The hermit crab species with a great number of interactions (species strength) was *D. insignis*, followed by *Loxopagurus loxochelis* (Moreira, 1901). For gastropods species *B. cochlidium* and *O. urceus* had higher values of specie strength. Also, *D. insignis* harbored a greater diversity of interactions (Partner diversity), followed by *P. exilis*. Regarding to specialization, *L. loxochelis* showed more unique interactions links with gastropods shells, followed by *Petrochirus diogenes* (Linnaeus, 1758). The network produced was modular with three highly distinguishable modules (Figure 2). The hermit crab *D. insignis* was classified as "Network hubs", *Pagurus crinitornis* (Dana, 1852), *L. loxochelis, P. exilis* and *P. diogenes* were "connectors" and and *Isocheles sawayai* Forest & de Saint Laurent, 1968 was "peripheral". The

most frequent shell species *B. cochlidium* was "Network hub". Only shell species acted as "Modules hubs", the large gastropod shell *Tonna galea* (Linnaeus, 1758), *Strombus pugilis* Linnaeus, 1758 and *Fusinus sp.* Among the hermit crabs, only *D. insignis* was "supergenaralist" (i.e. "network hub" or "module hub"), occupying a wide diversity of gastropods shells. The shells *O. urceus* and *T. galea* were occupied by a select group of hermit crabs, being more specialized than others.

Table 1. Network-level descriptors calculated for hermit crabs-shells networks. * indicates estimate outside the respective 95% confidence interval obtained under null model.

Descriptor	**Estimate**	2.5%	97.5%
Connectance	0.41*****	0.477	0.555
Modularity index (Q')	0.28*	0.039	0.079
Specialization (H2')	0.32*	0.017	0.044
wNODF	50.48*	59.555	76.527
Niche overlap (gastropods)	0.63	0.623	0.894
Niche overlap (hermit crabs)	0.47*	0.552	0.842

Table 1. Network-level descriptors calculated for hermit crabs-shells networks. * indicates estimate outside the respective 95% confidence interval obtained under null model.

Descriptor	**Estimate**	2.5%	97.5%
Connectance	0.41*****	0.477	0.555
Modularity index (Q')	0.28*	0.039	0.079
Specialization (H2')	0.32*	0.017	0.044
wNODF	50.48*	59.555	76.527
Niche overlap (gastropods)	0.63	0.623	0.894
Niche overlap (hermit crabs)	0.47*	0.552	0.842

Table 2. Species-level descriptors calculated for hermit crabs-shells networks.

	Species	Species strength	Partner diversity	Specialization (d')
Gastropods (Shells providers)	*Astraea sp.*	0.033	0.000	0.089
	B. cochlidium	1.813	0.629	0.098
	C. parthenopeum	0.540	0.496	0.064
	D. moniliferum	0.091	0.301	0.126
	F. marmoratus	0.062	0.301	0.033
	F. brasiliensis	0.016	0.000	0.000
	Fusinus sp.	0.372	0.415	0.090
	M. zebra	0.016	0.000	0.000
	O. urceus	0.649	0.400	0.455
	Oliva sp.	0.045	0.000	0.169

	P. granulatum	0.097	0.000	0.173
	S. haemastoma	0.761	0.543	0.015
	S. pugilis	0.450	0.228	0.201
	S. tenuivicarius	0.525	0.505	0.074
	T. galea	0.522	0.278	0.238
Hermit crabs	*D. insignis*	8.732	1.020	0.193
	I. sawayai	0.135	0.294	0.081
	L. loxochelis	2.704	0.669	0.526
	P. criniticornis	0.392	0.602	0.144
	P. diogenes	0.612	0.463	0.382
	P. exilis	2.424	0.800	0.238

Table 2. Species-level descriptors calculated for hermit crabs-shells networks.

	Species	Species strength	Partner diversity	Specialization (d')
Gastropods (Shells providers)	*Astraea sp.*	0.033	0.000	0.089
	B. cochlidium	1.813	0.629	0.098
	C. parthenopeum	0.540	0.496	0.064
	D. moniliferum	0.091	0.301	0.126
	F. marmoratus	0.062	0.301	0.033
	F. brasiliensis	0.016	0.000	0.000
	Fusinus sp.	0.372	0.415	0.090
	M. zebra	0.016	0.000	0.000
	O. urceus	0.649	0.400	0.455
	Oliva sp.	0.045	0.000	0.169
	P. granulatum	0.097	0.000	0.173
	S. haemastoma	0.761	0.543	0.015
	S. pugilis	0.450	0.228	0.201
	S. tenuivicarius	0.525	0.505	0.074
	T. galea	0.522	0.278	0.238
Hermit crabs	*D. insignis*	8.732	1.020	0.193
	I. sawayai	0.135	0.294	0.081
	L. loxochelis	2.704	0.669	0.526
	P. criniticornis	0.392	0.602	0.144
	P. diogenes	0.612	0.463	0.382
	P. exilis	2.424	0.800	0.238

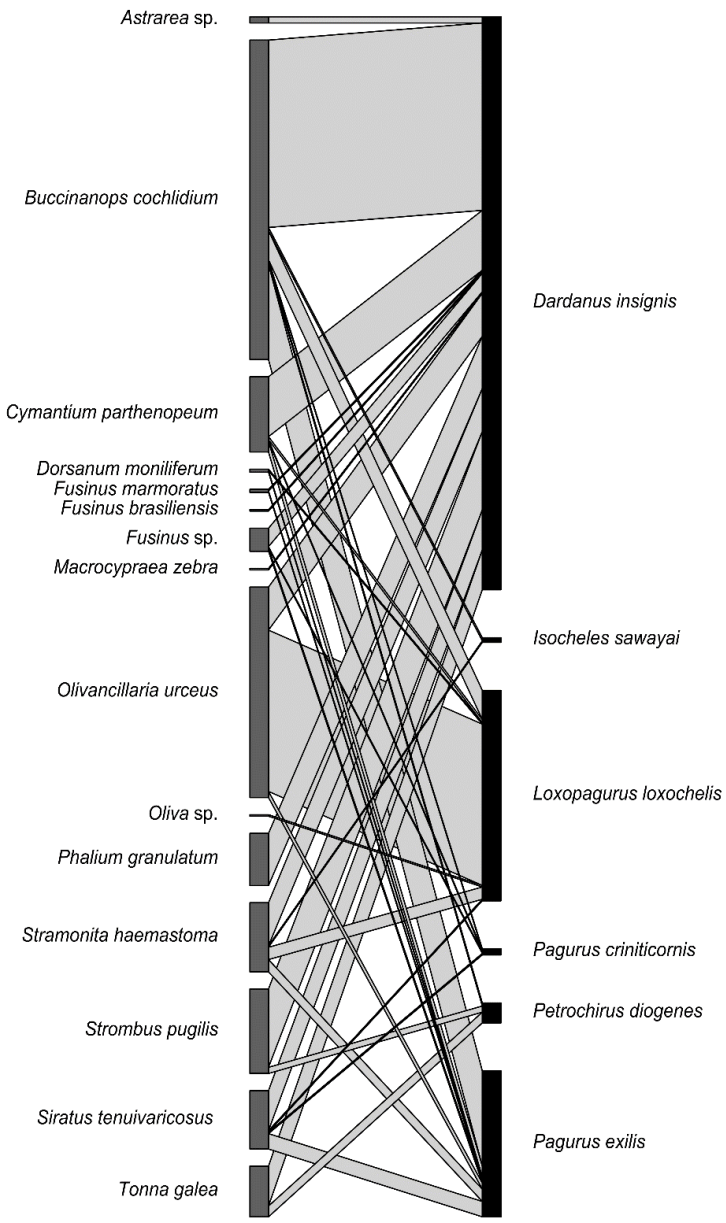


Figure 1. Quantitative hermit crabs-shells networks. The network was sampled with the same level of effort and are represented on the same scale. Network was drawn in bipartite package in the R platform 3.4.

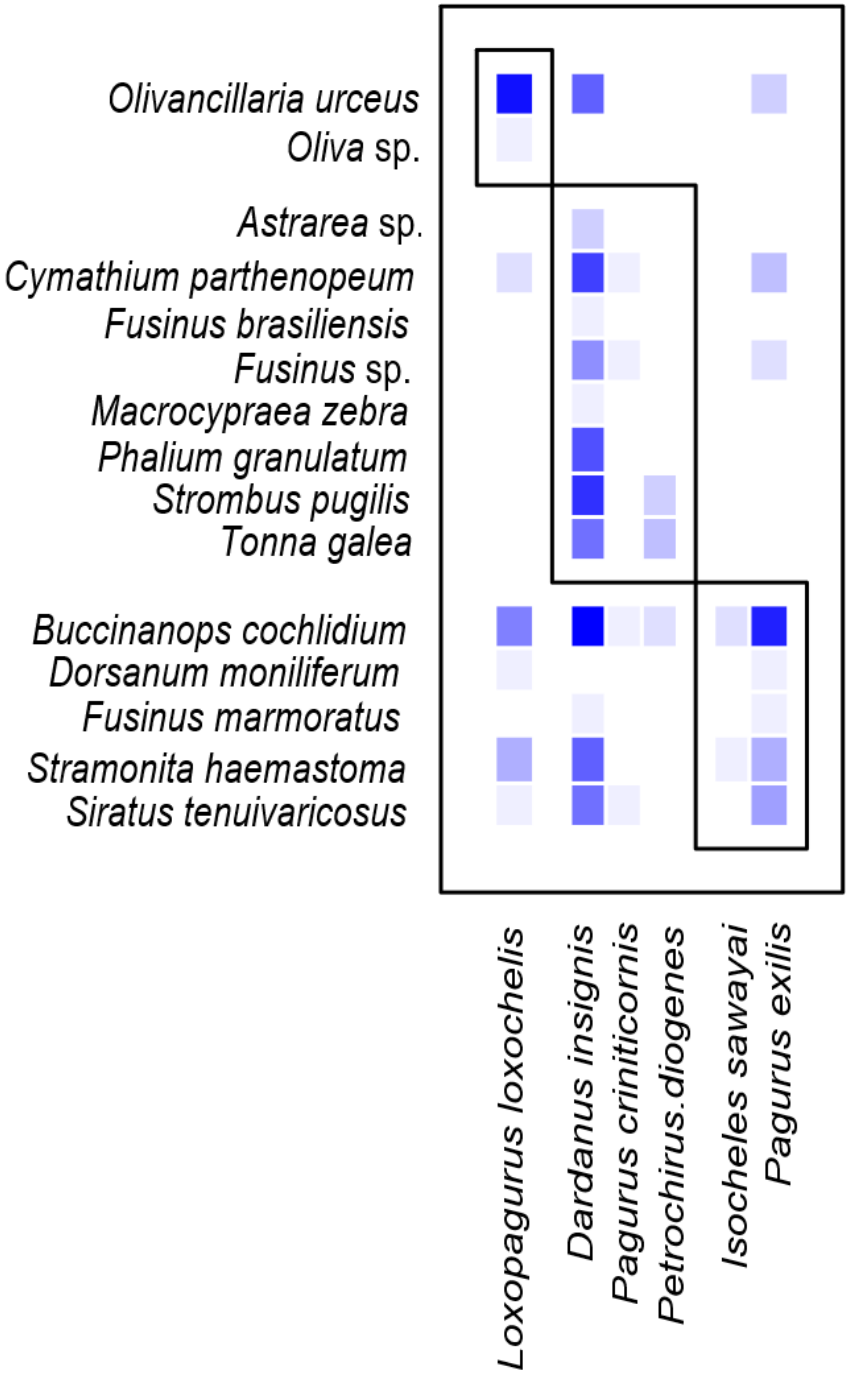


Figure 2. Graphical representation of modules between hermit crabs and gastropods shells at Ubatuba Bay, Brazil.

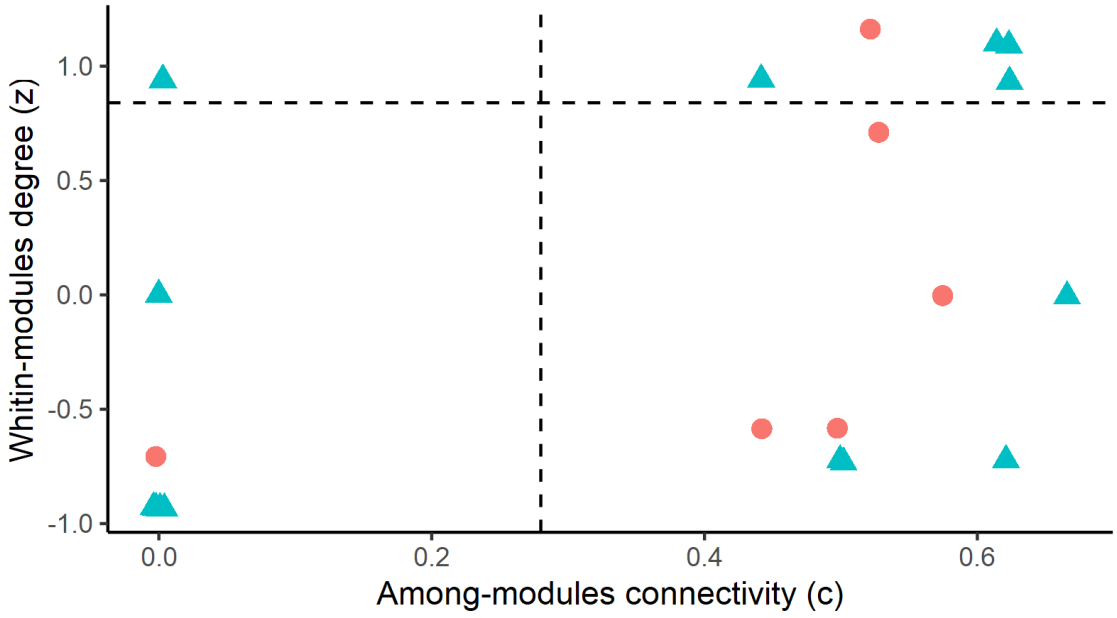


Figure 3. Distribution of gastropod shell (blue triangles) and hermit crab (red circles) species according to their values of "among-module connectivity" I and "within-module degree" (*z*) in the Southeastern Brazilian Coast. The threshold value of $z = 0.84$ and $c = 0.28$ based on standard deviations of *c* and *z* scores.

Discussion

In spite of hermit crabs-shells interactions differ in several ways from animal-plants or parasite-host interactions, where both sides represent living organisms rather than inanimate shells, we found similar patterns from ant-plant interactions (Dejean et al., 2018) and spatial network hummingbirds configuration (Araujo et al., 2018). Here we found a specialized and modular network structure, indicating that hermit crabs in Southeastern Brazilian Coast have clear preferences for certain species of gastropods shells. Some authors suggests that nonsymbiotic interactions will lead to nested networks in which there is a core of generalists and specialists often interact with generalists, due to the lack of coadaptation within nonsymbiotic

interactions (Guimarães et al., 2007a). Indeed, each hermit crab has the opportunity to interact with multiple shells of different species during its lifetime. However, there is compelling evidence that hermit crab species could actively choose certain suitable shells rather than random picks or modulated by frequency of encounters (Bertini & Fransozo, 2000; Benvenuto & Gherardi, 2001; Teoh et al., 2014; Vale et al., 2017; Ragagnin et al., 2018). Shell distribution among different hermit crab communities has been explained through interspecific differences in exploitation and fighting ability (Alcaraz & Kruesi, 2017). The niche partitioning possibly is determined by competition, sex and maximum body size reach in adulthood. Slight niche overlap observed among hermit crabs could be derived from intensive past resource competition, leading to hermit crabs minimize the shells overlap selecting different species. Competition among hermit crab species for optimal shells occur often in hermit crab communities (Gherardi & Vannini, 1993; Squires et al., 2001; Alcaraz & Kruesi, 2017; Peres et al., 2018), even intraspecific and intersexual competition occurs, where males get larger shells over the females, arising from different energy allocation (Asakura, 1995). Larger body size is associated with increased fitness by favoring competitive abilities, tolerance to environments stresses, and reduce predation risks (Bertness, 1981). Hermit crabs reach larger sizes faster when dwell suboptimal shells, being more competitive in further fights for shell and reducing the risk of being predated (Alcaraz et al., 2015). The males invest more energy in body growth for resource and reproductive competition, the females invest energy developing gonads that provide nutrients for the egg masses. Also, females tend to select shells with

greater internal volume that could provide more internal space for resident females to take care of egg masses (Hazlett, 1989; Biagi et al., 2006; Vale et al., 2017).

The large bodied hermit crab *Petrochirus diogenes* had a clear preference for large shells, occupying only three shells, mainly *Tonna galea* that bears a large aperture width. However, other study found that the juveniles occupied a wide diversity of shell species of very different shape (Bertini & Fransozo, 2000), possibly that behavior reduce competition for shells between juveniles and adults. Moreover, small-size hermit crabs *Pagurus criniticornis* and *Pagurus exilis* were not found in heavier shells like *Strombus pugilis* and *Phalium granulatum*. Carry heavier shells could delay the growth, reproduction and survival of hermit crabs (Alcaraz et al., 2015). Also, a generalist strategy performed by *Dardanus insignis*, which reach an intermediate size when comparing to the sampled fauna, were found in a wide array of shells from different features, providing a no limiting supply of suitable shells.

Species-level descriptors provide information for each both hermit crab and shell species in community structure. We may highlight the importance of *D. insignis* that are responsible for a great amount of the realized links (species strength = 8.732) and bear a great diversity of partner (Partner diversity = 1.020). The ability to occupy a wide diversity of shells allow *D. insignis* reach higher abundances in many soft-sediment habitats near Ubatuba bay (Fransozo et al., 1998, 2011; Frameschi et al., 2013). From resource perspective, *Buccinanops cochlidium* seems to be the most valuable shell for network structure, utilized for all hermit crabs found (Partner diversity = 0.629) and responsible for many interaction

(Specie strength = 1.813). We also noted an intimal relationship between *Loxopagurus loxochelis* and *Olivancillaria urceus* (d' = 0.526 and 0.455). *O. urceus* have a narrow elongated aperture that facilitate the protection of *L. loxochelis* due the well-developed and elongated left-chela fitting well in shell's aperture (Mantelatto et al., 2004; Ayres-Peres & Mantelatto, 2010).

In sum, detected network patterns may indicate clear preferences for certain shells species by hermit crabs rather than random picks entailed by neutral processes. Probably the environment and hermit crab morphology influences which shells are in an optimal condition. Also, we argue that hermit crab-shells interaction should be better investigate in distinct environments since the species role for both hermit crab and shell might change spatially and temporally.

References

Ahyong, S., 2009. Anomuran Phylogeny : New Insights from Molecular Data Decapod crustacean phylogenetics. CRC Press, Boca Raton, FL: 399–414.

Alcaraz, G., C. E. Chávez-Solís, & K. Kruesi, 2015. Mismatch between body growth and shell preference in hermit crabs is explained by protection from predators. Hydrobiologia 743: 151–156.

Alcaraz, G., & K. Kruesi, 2017. Niche overlap and resource partitioning between two intertidal hermit crab species. Journal of the Marine Biological Association of the United Kingdom 8–15.

Aldhous, P., 2014. We are killing species at 1000 times the natural rate. NewScientist. , https://www.newscientist.com/article/dn25645-we-are-killing-species-at-1000-times-the-natural-rate/.

Almeida-Neto, M., & W. Ulrich, 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. Environmental Modelling and Software Elsevier 26: 173–178, http://dx.doi.org/10.1016/j.envsoft.2010.08.003.

Alsaffar, Z., J. Cúrdia, A. Borja, X. Irigoien, & S. Carvalho, 2017. Consistent variability in beta-diversity patterns contrasts with changes in alpha-diversity along an onshore to offshore environmental gradient: the case of Red Sea soft-bottom macrobenthos. Marine Biodiversity 1–16.

Amaral, A. C. Z., & S. A. H. Nallin, 2017. Marine benthic biodiversity and ecosystems from the Northern coast of the State of São. UNICAMP/IB, Campinas - SP.

Anderson, M. J., 2001. A new method for non parametric multivariate analysis of variance. Austral ecology 26: 32–46.

Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. V Cornell, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, & N. G. Swenson, 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters 14: 19–28.

Angeler, D. G., 2013. Revealing a conservation challenge through partitioned long-term beta diversity: increasing turnover and decreasing nestedness of boreal lake metacommunities. Diversity and Distributions 19: 772–781.

Araujo, A. C., A. M. M. Gonzaléz, B. Sandel, P. K. Maruyama, E. Fischer, J. V. Francielle, G. Aline, F. Maria, G. L. Ariadna, V. Lopes, A. O. Machado, C. Graco, M. Isabel, C. Machado, J. A. Mcguire, A. Maria, R. Ivan, S. Marlies, S. Isabela, G. Varassin, Z. Wang, & B. Dalsgaard, 2018. Spatial distance and climate determine modularity in a cross-biomes plant – hummingbird interaction network in Brazil. Journal of Biogeography 1–13.

Asakura, A., 1995. Sexual differences in life history and resource utilization by the hermit crab. Ecology. .

Ávila-da-Silva, A. O., M. H. Carneiro, J. T. Mendonça, G. C. C. Bastos, L. V. de Miranda, W. do R. Ribeiro, & S. dos Santos, 2017. Produção Pesqueira Marinha e Estuarina no Estado de São Paulo Setembro de 2017. Informe Pesqueiro de São Paulo São Paulo 89: 1–4.

Ayres-Peres, L., & F. L. Mantelatto, 2008. Patterns of distribution of the hermit crab Loxopagurus loxochelis (Moreira, 1901) (Decapoda, Diogenidae) in two coastal areas of southern Brazil. Revista De Biologia Marina Y Oceanografia 43: 399–411.

Ayres-Peres, L., & F. L. Mantelatto, 2010. Epibiont occurrence on gastropod shells used by the hermit crab Loxopagurus loxochelis (Anomura: Diogenidae) on the northern coast of Sao Paulo, Brazil. Zoologia

27: 222–227.

Barnes, D. K. A., 1999. Ecology of tropical hermit crabs at Quirimba Island, Mozambique: Shell characteristics and utilisation. Marine Ecology Progress Series 183: 241–251.

Bascompte, J., P. Jordano, C. J. Melian, & J. M. Olesen, 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences 100: 9383–9387, http://www.pnas.org/cgi/doi/10.1073/pnas.1633576100.

Bascompte, J., P. Jordano, & J. M. Olesen, 2006. Facilitate Biodiversity Maintenance. Science 431: 3–6.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19: 134–143.

Baselga, A., & C. D. L. Orme, 2012. Betapart: An R package for the study of beta diversity. Methods in Ecology and Evolution 3: 808–812.

Bax, N., A. Williamson, M. Aguero, E. Gonzalez, & W. Geeves, 2003. Marine invasive alien species: A threat to global biodiversity. Marine Policy 27: 313–323.

Benvenuto, C., & F. Gherardi, 2001. Population structure and shell use in the hermit crab, Clibanarius erythropus: a comparison between Mediterranean and Atlantic shores. Journal of the Marine Biological Association of the UK 81: 77–84.

Bertini, G., & A. Fransozo, 1999. Spatial and seasonal distribution of *Petrochirus diogenes* (Anomura, Diogenidae) in the Ubatuba Bay, Sao Paulo, Brazil. Iheringia Serie Zoologia 86: 145–150, http://biostor.org/reference/80049.

Bertini, G., & A. Fransozo, 2000. Patterns of shell utilization in Petrochirus diogenes (Decapoda, Anomura, Diogenidae) in the Ubatuba region, Sao Paulo, Brazil. Journal of Crustacean Biology 20: 468–473.

Bertini, G., A. Fransozo, & A. A. Braga, 2004. Ecological distribution and reproductive period of the hermit crab *Loxopagurus loxochelis* (Anomura, Diogenidae) on the northern coast of Sao Paulo State, Brazil. Journal of Natural History 38: 2331–2344.

Bertness, M. D., 1981. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana 40: 197–205.

Biagi, R., A. L. Meireles, M. A. Scelzo, & F. L. Mantelatto, 2006. Comparative study of shell choice by the southern endemic hermit crab Loxopagurus loxochelis from Brazil and Argentina. Revista Chilena De Historia Natural 79: 481–487.

Blüthgen, N., F. Menzel, & N. Blüthgen, 2006. Measuring specialization in species interaction networks. BMC Ecology 6:.

Burone, L., & A. M. S. Pires-Vanin, 2006. Foraminiferal assemblages in Ubatuba Bay, South - Eastern Brazilian coast. Scientia Marina 70: 203–217.

Caine, E. A., 1975. Feeding and matiscatory structures of selected ANOMURA (CRUSTACEA). journal experimental marine biology and ecology 18: 277–301.

Cardone, F., G. Corriero, A. Fianchini, M. F. Gravina, & C. Nonnis Marzano, 2014. Biodiversity of transitional waters: Species composition and comparative analysis of hard bottom communities from the south-eastern Italian coast. Journal of the Marine Biological Association of the United Kingdom 94: 25–34.

Carrington, D., 2016. Overfishing causing global catches to fall three times faster than estimated. The Guardian. , https://www.theguardian.com/environment/2016/jan/19/overfishing-causing-global-catches-to-fall-three-times-faster-than-estimated.

Castro Filho, B. M. de, L. B. de Miranda, & S. Y. Miyao, 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. Boletim do Instituto Oceanográfico 35: 135–151.

Chablais, J., R. M. Feldmann, & C. E. Schweitzer, 2011. A new Triassic decapod, *Platykotta akaina*, from the Arabian shelf of the northern United Arab Emirates: earliest occurrence of the Anomura. Paläontologische Zeitschrift Springer 85: 93–102.

Chatzinikolaou, E., M. Mandalakis, P. Damianidis, T. Dailianis, S. Gambineri, C. Rossano, F. Scapini, A. Carucci, & C. Arvanitidis, 2018. Spatio-temporal benthic biodiversity patterns and pollution pressure in three Mediterranean touristic ports. Science of the Total Environment 624: 648–660.

Childress, J. R., 1972. Behavioral ecology and fitness theory in a tropical hermit crab. Ecology 53: 960–964.

Clarke, K. R., & R. M. Warwick, 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35: 523–531.

Clarke, K. R., & R. M. Warwick, 2001. A further biodiversity index applicable to species lists: Variation in taxonomic distinctness. Marine Ecology Progress Series 216: 265–278.

Coelho, P. A., & M. de A. Ramos, 1972. A constituição e a distribuição da fauna de decapodos do litoral leste da América do Sul entre as latitudes 5 N e 30 S. Trabalhos Oceanograficos da Universidade Federal de Pernambuco. Recife, 133–236.

Connell, J. H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science 199: 1302–1310.

Cunningham, C. ., N. W. Blackstone, & L. W. Buss, 1992. Evolution of kings crabs from hermit crab ancestors. Nature 355: 539–542.

De Grave, S., N. D. Pentcheff, S. T. Ahyong, T. Chan, K. a Crandall, P. C. Dworschak, D. L. Felder, R. M. Feldmann, C. H. J. M. Fransen, L. Y. D. Goulding, R. Lemaitre, M. E. Y. Low, J. W. Martin, P. K. L. Ng, C. E. Schweitzer, S. H. Tan, D. Tshudy, & R. Wetzer, 2009. A classification of living and fossil genera of decapod crustacea. Raffles Bulletin of Zoology Supplement Series 21: 1–109.

De Léo, F. C., & A. M. S. Pires-Vanin, 2006. Benthic megafauna communities under the influence of the South Atlantic Central Water intrusion onto the Brazilian SE shelf: A comparison between an upwelling and a non-upwelling ecosystem. Journal of Marine Systems 60: 268–284.

Dejean, A., F. Azémar, F. Petitclerc, J. H. C. Delabie, B. Corbara, C. Leroy, R. Céréghino, & A. Compin, 2018. Highly modular pattern in ant-plant interactions involving specialized and non-specialized myrmecophytes. Science of Nature The Science of Nature 105:.

Devictor, V., R. Julliard, & F. Jiguet, 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117: 507–514.

Dormann, C. F., J. Frueund, N. Bluethgen, & B. Gruber, 2009. Indices, graphs and null models: analyzing bipartite ecological networks. The Open Ecology Journal 2: 7–24.

Dormann, C. F., B. Gruber, & J. Fruend, 2008. Introducing the bipartite Package: Analysing Ecological Networks. R News 8: 8–11.

Dormann, C. F., & R. Strauss, 2014. A method for detecting modules in quantitative bipartite networks. Methods in Ecology and Evolution 5: 90–98.

Dowds, B. M., & R. W. Elwood, 1985. Shell wars II: the influence of relative size on decisions made during hermit crab shell fights. Animal Behaviour 33: 649–656.

Ehrlich, P. R., & E. 0. Wilson, 1991. Biodiversity Studies: Science and Policy. Science .

Fernandes, D., & R. Alves, 2018. Composition, density, and shell use of hermit crabs (Crustacea : Paguroidea) from subtidal boulder fields in southeastern Brazil. Latin American Journal of Aquatic Research 46: 72–82.

Fortuna, M. A., D. B. Stouffer, J. M. Olesen, P. Jordano, D. Mouillot, B. R. Krasnov, R. Poulin, & J. Bascompte, 2010. Nestedness versus modularity in ecological networks: Two sides of the same coin?. Journal of Animal Ecology 79: 811–817.

Frameschi, I. F., L. S. De Andrade, F. G. Taddei, V. Fransozo, & L. C. Fernandes-Goés, 2013. Assemblage of hermit crabs near coastal islands in southeastern Brazil. Neotropical Biology and Conservation 9: 9–19.

Fransozo, A., G. Bertini, A. A. Braga, & M. L. Negreiros-Fransozo, 2008. Ecological aspects of hermit crabs (Crustacea, Anomura, Paguroidea) off the northern coast of Sao Paulo State, Brazil. Aquatic Ecology 42: 437–448.

Fransozo, A., L. Fernandes-Góes, V. Fransozo, J. Góes, V. Cobo, G. Teixeira, & R. Gregati, 2011. Marine anomurans (Decapoda) from the non-consolidated sublittoral bottom at the southeastern coast of Brazil. Crustaceana 84: 435–450.

Fransozo, A., F. L. M. Mantelatto, G. Bertini, L. C. Fernandez-Góes, & J. M. Martinelli, 1998. Distribution and assemblages of anomuran crustaceans in Ubatuba bay, north coast of São Paulo state, Brazil. Acta Biológica Venezuelana 18: 17–25.

Fründ, J., K. S. Mccann, & N. M. Williams, 2016. Sampling bias is a challenge for quantifying specialization and network structure: Lessons from a quantitative niche model. Oikos 125: 502–513.

Furlan, M., A. L. Castilho, L. C. Fernandes-Goes, V. Fransozo, G. Bertini, & R. C. da Costa, 2013. Effect of environmental factors on the abundance of decapod crustaceans from soft bottoms off southeastern Brazil. Anais Da Academia Brasileira De Ciencias 85: 1345–1356.

Gherardi, F., & M. Vannini, 1993. Hermit crabs in a mangrove swamp: proximate and ultimate factors in the clustering of Clibanarius laevimanus. Journal of Experimental Marine Biology and Ecology 168: 167–187.

Gotelli, N. J., & A. M. Ellison, 2016. Princípios de estatística em ecologia. Artmed Editora, Porto Alegre.

Gray, J. S., 2001. Marine diversity : the paradigms in patterns of species richness examined *. 65: 41–56.

Greenaway, P., 2003. Terrestrial adaptations in the Anomura (Crustacea : Decapoda). Memoirs of Museum Victoria 60: 13–26.

Guimarães, P. R., V. Rico-Gray, P. S. Oliveira, T. J. Izzo, S. F. dos Reis, & J. N. Thompson, 2007a. Interaction Intimacy Affects Structure and Coevolutionary Dynamics in Mutualistic Networks. Current Biology 17: 1797–1803.

Guimarães, P. R., C. Sazima, S. F. Dos Reis, & I. Sazima, 2007b. The nested structure of marine cleaning symbiosis: Is it like flowers and bees?. Biology Letters 3: 51–54.

Hahn, D. R., 1998. Hermit crab shell use patterns: response to previous shell experience and to water flow. Journal of Experimental Marine Biology and Ecology 228: 35–51.

Hawkins, B. A., 2001. Ecology's oldest pattern? Trends in Ecology & Evolution 16: 470.

Hazlett, B., 1981. The behavioral ecology of hermit crabs. Annual Review of Ecology and Systematics 12: 1–22.

Hazlett, B. A., 1989. Mating success of male hermit crabs in shell generalist and shell specialist species. Behavioral Ecology and Sociobiology 25: 119–128.

Hazlett, B. A., & W. Herrnkind, 1980. ORIENTATION TO SHELL EVENTS BY THE HERMIT CRAB

CLIBANARIUS VITTATUS (BOSC) (DECAPODA, PAGURIDEA). Crustaceana 39: 311–314.

Hazlett, B. A., D. Rittschof, & C. E. Bach, 2005. The effects of shell size and coil orientation on reproduction in female hermit crabs , Clibanarius vittatus. Journal of experimental maine biology and ecology 323: 93–99.

Hebling, N. J., F. L. Mantelatto, M. L. Negreiros-Fransozo, & A. Fransozo, 1994. Levantamento e distribuição de braquiúros e anomuros (Crustacea, Decapoda) dos sedimentos sublitorais da região da Ilha Anchieta, Ubatuba (SP). Boletim Do Instituto De Pesca 21: 1–9.

Hieri, O., A. F. Lotter, & G. Lemcke, 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25: 101–110.

Hollander, M., & D. A. Wolfe, 1999. Nonparametric statistical methods. Wiley-Interscience.

Humboldt, A. Von, 1808. Ansichten der natur. JG Cotta.

Hunt, H. L., R. A. Wahle, J. Tremblay, M. Comeau, A. Silva, & R. Rochette, 2017. Spatial patterns of richness and abundance of benthic decapod crustaceans and fishes in the North-west Atlantic as measured by cobble-filled bio-collectors. Marine Biology Research 1000: 1–19.

Huston, M., 1979. A General Hypothesis of Species Diversity. The American Naturalist 113: 81–101.

Hutchinson, G. E., 1957. Concluding remarks Cold spring symposia on quantitative. : 415–427.

IBAMA, 2008. Normative Instruction No. 189, 23th September, 2008. .

Johnson, W. S., 2015. Suprabenthic species distributions relative to small-scale bathymetric features along the Virginia coast, USA. Marine Biology Research 11: 1009–1020.

Jordano, P., 1987. Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance, Dependence Asymmetries, and Coevolution. The American Naturalist 129: 657–677.

Jowit, J., 2018. Half of world's oceans now fished industrially, maps reveal. The Guardian. , https://www.theguardian.com/environment/2018/feb/22/half-of-worlds-oceans-now-fished-industrially-maps-reveal.

Kaiser, M. J., K. R. Clarke, H. Hinz, M. C. V. Austen, P. J. Somerfield, & I. Karakassis, 2006. Global analysis of response and recovery of benthic biota to fishing. Marine Ecology Progress Series 311: 1–14.

Kaiser, M. J., & B. E. Spencer, 1995. Survival of by-catch from a beam trawl. Marine Ecology Progress Series 126: 31–38.

Kaiser, M. J., & B. E. Spencer, 1996. Behavioural responses of scavengers to beam trawl disturbance. Aquatic predators and their prey Blackwell Scientific Publications Oxford 116: 123.

Kellogg, C. W., 1976. Gastropod shells: A potentially limiting resource for hermit crabs. Journal of Experimental Marine Biology and Ecology .

Kellogg, C. W., 1977. Coexistence in a hermit crab species ensemble. The Biological bulletin 153: 133–144, http://www.biolbull.org/content/153/1/133.abstract.

Kolbert, E., 2014. The sixth extinction: An unnatural history. A&C Black.

Laidre, M. E., 2011. Ecological relations between hermit crabs and their shell-supplying gastropods: Constrained consumers. Journal of Experimental Marine Biology and Ecology Elsevier B.V. 397: 65–70, http://dx.doi.org/10.1016/j.jembe.2010.10.024.

Laidre, M. E., 2012. Niche construction drives social dependence in hermit crabs. Current Biology

Elsevier 22: R861–R863, http://dx.doi.org/10.1016/j.cub.2012.08.056.

Laity, T., S. W. Laffan, C. E. González-Orozco, D. P. Faith, D. F. Rosauer, M. Byrne, J. T. Miller, D. Crayn, C. Costion, C. C. Moritz, & K. Newport, 2015. Phylodiversity to inform conservation policy: An Australian example. Science of the Total Environment Elsevier B.V. 534: 131–143.

Lancaster, I., 1986. Pagurus bernhardus (L.)–an introduction to the natural history of hermit crabs. Field studies 7: 189–238.

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Global Ecology and Biogeography 23: 1324–1334.

Lemaitre, R., & P. McLaughlin, 2009. Recent advances and conflicts in concepts of anomuran phylogeny (Crustacea: Malacostraca). Arthropod Systematics & Phylogeny 67: 119–135, http://www.arthropod-systematics.de/ASP_67_2/ASP_67_2_LeMaitre&McLaughlin_119-135.pdf.

Lemaitre, R., & M. Tavares, 2015. New taxonomic and distributional information on hermit crabs (Crustacea: Anomura: Paguroidea) from the Gulf of Mexico, Caribbean Sea, and Atlantic coast of South America. Zootaxa 3994: 451–506.

Leprieur, F., J. D. Olden, S. Lek, & S. Brosse, 2009. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. Journal of Biogeography 36: 1899–1912.

Magurran, A. E., 2004. Measuring biological diversity. John Wiley & Sons.

Mahiques, M. M. de, E. Siegle, J. Alcántara-Carrió, F. G. Silva, P. H. G. de Sousa, & C. C. Martins, 2016. The Beaches of the State of São Paulo In Short, A. D., & A. H. da F. Klein (eds), Brazilian Beach Systems. Springer: 397–418.

Mahiques, M. M., M. G. Tessler, & V. V. Furtado, 1998. Characterization of energy gradient in enclosed bays of Ubatuba region, south-eastern Brazil. Estuarine, Coastal and Shelf Science 47: 431–446.

Mantelatto, F. L., C. H. Bernardo, T. E. Silva, V. P. Bernardes, V. J. Cobo, & A. Fransozo, 2016. Composition and distribution of decapod crustaceans associated by fisheries of seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) at the northern coast of Sao Paulo. Boletim Do Instituto De Pesca 42: 307–326.

Mantelatto, F. L., R. Biagi, A. L. Meireles, & M. A. Scelzo, 2007a. Shell preference of the hermit crab Pagurus exilis (Anomura: Paguridae) from Brazil and Argentina: A comparative study. Revista de Biologia Tropical 55: 153–161.

Mantelatto, F. L., D. L. a. Espósito, M. Terossi, R. Biagi, & a. L. Meireles, 2007b. Population features of the Western Atlantic hermit crab Pagurus exilis (Anomura, Paguridae) in Brazil. Atlantica 29: 107–114.

Mantelatto, F. L. M., & A. Franzoso, 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, Northern coast of São Paulo State, Brazil. Revista Brasileira de Biologia 59: 23–31.

Mantelatto, F. L. M., & R. B. Garcia, 2002. Hermit crab fauna from the infralittoral zone of Anchieta Island (Ubatuba, Brazil) In Escoba-Briones, E., & F. Alvarez (eds), Modern approaches to the study of Crustacea. : 137–143.

Mantelatto, F. L. M., J. M. Martinelli, & A. Fransozo, 2004. Temporal-spatial distribution of the hermit crab *Loxopagurus loxochelis* (Decapoda : Diogenidae) from Ubatuba Bay, Sao Paulo State, Brazil. Revista De Biologia Tropical 52: 47–55.

Mantelatto, F. L., M. Terossi, M. Negri, R. C. Buranelli, R. Robles, T. Magalhães, A. F. Tamburus, N. Rossi, & M. J. Miyazaki, 2018. DNA sequence database as a tool to identify decapod crustaceans on the São Paulo coastline. Mitochondrial DNA Part A: DNA Mapping, Sequencing, and Analysis Informa UK Ltd. 29: 805–815, https://doi.org/10.1080/24701394.2017.1365848.

Martello, F., F. de Bello, M. S. de C. Morini, R. R. Silva, D. R. de Souza-Campana, M. C. Ribeiro, & C. P. Carmona, 2018. Homogenization and impoverishment of taxonomic and functional diversity of ants in Eucalyptus plantations. Scientific Reports 8: 3266, http://www.nature.com/articles/s41598-018-20823-1.

Maruyama, P. K., J. Vizentin-Bugoni, B. Dalsgaard, I. Sazima, & M. Sazima, 2015. Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. Oecologia Springer Berlin Heidelberg 178: 783–793, http://dx.doi.org/10.1007/s00442-015-3275-9.

Maruyama, P. K., J. Vizentin-Bugoni, G. M. Oliveira, P. E. Oliveira, & B. Dalsgaard, 2014. Morphological and {Spatio}-{Temporal} {Mismatches} {Shape} a {Neotropical} {Savanna} {Plant}-{Hummingbird} {Network}. Biotropica 46: 740–747, http://onlinelibrary.wiley.com/doi/10.1111/btp.12170/abstract.

Mazor, T. K., C. R. Pitcher, N. Ellis, W. Rochester, S. Jennings, J. G. Hiddink, R. A. McConnaughey, M. J. Kaiser, A. M. Parma, P. Suuronen, M. Kangas, & R. Hilborn, 2017. Trawl exposure and protection of seabed fauna at large spatial scales. Diversity and Distributions 23: 1280–1291.

Mcclain, C. R., & J. P. Barry, 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. Ecological Society of America 91: 964–976.

McDermott, J. J., J. D. Williams, & C. B. Boyko, 2010. The unwanted guests of hermits: A global review of the diversity and natural history of hermit crab parasites. Journal of Experimental Marine Biology and Ecology 394: 2–44.

McLaughlin, P. A., 2003. Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. Memoirs of Museum Victoria 60: 111–144.

Mclaughlin, P. a., T. Komai, R. Lemaitre, & D. L. Rahayu, 2010. Annotated checklist of anomuran decapod crustaceans of the world. PART I: Lithodoidea, Lomisoidea and Paguroidea. The raffles bulletin of zoology 5–107.

Mclaughlin, P. A., R. Lemaitre, & U. Sorhannus, 2007. HERMIT CRAB PHYLOGENY : A REAPPRAISAL AND ITS ‘“ FALL-OUT .”’ 27: 97–115.

McLean, R., 1983. Gastropod shells: a dynamic resource that helps shape benthic community structure. Journal of Experimental Marine Biology and Ecology Elsevier 69: 151–174.

McNatty, A., K. L. Abbott, & P. J. Lester, 2009. Invasive ants compete with and modify the trophic ecology of hermit crabs on tropical islands. Oecologia 160: 187–194.

Meireles, A. de L., R. G. Biagi, A. Fransozo, & F. L. M. Mantelatto, 2012. Os Ermitões (Crustacea, Anomura) In Amaral, A. C. Z., & S. A. H. Nallin (eds), Biodiversidade e ecossistemas bentônicos marinhos do Litoral Norte de São Paulo - Sudeste do Brasil. UNICAMP/IB, Campinas - SP: 479–488.

Mellin, C., M. Aaron Macneil, A. J. Cheal, M. J. Emslie, & M. Julian Caley, 2016. Marine protected areas increase resilience among coral reef communities. Ecology Letters 19: 629–637.

Melo, G. A. S., 1998. Manual de identificação dos Crustacea Decapoda do litoral Brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea. Editora Plêiade. São Paulo.

Miranda, I., A. L. Meireles, R. Biagi, & F. L. Mantelatto, 2006. Is the abundance of the red brocade hermit crab *Dardanus insignis* (Decapoda: Anomura: Diogenidae) in the infralittoral region of southern Brazil determined by reproductive potential? Crustacean Research 6: 45–55.

Miserendino, M. L., C. Brand, L. B. Epele, C. Y. Di, G. H. Omad, M. Archangelsky, O. Martínez, & A. M. Kutschker, 2018. Environment Biotic diversity of benthic macroinvertebrates at contrasting glacier-fed systems in Patagonia Mountains: The role of environmental heterogeneity facing global warming. Science of the Total Environment 622–623: 152–163.

Nagabhushanam, R., & R. Sarojini, 1968. Digestive enzymes in *Diogenes bicristimanus* (Crustacea: Decapoda). .

Negreiros-Fransozo, M. L., A. Fransozo, F. L. M. Mantelatto, M. A. Pinheiro, & S. Santos, 1997. Anomuran species (Crustacea, Decapoda) and their ecological distribution at Fortaleza Bay sublittoral, Ubatuba, São Paulo, Brazil. Iheringia Série Zoologia 194: 187–194.

Oba, T., & S. Goshima, 2004. Temporal and spatial settlement patterns of sympatric hermit crabs and the influence of shell resource availability. 871–879.

Oksanen, A. J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O. Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, & H. Wagner, 2015. Package ' vegan .' .

Olden, J. D., N. L. R. Poff, M. R. Douglas, M. E. Douglas, & K. D. Fausch, 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19: 18–24.

Olesen, J. M., J. Bascompte, Y. L. Dupont, & P. Jordano, 2007. The modularity of pollination networks. Proceedings of the National Academy of Sciences 104: 19891–19896, http://www.pnas.org/cgi/doi/10.1073/pnas.0706375104.

Oliveira, C. D. L. de, A. M. S. Quirino, E. A. da Silva, E. F. Costa, D. da S. Santos, A. N. C. Menezes, M. de M. Junior, & F. M. S. da Silva, 2018. Shell choice and occupation by the hermit crab (Crustacea : Diogenidae) in laboratory environment. International Journal of Aquatic Biology. .

Patefield, W. M., 1981. Confidence intervals for the slope of a linear functional relationship. Communications in Statistics - Theory and Methods Taylor & Francis 10: 1759–1764, https://doi.org/10.1080/03610928108828147.

Peres, P. A. S., A. P. Ferreira, & F. P. P. Leite, 2018. Expanding the "shell exchange market" hypothesis for clustering behavior in intertidal hermit crabs: Mating and tide as proximate factors. Journal of Experimental Marine Biology and Ecology Elsevier 500: 100–104, https://doi.org/10.1016/j.jembe.2017.12.019.

Peterson, B. G., & P. Carl, 2018. PerformanceAnalytics: Econometric Tools for Performance and Risk Analysis. , https://cran.r-project.org/package=PerformanceAnalytics.

Pianka, E. R., 1966. Latitudinal Gradients in Species Diversity: A Review of Concepts. The American Naturalist 100: 33–46, http://www.journals.uchicago.edu/doi/10.1086/282398.

Pianka, E. R., 1970. On r- and K- selection. The American Naturalist 592–597.

Pianka, E. R., 1972. r and K Selection or b and d Selection ?. The American naturalist 106: 581–588.

Pohlert, T., 2014. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR). , https://cran.r-project.org/package=PMCMR.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria, https://www.r-project.org/.

Ragagnin, M. N., D. Gorman, I. D. McCarthy, B. S. Sant'Anna, C. C. De Castro, & A. Turra, 2018. Gastropod shell size and architecture influence the applicability of methods used to estimate internal volume. Scientific Reports 8: 1–11.

Ramalho, S. P., L. Lins, J. Bueno-Pardo, E. A. Cordova, J. M. Amisi, N. Lampadariou, A. Vanreusel, & M. R. Cunha, 2017. Deep-Sea Mega-Epibenthic Assemblages from the SW Portuguese Margin (NE Atlantic) Subjected to Bottom-Trawling Fisheries. Frontiers in Marine Science 4: 1–16.

Ramsay, K., M. J. Kaiser, & R. N. Hughes, 1996. Changes in hermit crab feeding patterns in response to trawling disturbance. Marine Ecology Progress Series 144: 63–72.

Ramsay, K., M. J. Kaiser, & R. N. Hughes, 1997. A Field Study of Intraspecific Competition for Food in Hermit Crabs (Pagurus bernhardus). Estuarine, Coastal and Shelf Science 44: 213–220.

Rios, E., 1994. Seashells of Brazil. Editora da Fundaçao Cidade do Rio Grande, Rio Grande - RS, Museu Oceanográfico de Rio Grande.

Rodrigues, G. F. B., I. F. Frameschi, V. P. Bernardes, & A. Fransozo, 2016. Dinâmica populacional do ermitão endêmico Pagurus exilis (Benedict , 1892) (Crustacea : Decapoda : Paguridae) na região de Ubatuba-SP. Ciência et Praxis 9: 17–24.

Rodrigues, L. C., B. M. Pivato, L. C. G. Vieira, V. M. Bovo-Scomparin, J. C. Bortolini, A. Pineda, & S. Train, 2017. Use of phytoplankton functional groups as a model of spatial and temporal patterns in reservoirs: a case study in a reservoir of central Brazil. Hydrobiologia 805: 147–161.

Rosenberg, R., M. Blomqvist, H. C. Nilsson, H. Cederwall, & A. Dimming, 2004. Marine quality assessment by use of benthic species-abundance distributions: A proposed new protocol within the European Union Water Framework Directive. Marine Pollution Bulletin 49: 728–739.

Sazatornil, F. D., M. Moré, S. Benitez-Vieyra, A. A. Cocucci, I. J. Kitching, B. O. Schlumpberger, P. E. Oliveira, M. Sazima, & F. W. Amorim, 2016. Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks. Journal of Animal Ecology 85: 1586–1594.

Schemske, D. W., & G. G. Mittelbach, 2017. "Latitudinal Gradients in Species Diversity": Reflections on Pianka's 1966 Article and a Look Forward. The American Naturalist 000–000, http://www.journals.uchicago.edu/doi/10.1086/691719.

Schemske, D. W., G. G. Mittelbach, H. V Cornell, J. M. Sobel, & K. Roy, 2009. Is There a Latitudinal Gradient in the Importance of Biotic Interactions ?. The Annual Review ofEcology, Evolution, and Systematics 40: 245–269.

Schwinghamer, P., J. Y. Guigné, & W. C. Siu, 1996. Quantifying the impact of trawling on benthic habitat structure using high resolution acoustics and chaos theory. Canadian Journal of Fisheries and Aquatic Sciences 53: 288–296.

Scully, E. P., 1979. The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. Journal of Experimental Marine Biology and Ecology 37: 139–152.

Seitz, R. D., K. E. Knick, T. M. Davenport, & G. G. Saluta, 2017. Human influence at the Coast: upland and shoreline stressors affect coastal macrofauna and are mediated by salinity. Estuaries and Coasts Estuaries and Coasts 1–17.

Selin, N. I., E. S. Kornienko, & O. M. Korn, 2016. The species composition and pattern of distribution of hermit crabs (Decapoda: Paguroidea) in Vostok Bay, Sea of Japan. Russian Journal of Marine Biology 42: 481–488.

Small, C., & R. J. Nicholas, 2003. A global analysis of human settlement in coastal zones. Journal of coastal research 19: 584–599.

Sommer, B. R., P. L. Harrison, Ma. Beger, & J. M. Pandolfi, 2014. Trait-mediated environmental filtering drives assembly at biogeographic transition zones. Ecology 95: 1000–1009.

Squires, H. J., G. P. Ennis, & G. Dawe, 2001. On biology of two sympatric species of Hermit Crab (Crustacea, Decapoda, Paguridae) at St. Chads, Newfoundland. NAFO Scientific Council Studies 7–17.

Stanski, G., F. L. Mantelatto, & A. Leão-Castilho, 2016. Hermit crab bycatch fauna (Decapoda, Anomura) off the coast of Santa Catarina State, Brazil: diversity and spatial-temporal distribution. Latin American Journal of Aquatic Research 44: 546–556.

Stuer-lauridsen, F., G. Drillet, F. Thorbjørn, & J. Saunders, 2018. Same Risk Area : An area-based

approach for the management of bio- invasion risks from ships ' ballast water. Marine Policy Elsevier Ltd 97: 147–155, https://doi.org/10.1016/j.marpol.2018.05.009.

Suguio, K., 1973. Introdução à sedimentologia. Edgard Blucher, EDUSP, São Paulo.

Tagliapietra, D., & M. Sigovini, 2010. Benthic fauna : collection and identification of macrobenthic invertebrates. Terre et Environnement 88: 253–261.

Teoh, H. W., M. Ali, S. Hussein, & V. C. Chong, 2014. Influence of habitat heterogeneity on the assemblages and shell use of hermit crabs (Anomura : Diogenidae). Zoological Studies 53: 1–9.

Terossi, M., L. S. Torati, I. Miranda, M. A. Scelzo, & F. L. Mantelatto, 2010. Comparative reproductive biology of two southwestern Atlantic populations of the hermit crab *Pagurus exilis* (Crustacea: Anomura: Paguridae). Marine Ecology 31: 584–591.

Thrush, S. F., & P. K. Dayton, 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annual Review of Ecology and Systematics 33: 449–473.

Thrush, S. F., K. E. Ellingsen, & K. Davis, 2016. Implications of fisheries impacts to seabed biodiversity and ecosystem-based management. Ices Journal of Marine Science 73: 144–150.

Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences 101: 10854–10861, http://www.pnas.org/cgi/doi/10.1073/pnas.0403458101.

Tran, M. V., 2014. Coexisting generalist scavengers occupy different feeding niches. Marine Biology .

Tricarico, E., & F. Gherardi, 2007. Resource assessment in hermit crabs: The worth of their own shell. Behavioral Ecology 18: 615–620.

Tsang, L. M., T. Y. Chan, S. T. Ahyong, & K. H. Chu, 2011. Hermit to king, or hermit to all: Multiple transitions to crab-like forms from hermit crab ancestors. Systematic Biology 60: 616–629.

Tucker, M. E., 1988. Techniques in sedimentology. Blackwell Scientific Publications, Oxford - UK.

Turra, A., & D. Gorman, 2014. Subjective resource value and shell abandoning behavior in hermit crabs. Journal of Experimental Marine Biology and Ecology Elsevier B.V. 452: 137–142, http://dx.doi.org/10.1016/j.jembe.2013.12.018.

Tylianakis, J. M., A. M. Klein, & T. Tscharntke, 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. Ecology 86: 3296–3302.

Underwood, A. J., 1979. The ecology of intertidal gastropods. Advances in Marine Biology 16: 111–210.

Vale, V. F., S. A. S. N. Moraes, V. L. G. Brito, C. E. R. D. Alencar, & F. A. M. Freire, 2017. Shell use by sympatric hermit crab species in a seasonally open coastal lagoon in Northeastern Brazil. Marine Ecology 38: 1–14.

Van Denderen, P. D., S. G. Bolam, J. G. Hiddink, S. Jennings, A. Kenny, A. D. Rijnsdorp, & T. Van Kooten, 2015. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Marine Ecology Progress Series 541: 31–43.

Vázquez, D. P., N. Bluthgen, L. Cagnolo, & N. P. Chacoff, 2009. Uniting pattern and process in plant-animal mutualistic networks: A review. Annals of Botany 103: 1445–1457.

Veale, L. O., A. S. Hill, S. J. Hawkins, A. R. Brand, & S. A. Hill, 2000. Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats. Marine Biology 137: 325–337.

Vellend, M., 2010. Conceptual Synthesis in Community Ecology. The Quarterly Review of Biology 85:

183–206, http://www.journals.uchicago.edu/doi/10.1086/652373.

Vianna, M., & H. Valentini, 2004. Observações Sobre a Frota Pesqueira Em Ubatuba , Litoral norte Do Estado De São Paulo, Entre 1995 E 1996. Boletim Do Instituto De Pesca 30: 171–176.

Vizentin-Bugoni, J., P. K. Maruyama, V. J. Debastiani, L. da S. Duarte, B. Dalsgaard, & M. Sazima, 2016. Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant-hummingbird network. Journal of Animal Ecology 85: 262–272.

Watling, L., & E. A. Norse, 1998. Disturbance of the Seabed by Mobile Fishing Gear: A comparison to Forest Clearcutting. Conservation Biology 12: 1180–1197.

Wells, R. M. G., P. E. McShane, N. Ling, R. J. Wong, T. O. C. Lee, & J. Baldwin, 1998. Effect of wave action on muscle composition, metabolites and growth indices in the New Zealand abalone, Paua (*Haliotis iris*), with implications for harvesting and aquaculture. Comparative Biochemistry and Physiology - B Biochemistry and Molecular Biology 119: 129–136.

Williams, J. D., & J. J. McDermott, 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. Journal of Experimental Marine Biology and Ecology 305: 1–128.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, & K. A. Selkoe, 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science 314: 787–791.

Wright, D. H., & J. H. Reeves, 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia 92: 416–428.

Yoshimura, M., & M. Yamashita, 2012. Measurement of tropical rainforest three- dimensional light environment and its diurnal change. 1161:.

Zajac, R. N., J. M. Vozarik, & B. R. Gibbons, 2013. Spatial and temporal patterns in macrofaunal diversity components relative to sea floor landscape Structure. PLoS ONE 8: 1–11.

Zar, J. H., 1999. Biostatistical analysis. Upper Saddle River, New Jersey - NY.

Zeileis, A., & T. Hothorn, 2002. Diagnostic Checking in Regression Relationships. R News 2: 7–10, https://cran.r-project.org/doc/Rnews/.

Considerações finais

Mudança na fauna de caranguejos ermitões

Um dos temas centrais da ecologia de comunidades é o estudo da variação espaço-temporal da abundância, riqueza e diversidade. Utilizando os caranguejos ermitões como modelo, foi possível notar uma alteração em escala temporal e espacial dentro de uma enseada localizada no litoral norte paulista.

Ao comparar a abundância dos ermitões com intervalo de 20 anos identificou-se um aumento de ermitões no segundo período amostrado. Fatores de origem ambiental e/ou antrópico podem ser responsável pela alteração da abundância de algumas espécies, dessa forma destaca-se a pesca de arrasto (fator antrópico) como possível responsável por alterar a abundância desses organismos. Sabe-se que a pesca de arrasto é prejudicial aos ecossistemas costeiros pelos diversos distúrbios que esse aparato causa, no entanto, algumas espécies são mais resistentes e podem ser favorecidas pela ação pesqueira. Os ermitões são conhecidos por ocuparem conchas vazias de gastrópodes, essa "armadura" pode fornecer uma vantagem contra os danos físicos causados pelo arrasto, em relação a outras espécies costeiras. Porém, embora a abundância de algumas espécies tenha aumentado (principalmente espécies generalistas), outras espécies foram menos encontradas ou então desapareceram durante o segundo período. Os resultados indicaram que a própria comunidade de ermitões se alterou nesse intervalo de 20 anos, o que indica que possivelmente as relações ecológicas desses organismos mudaram.

Ao investigar os padrões de riqueza e diversidade, várias métricas indicaram uma similaridade entre os períodos amostrados, no entanto, no primeiro período foi capturado um maior número de espécies. Vale ressaltar a utilização de várias métricas de diversidade alfa para detectar alterações na diversidade local de uma dada comunidade. Existe uma ampla gama de medidas de diversidade e cada uma pode responder de forma satisfatória uma questão de interesse. Adicionalmente a abordagem da diversidade beta particionada possibilitou entender que a alteração na estrutura da comunidade de ermitões não ocorreu de forma uniforme nos pontos amostrados (em alguns locais houve reposição de algumas espécies por outras, enquanto que em outros obteve-se um padrão de subconjuntos). Destaca-se a utilização da diversidade beta particionada como uma ferramenta útil para entender processos ecológicos e gerar medidas de conservação.

Mudança nos fatores ambientais

Em relação fatores ambientais mensurados nos dois períodos de estudo, a mudança da textura do sedimento foi nítida, enquanto que no primeiro período menores valores de phi indicavam um substrato com grãos mais grossos, durante o segundo período obteve-se (no geral) maiores valores de phi, apontando para um substrato mais fino composto principalmente por silte e argila. No entanto, essa alteração não ocorreu de forma uniforme em todos os locais amostrados. O local 5m está localizado mais próximo a linha da costa foi o que obteve os maiores valores de phi durante o segundo período, já o local 15m que está localizado na

boca da enseada, apresentou um aumento nos valores de phi, no entanto, de forma não tão acentuada como em outros locais amostrados. Um dos possíveis motivos que tenham causado essa alteração nos valores do phi pode ter sido a expansão imobiliária que a cidade de Ubatuba-SP passou nas últimas décadas, movida principalmente pela expansão do turismo na região. Outros fatores ambientais não se alteraram de forma significativa nos períodos estudados.

Redes de interação para ermitões e conchas de gastrópodes

A utilização da ferramenta de redes para elucidar padrões de utilização de recursos e frequência de interações vem sendo utilizada há algumas décadas para investigar as relações de polinizadores-plantas e parasita-hospedeiro. A relação entre ermitões e conchas (recurso) é uma das mais fascinantes e indispensáveis relações da natureza, assim investigar como está estruturada essas redes em uma dada comunidade pode elucidar questões e mostrar padrões interessantes sobre esses organismos. A rede estudada apresentou-se mais especializada (H_2) e mais modular (Q') do que esperada ao acaso, indicando que os ermitões não ocupam as conchas somente por processos neutros (como abundância) mas também por características apresentadas por ambos ermitões e conchas.

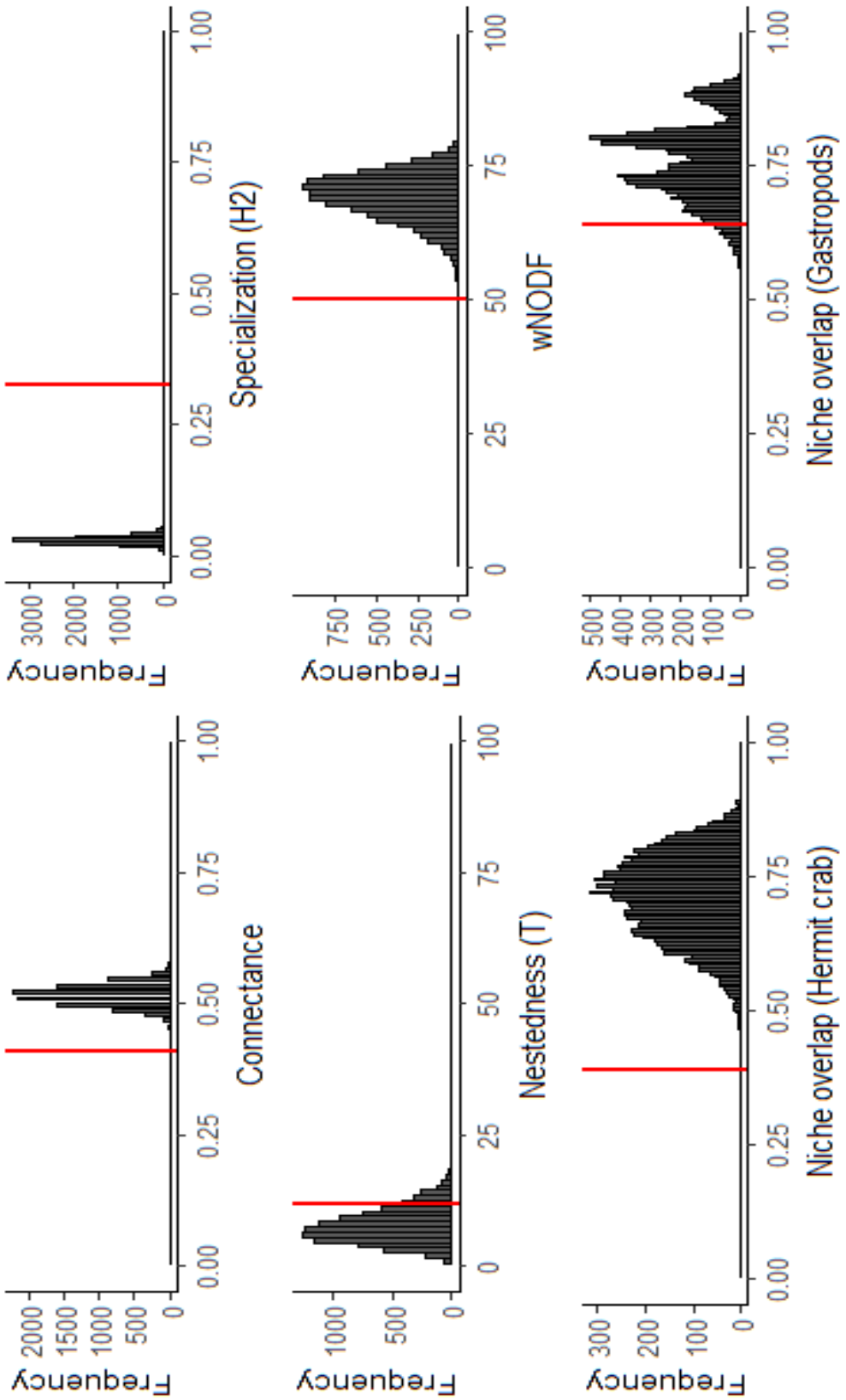
No geral, a utilização de uma abordagem comparativa com um intervalo de tempo considerável permitiu identificar como a fauna de ermitões mudou na enseada de Ubatuba e quais fatores podem ter causado essas alterações. Tendo em

vista que a diversidade variou espacialmente na enseada é possível detectar localidades com maior necessidade de preservação (com número de espécies), assim o local Abridado (*Sheltered*) deve ser levado em conta por abrigar uma maior diversidade de ermitões. O local *5m* também contribui de forma significativa para a manutenção da diversidade de ermitões na região. Dentre as métricas utilizadas a distinção taxonômica — por incorporar relações filogenéticas — indicou um aumento significativo após o intervalo de tempo. Em relação a interação ermitões e conchas a ferramenta utilizada (pacote *bipartite*) possibilitou encontrar padrões até então nunca visto antes, mostrando ser extremamente útil no estudo dessa relação. Contudo destaca-se a importância de ações que visem a preservação da biodiversidade de ambientes costeiros que estão em constante mudança, seja por influência natural ou antrópica. Os caranguejos ermitões se mostraram um interessante modelo para o estudo da ecologia de comunidades com uma abordagem espaço-temporal e devem ser amplamente estudados.

Sumarizando, para conservar a biodiversidade local é necessário entender como a paisagem se altera e quais consequências para o ecossistema essas mudanças causam. Detectar distúrbios em processos ecológicos centrais, como dispersão, predação, competição torna-se imprescindível para um melhor entendimento da origem, manutenção e funcionamento da biodiversidade costeira tropical. Pode-se destacar também a importância da preservação não só das espécies em si, mas também as próprias interações entre elas, como percebeu Janzen (1974) " *O que escapa aos olhos, no entanto, é um tipo muito mais traiçoeiro de extinção: a extinção das interações ecológicas*."

Recorte da Enseada de Ubatuba, Ubatuba, São Paulo, Brasil em 2017 evidenciando a proximidade da Serra do Mar com a enseada.

Anexo 1. Ermitões encontrados em maior abundância durante o período de estudos na Enseada de Ubatuba-SP.



Anexo 2. Histogramas mostrando a frequência das distribuições de 5,000 simulações para cada métrica. Linhas vermelhas verticais indicam o valor observado de cada métrica na comunidade de estudos.