UNIVERSIDADE ESTADUAL DE CAMPINAS

INSTITUTO DE BIOLOGIA

PEDRO AUGUSTO DOS SANTOS LONGO

GENÔMICA POPULACIONAL E SEUS FATORES MODULADORES EM INVERTEBRADOS ASSOCIADOS A MACROALGAS MARINHAS

POPULATION GENOMICS AND THEIR MODULATING FACTORS IN SEAWEED-ASSOCIATED INVERTEBRATES

Campinas

2023

PEDRO AUGUSTO DOS SANTOS LONGO

GENÔMICA POPULACIONAL E SEUS FATORES MODULADORES EM INVERTEBRADOS ASSOCIADOS A MACROALGAS MARINHAS

POPULATION GENOMICS AND THEIR MODULATING FACTORS IN SEAWEED-ASSOCIATED INVERTEBRATES

Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do título de Doutor em Ecologia

Thesis presented to the Institute of Biology of the University of Campinas in partial fulfillment of the requirements for the degree of Doctor in Ecology

Orientadora: Profª. Drª. FOSCA PEDINI PEREIRA LEITE

ESTE ARQUIVO DIGITAL CORRESPONDE À VERSÃO FINAL DA TESE DEFENDIDA PELO ALUNO **PEDRO AUGUSTO DOS SANTOS LONGO**, E ORIENTADA PELA PROFª. DRª. **FOSCA PEDINI PEREIRA LEITE**

Campinas

2023

Ficha catalográfica
Universidade Estadual de Campinas
Biblioteca do Instituto de Biologia
Mara Janaina de Oliveira - CRB 8/6972

L864g

Longo, Pedro Augusto dos Santos, 1992-
Genômica populacional e seus fatores moduladores em invertebrados associados a macroalgas marinhas / Pedro Augusto dos Santos Longo. – Campinas, SP : [s.n.], 2023.

Orientador: Fosca Pedini Pereira Leite.
Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Ecologia marinha. 2. Ecologia molecular. 3. Conectividade de paisagens. 4. Fluxo gênico. I. Leite, Fosca Pedini Pereira, 1947-. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Informações Complementares

Título em outro idioma: Population genomics and their modulating factors in seaweed-associated invetebrates
Palavras-chave em inglês:
Marine ecology
Molecular ecology
Landscape connectivity
Gene flow
Área de concentração: Ecologia
Titulação: Doutor em Ecologia
Banca examinadora:
Fosca Pedini Pereira Leite [Orientador]
Vera Nisaka Solferini
Sónia Cristina da Silva Andrade
Marina Corrêa Côrtes
Guilherme Henrique Pereira Filho
Data de defesa: 03-03-2023
Programa de Pós-Graduação: Ecologia

Identificação e informações acadêmicas do(a) aluno(a)
- ORCID do autor: https://orcid.org/0000-0003-2550-2157
- Currículo Lattes do autor: https://lattes.cnpq.br/2226681449218418

Campinas, 03 de março de 2023

COMISSÃO EXAMINADORA

Profª. Drª. Fosca Pedini Pereira Leite

Profª. Drª. Vera Nisaka Solferini

Profª. Drª. Sónia Cristina da Silva Andrade

Profª. Drª. Marina Corrêa Côrtes

Prof. Dr. Guilherme Henrique Pereira Filho

Os membros da Comissão Examinadora acima assinaram a Ata de Defesa, que se encontra no processo de vida acadêmica do aluno.

A Ata da defesa com as respectivas assinaturas dos membros encontra-se no SIGA/Sistema de Fluxo de Dissertação/Tese e na Secretaria do Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Universidade Estadual de Campinas.

DEDICATÓRIA

Dedico essa tese aos meus pais, que me fortaleceram e me apoiaram durante toda essa trajetória, e sonharam comigo em cada instante desta conquista! Amo vocês!

AGRADECIMENTOS

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001 e pelo programa Biota-FAPESP da Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), pelos projetos de Nº 2018/10313-0 e Nº 2017/16837-8.

Agradeço a Deus e aos queridos espíritos protetores por terem me dado forças de enfrentar momentos tão difíceis e chegar até aqui, tendo conseguido construir este trabalho do qual tanto nos orgulhamos.

Mas eu definitivamente não estive só. Estando só, definitivamente não teria conseguido.

Agradeço primeiramente à minha família. Meu suporte, meus amores, minha trupe. A meus pais, Cidinha e Edson, por sempre terem feito absolutamente tudo – e além – do que estava ao alcance deles para me verem feliz e conquistando esse sonho. Mesmo nos momentos mais difíceis, e quando dar este apoio não foi fácil. Este trabalho é totalmente fruto do amor de vocês. A minhas irmãs, Carol e Gabi, minhas grandes companheiras dessa vida, sempre tão presentes, e que sempre me ensinam tanto sobre amor e companheirismo, ter vocês ao meu lado torna sempre tudo tão mais fácil, leve e lindo, obrigado por sempre me incentivarem e me impulsionarem a enxergar o melhor de mim. Ao meu cunhado Luís Eduardo, por tanto carinho e suporte, inclusive nos momentos mais difíceis desse período. Ao meu sobrinho Gabriel, meu eterno parceirinho, meu companheiro, seu olhar de amor e admiração me fortalecem sempre a seguir em frente e ser uma pessoa melhor. À minha sobrinha Dudinha, que chegou esse ano abrilhantando e acrescentando tanto às nossas vidas com seu olhar amoroso, forte e atento e com toda sua fofura. Ao meu cachorro Cacau, meu anjo, porque uma das manifestações mais puras de amor é o canino. Minha família, vocês são meus tudo. Amo vocês infinitamente.

Agradeço também a tantas pessoas e amigos queridos que estiveram ao meu lado. À Karine, minha amiga tão querida e parceira de jornada, que comprou, sonhou e construiu cada mínima etapa deste projeto, mas que vem sendo minha companheira deste muito antes, sempre nos fortalecendo, nos ouvindo, nos ajudando, e rindo muito de tudo. Só a gente sabe cada detalhe do que a gente passou, cada perrengue, como tudo foi mais leve com você! Te amo pra vida!! À Mari, minha tão querida amiga há mais de dez anos, desde o início de tudo, e com quem agora eu tive a enorme alegria de também trabalhar juntos, e que se dedicou em tudo que pode pra me ajudar, me ensinando muitas coisas do zero, com todo o afeto possível sempre. Amore, sem o seu apoio incondicional desde o início, se você não tivesse comprado essa ideia comigo, nada teria sido possível! Eu te amo!! À Vanessa, amiga querida que também foi fundamental no desenvolvimento de nosso projeto. Gostaria de agradecer ao Jason, meu amigo tão amado, meu companheiro de vida, que acompanhou de muito perto – ainda quando longe fisicamente – todos os momentos e as dificuldades para conseguir chegar até aqui, sempre me fortalecendo em tudo que podia, e me lembrando de celebrar cada passo dado e cada conquista. Migo

do coração, obrigado por todo seu apoio, nossa amizade e a nossa rede de suporte incondicional que construímos são preciosas para mim. Te amo muito sempre!!! Agradeço à Thais, minha querida amiga da malacologia pra vida, por seu apoio sempre, te amo! Obrigado à Nati e a Fer, grandes amigas e pessoas tão importantes em minha vida há tantos anos, amo vocês! Agradeço ao Saulo, que apareceu este ano em minha vida de maneira muito especial, sendo meu companheiro e compartilhando de tantos momentos, nos dando apoio em nossas dificuldades. Você tem um lugar especial em minha vida! Agradeço a Zizi, Grazi, Dani, André, Jhon, Ju, Allan, e tantas outras pessoas especiais de minha vida.

Agradeço à Profa. Anete Pereira, pela colaboração e por tão gentilmente ceder a infraestrutura de seu laboratório para a execução de boa parte deste projeto. Obrigado também ao Danilo, à Aline e à Patrícia, e a todos os colegas do LAGM – UNICAMP.

Agradeço também a todos os colegas do LICOMAR – UNICAMP, em especial à Tammy e à Silvana, pela ajuda em algumas partes do trabalho.

Agradeço aos técnicos e funcionários do Centro de Biologia Marinha da USP (CEBIMAR – USP) e da base de pesquisa "Clarimundo de Jesus" do Instituto Oceanográfico da USP (IO-USP) pelo apoio fundamental durante a coleta de dados deste trabalho. Agradeço também a toda a equipe do ICMBio – Alcatrazes por viabilizarem e darem apoio incondicional nas coletas em Alcatrazes e na Ilha das Palmas, em especial à Sílvia, ao Geraldo, ao Felipe e ao Anderson.

Agradeço ao Prof. Yoshihisa Suyama, da Universidade de Tohoku no Japão e ao prof. Joseph Harari, da Universidade de São Paulo, pelas colaborações essenciais a este trabalho.

Agradeço às professoras e aos professores membros das minhas bancas de análise prévia e defesa de tese, pela disponibilidade e pelo apoio à finalização de nosso trabalho.

Gostaria de agradecer ao Prof. Gustavo Mori, que além de grande amigo, me coorientou neste doutorado. Seu apoio incondicional, em cada etapa, sempre tão atento, dedicado e atencioso, fizeram toda a diferença na construção, execução e finalização deste trabalho. É uma grande alegria poder trabalhar com você.

Agradeço à Profa. Fosca Leite, minha querida orientadora. Já são tantos anos de parceria, você é um exemplo de pesquisadora e de professora, sempre tão humana, afetuosa, disposta a abraçar novas ideias e a potencializar os diferenciais de seus alunos. Obrigado por me acolher sempre de braços tão abertos em seu laboratório e por me apresentar ao universo das algas marinhas, pelo qual me apaixonei e venho estudando há tantos anos de minha carreira. Uma enorme alegria trabalhar com você durante todos esses anos, conte sempre comigo, Fosca!

Agradeço ao Programa de Pós-Graduação em Ecologia da Unicamp, por todo apoio, contribuição e ensinamentos ao longe destes anos.

Agradeço do fundo do coração à minha universidade, a Universidade Estadual de Campinas, que tem sido minha casa desde 2010, onde construí minha formação como profissional e onde cresci e me desenvolvi tanto como ser humano. Que orgulho em fazer parte deste lugar. Viva a universidade pública, as pesquisadoras e pesquisadores e a ciência brasileira!!!

RESUMO

Compreender os padrões de estruturação genética e de conectividade em populações marinhas, bem como quais são os principais fatores moduladores destes padrões, são informações de fundamental importância para se determinar medidas efetivas de conservação das espécies neste ambiente e, consequentemente, dos habitats que elas ocupam. As macroalgas marinhas formam extensos bancos, que constituem habitats para uma grande diversidade de invertebrados associados, os quais podem apresentar uma grande variedade de formas, modos de vida e potencial de dispersão. Neste trabalho, investigamos a estruturação e diversidade genética de algumas espécies de invertebrados associados aos bancos de macroalgas marinhas no litoral paulista, e avaliamos a influência de alguns fatores moduladores. Primeiramente, estudamos o anfípode *Hyale niger* e os efeitos da distância geográfica, distância ambiental e variações morfológicas sobre a diferenciação genética, a partir de marcadores COI e SNPs. Em um segundo momento, avaliamos: (1) a estrutura genética e o fluxo gênico em quatro espécies com diferentes potenciais de dispersão (os anfípodes *H. niger* e *Cymadusa filosa*, com desenvolvimento direto, e os moluscos *Pinctada imbricata* e *Costoanachis sertulariarum*, com larva planctônica), a partir de marcadores SNPs; (2) variações na diversidade e composição de espécies entre as assembleias de invertebrados associados às macroalgas marinhas; (3) a influência da distância geográfica, da variabilidade ambiental e do padrão de correntes sobre as dissimilaridades genética e da comunidade; e (4) a correlação entre a diversidade genética das quatro espécies e a diversidade de espécies da assembleia de invertebrados. Nós inicialmente verificamos que, para *Hyale niger*, apesar dos marcadores SNPs terem retomado um padrão de estruturação genética mais refinado do que os marcadores do gene COI, ambos indicaram que a distância ambiental foi a mais importante para explicar a diferenciação genética entre as populações, e que variações na morfologia do gnatópode 2 dos machos não apresentam relação com a genética, tratando-se possivelmente de plasticidade fenotípica. Observamos também que as espécies de desenvolvimento direto (anfípodes) apresentaram alguma estrutura genética, ao passo que os moluscos, com larvas planctônicas, não apresentaram nenhuma estrutura. *H. niger* apresentou maior estrutura genética que *C. filosa*, e o padrão de correntes teve o maior efeito sobre sua diferenciação genética. A maior diversidade de espécies foi encontrada em Ilha das Palmas, uma área de proteção integral, enquanto a menor diversidade foi observada no Lamberto, uma área impactada e desprotegida. Variações nos parâmetros de comunidade estão muito relacionadas a variações na abundância relativa de *H. niger*, indicando que esta espécie tem um papel chave na estruturação das assembleias de invertebrados de algas. Somente valores

de correlação não-positivos foram observados entre a diversidade genética das espécies e a diversidade de espécies, indicando que processos não-paralelos atuam sobre cada nível de diversidade, e que não se pode fazer inferências sobre um a partir do outro. Nosso trabalho traz uma nova contribuição acerca de estudos genômicos e seus fatores moduladores para invertebrados de algas, sendo um tópico ainda escasso na literatura, ainda que de grande importância para contribuir para a conservação destes hábitats costeiros.

ABSTRACT

Understanding the patterns of genetic structuring and connectivity in marine populations, as well as disentangling the modulating factors generating those patters, are crucial information allowing the elaboration of effective conservation measures of species in marine environment and, consequently, the marine habitats they occupy. Marine macroalgae form extensive beds that will constitute habitat for a great diversity of associated invertebrates, which can present a wide variety of shapes, life habits and dispersion potentials. In this work, we investigated the genetic structure and diversity of some seaweed-associated invertebrate species along São Paulo coast and evaluated the influence of some modulating factors. Initially, we studied the amphipod *Hyale niger* and the effects of geographic distances, environmental distances, and morphological variations on genetic differentiations, using both COI and SNPs molecular markers. Afterwards, we evaluated: (1) the genetic structure and gene flow patterns of four seaweed-associated invertebrate species with distinct dispersion potentials (the amphipods *H. niger* and *Cymadusa filosa*, both direct developers, and the mollusks *Pinctada imbricata* and *Costoanachis sertulariarum*, with a planktonic larva), using SNP markers; (2) variations in species diversity and composition among seaweed-associated invertebrate assemblages; (3) the influence of geographic distance, environmental variability, and water flow patterns on the genetic and assemblage dissimilarities; and (4) the correlations between genetic diversity of the four species and species diversity of seaweed-associated invertebrate assemblages. We initially verified that, for *H. niger*, even though SNPs revealed a finer spatial genetic structure than COI marker, both indicated that environmental distance better explained genetic differentiation among populations, and that variations in the morphology of the ganothopod 2 of males was not genetic-related, possibly being a case of phenotypic plasticity. We also observed that direct developers (amphipods) presented some genetic structure, whilst mollusks, with a planktonic larva, showed no structure among populations. *H. niger* presented a stronger genetic structure than *C. filosa*, and water flow patterns presented the higher effect on its genetic differentiation. The higher species diversity was found in Palmas Island, a marine protected area, while the lowest species diversity was found in Lamberto, an impacted unprotected area. Variations in community parameters were highly associated with variations in the relative abundance of *H. niger*, indicating the key role of this species for structuring seaweed-associated invertebrate assemblages. Only non-positive correlations values were found between genetic diversity of the four species and species diversity, indicating that non-parallel processes act on each diversity level, therefore one cannot be used as a surrogate for the other. Our work brings a new

contribution on genomic studies and their modulating factors for seaweed invertebrates, which is a scientific topic still scarce on literature, although of great relevance for the effective conservation of those coastal habitats.

SUMÁRIO

INTRODUÇÃO GERAL

As águas oceânicas recobrem cerca de 70% da superfície do mundo, e diante desta vastidão, os limites existentes entre os diferentes ambientes, hábitats e ecossistemas marinhos são muitas vezes difíceis de serem identificados, não só por sua amplidão, mas também pela existência de correntes marinhas, que conseguem conectar diferentes hábitats e regiões localizadas a milhares de quilômetros de distância umas das outras (Oleksiak 2018). Nas águas marinhas, uma enorme diversidade de organismos pode ser encontrada, com cerca de 2,2 milhões de espécies estimadas (Mora et al. 2011).

As espécies marinhas, de modo geral, podem ser divididas quanto ao local em que elas ocorrem na coluna d'água, entre espécies pelágicas – aquelas que vivem na coluna d'água, e espécies betônicas – aquelas que vivem sobre o fundo marinho. Dentre as espécies betônicas, os organismos podem ser classificados também quanto ao seu grau de movimentação, podendo ser sésseis (ou seja, completamente fixos ao substrato), sedentários (não são totalmente fixos ao substrato, mas se movimentam pouco) ou errantes (movimentam-se livremente pelo substrato) (Pereira & Soares-Gomes 2009).

As espécies bentônicas podem apresentar desenvolvimento direto, ou seja, não apresentarem uma fase larval, dessa maneira apresentando todo o seu ciclo de vida no bentos (ciclo de vida holobentônico), ou então podem apresentar desenvolvimento indireto, com uma fase larval pelágica que, após viver algum tempo na coluna d'água, irá se assentar e dar origem aos juvenis de hábito bentônico (Pereira & Soares-Gomes 2009).

Supostamente, as espécies bentônicas com desenvolvimento indireto e uma fase larval pelágica são capazes de dispersar-se por longas distâncias, através da ação das correntes marinhas, mesmo apresentando mobilidade reduzida após completarem seu desenvolvimento e assentarem ao substrato (Bierne et al. 2016). Este seria um dos principais modos de dispersão de espécies bentônicas no ambiente marinho, e espécies com ciclo de vida holobentônico apresentariam um menor potencial de deslocamento, ficando mais restritas ao seu local de origem (Foggo et al. 2007; Cowen & Sponaugle 2009). No entanto, outros modos de dispersão para estas espécies também são conhecidos e já foram descritos, como por exemplo a emissão de propágulos por muitas espécies de algas marinhas (Norton 1992); pequenos invertebrados de tamanho reduzido que emergem à coluna d'água e dispersam-se através das correntes ("drifting") (Havermans et al. 2007), ou então o transporte de organismos em associação com estruturas flutuantes, tais como macroalgas, detritos marinhos e estruturas abióticas como pedra-pomes e itens plásticos, processo conhecido como "rafting" (Thiel & Gutow 2004; Bravo

et al. 2011). Entretanto, o modo e o potencial de dispersão de muitas espécies marinhas permanecem desconhecidos até hoje, devido à dificuldade de se rastrear e estudar tais eventos e o uso de ferramentas moleculares para melhor compreender-se os padrões de dispersão, fluxo gênico e conectividade dos organismos e de suas populações tem se mostrado uma alternativa essencial para se compreender os limites existentes no vasto ambiente marinho.

Tradicionalmente, estudos genéticos populacionais têm usado marcadores moleculares neutros de genes específicos para se estimar os padrões de diferenciação genética entre populações marinhas (Oleksiak 2018). Devido a seu suposto alto grau de dispersão, associado a uma alta fecundidade e elevados tamanhos populacionais, características normalmente atreladas a essas populações (Bierne et al. 2016), espera-se qu e estas apresentem baixa diferenciação genética entre populações para estes loci neutros. Eventos de dispersão por longa distância, ainda que raros, podem levar a um processo mais acentuado de homogeneização genética entre as populações (Waples 1998). Além disso, em populações maiores (elevado tamanho populacional), processos neutros apresentariam um menor efeito sobre as alterações populacionais, com uma menor diferenciação genética entre elas devido à deriva genética (Kliman et al. 2008). No entanto, o advento de novas técnicas moleculares, que nos permitem deixar de olhar somente para genes específicos e passar a olhar para genomas completos ou pequenas e numerosas representações ao longo do genoma, tem mudado essa perspectiva e mostrado que populações marinhas podem apresentar elevada diferenciação genética, diferentes padrões de conectividade, podendo ser influenciados por fatores físicos, biológicos, e elucidando o papel de processos adaptativos também na determinação destes padrões (Oleksiak 2018), sendo estes temas de interesse da Genômica Populacional.

Estudos genômicos, ao permitirem uma amostragem mais ampla do genoma, avaliando polimorfismo em diferentes loci ao longo do genoma em paralelo e simultaneamente, conseguem revelar padrões de variabilidade genética em escalas ecológicas, espaciais e temporais mais refinadas (Mardis 2008; Hohenlohe et al. 2018; Oleksiak & Rajora 2019). Além disso, as análises genômicas requerem poucas informações genéticas e moleculares disponíveis a priori sobre as espécies em estudo, o que é de extrema importância para se estudar a diversidade marinha, visto que conhecimentos prévios acerca de muitas das espécies que vivem neste ambiente ainda são escassos, devido à dificuldade de estudá-las (Oleksiak & Rajora 2019).

Conforme foram se estabelecendo conhecimentos mais aprofundados sobre os padrões de estruturação genética e conectividade para as espécies marinhas, novas questões

passam a se tornar centrais no estudo destes organismos, como por exemplo quais seriam os principais fatores responsáveis por determinar os padrões demográficos das populações marinhas, para isso buscando integrar informações genômicas, conhecimento sobre os padrões de movimentação e modo de vida das espécies e características ambientais e modelos oceanográficos (Pérez-Portela & Riesgo 2018; Oleksiak & Rajora 2019). Compreender como variações espaciais e ambientais podem atuar como moduladores da resposta genômica das espécies é interesse da área conhecida como "Seascape Genomics", que integra conceitos de Ecologia da Paisagem, análises espaciais e processos oceanográficos, buscando quantificar gradientes espaciais de características ambientais que possam ser relevantes enquanto atributos da paisagem, gerando variabilidade genômica (Riginos et al. 2016).

O conhecimento acerca dos padrões de estruturação genômica das espécies marinhas, conectividade entre suas populações e o levantamento de características essenciais da paisagem marinha para determinar tais padrões é de extrema importância para o desenvolvimento de planos efetivos de conservação desta biodiversidade (Chatzigeorgiou et al. 2014; Heyden et al. 2014; Selkoe et al. 2016). O estabelecimento de áreas protegidas nos ecossistemas marinhos é de particular importância, visto que: (1) grande parte da biodiversidade presente nesses ambientes, incluindo aspectos da história de vida e dinâmica populacional das espécies que ali vivem, ainda é amplamente desconhecida, o que dificulta a previsibilidade dos efeitos e das respostas destas espécies a distúrbios naturais e antrópicos; (2) os ecossistemas marinhos promovem importantes serviços ambientais, como ciclagem de nutrientes, sequestro de carbono e proteção das regiões costeiras; e (3) os ecossistemas marinhos apresentam um papel essencial para populações humanas, cujo desenvolvimento econômico-social gera um impacto sobre as águas marinhas (Parsons et al. 2014).

A degradação de habitats, o aquecimento global e a poluição estão entre os principais impactos cujos efeitos vêm sendo observados sobre os ambientes costeiros (Miller & Ayre 2008; Parsons et al. 2014), e a preocupação com o crescimento de tais impactos sobre o oceano têm aumentado o enfoque da comunidade científica sobre o estabelecimento de áreas de proteção marinhas ("marine protected areas", ou MPAs) (Lubchenco et al. 2003; Miller & Ayre 2008; Gill et al. 2017), as quais devem atuar tanto como fontes de recrutas para áreas adjacentes desprotegidas, como possibilitar uma dispersão suficiente entre elas para manutenção da conectividade entre áreas protegidas, dessa maneira assegurando a essas áreas um papel eficiente de conservação (Palumbi 2003; Miller & Ayre 2008; Christie et al. 2010).

Dentre os habitats costeiros, os bancos de macrófitas possuem ampla susceptibilidade a impactos antropogênicos, uma vez que podem acumular diferentes tipos de

contaminantes em seus tecidos e terem sua abundância e diversidade afetadas em locais muito impactados (Roberts et al. 2008). Estima-se que aproximadamente 29% dos habitats de algas marinhas desapareceram desde o século XIX, totalizando cerca de 110km² perdidos ao ano desde 1980 (Waycott et al. 2009). As macroalgas destacam-se devido a sua alta produtividade (Christie et al. 2009; Roberts et al. 2008) e complexidade estrutural que propicia sítios reprodutivos, abrigo contra predadores, maior estabilidade de fatores abióticos, e recurso alimentar para uma grande diversidade de espécies que vivem associadas a elas (Christie et al. 2009). Desta forma, impactos antropogênicos sobre os bancos de macroalgas resultam em desequilíbrios neste sistema com consequências para as muitas espécies de animais que ali vivem associadas (Roberts et al. 2008).

As macrófitas e sua fauna associada também atuam como um elo entre diferentes níveis tróficos em ambientes costeiros, uma vez que exportam grandes quantidades de nutrientes, como carbono, fósforo e nitrogênio, para cadeias tróficas marinhas, tanto por transferência direta de matéria, como através de matéria orgânica dissolvida e/ou particulada, assim, sua perda pode afetar negativamente a produtividade de espécies individuais ou grupo de espécies, com propagação de seus efeitos (Airoldi et al. 2008). Portanto, a análise sobre a diversidade de macroalgas e invertebrados associados pode fornecer informações importantes e que implicam em consequências relevantes para os demais níveis tróficos e, então, para todo equilíbrio das cadeias tróficas dos ecossistemas marinhos em que estão inseridos.

Portanto, uma melhor compreensão dos padrões de estruturação, dispersão e conectividade das populações de espécies que vivem associadas às macroalgas marinhas, bem como sobre os principais fatores moduladores destes padrões, é de fundamental importância para servirem de subsídio ao estabelecimento de medidas efetivas de conservação destes importantes habitats marinhos. Neste estudo, investigamos a influência de diferentes fatores moduladores – distância geográfica, variabilidade ambiental, variações fenotípicas, parâmetros da comunidade e modelos oceanográficos – sobre a genética e genômica populacional e diferentes espécies-chave de invertebrados associados a macroalgas marinhas ao longo do litoral paulista, incluindo no estudo áreas com diferentes status de conservação. No capítulo 1, buscamos investigar, a partir do uso de diferentes marcadores moleculares (COI e SNPs), a diferenciação genética e a história demográfica do anfípode *Hyale niger* na área de estudo, bem como avaliar as contribuições da distância geográfica, fatores ambientais e alterações morfológicas na estruturação de suas populações. No capítulo 2, nós comparamos os padrões de estruturação genômica, fluxo gênico e suas relações com a distância geográfica, variáveis ambientais e modelos oceanográficos de circulação de correntes, entre quatro espécies de

invertebrados associados a macroalgas com diferentes tipos de desenvolvimento, sendo dois anfípodes com desenvolvimento direto holobentônicos – *Hyale niger* e *Cymadusa filosa*, e duas espécies de moluscos com desenvolvimento indireto e larvas planctônicas – o bivalve *Pinctada imbricata* e o gastrópode *Costoanachis sertulariarum*.

CHAPTER 1: DIFFERENT FACTORS MODULATING GENETIC AND MORPHOLOGICAL VARIATIONS OF A SEAWEED-ASSOCIATED MARINE AMPHIPOD

Pedro A. S. Longo; Marianne Azevedo-Silva; Karine F. R. Mansur; Thais A. Marinho; André G. Madeira; Anete P. de Souza; Shun K. Hirota; Yoshihisa Suyama; Gustavo M. Mori; Fosca P. P. Leite

Introduction

Unraveling the patterns of dispersal and connectivity in natural populations is fundamental for better understanding species dynamics in nature, how they interact with their habitats, and ultimately to guide decision for the conservation of species and habitats (Levin 2006; Christie et al. 2010; Magris et al. 2016; Pessanha et al. 2021). In marine systems, tracking the dispersal and connectivity of benthic species is challenging due to their general high capacity of displacement through water currents, either by larval dispersion during planktonic life stages or as adults, using, for instance, buoyant structures (Thiel & Gutow 2005; Levin 2006; Buston & D'Aloia 2013; D'Aloia et al. 2015). Genetic studies and the use of molecular techniques have risen as fundamental mechanisms for dealing with those issues and for revealing patterns of distribution of marine species (Burton 2009; Heyden et al. 2014; Xuereb et al. 2019).

Genetic structure and gene flow among populations may be modulated by geographic distances, which can limit dispersal and thus increase genetic divergence in allele frequencies, a model known as Isolation by Distance (IBD) (Wright 1943; Bradburd et al. 2013). Alternatively, variations in environmental features can result in processes such as dispersal limitation, biased dispersal or selection against immigrants leading to local adaptation of populations, a model known as Isolation by Environment (IBE) (Bradburd et al. 2013; Wang & Bradburd 2014). Ultimately, phenotypes can also lead to genetic differentiation, depending on the trait function and how it interacts with the environment, even though phenotypic variation can also occur without an associated genetic divergence, and different biological and evolutionary mechanisms can be responsible for partitioning genetic and phenotypic variations among populations (Zamudio et al. 2016). Understanding how those non-mutually exclusive factors (Sexton et al. 2014), can explain the distribution of genetic variability in marine species over space is a topic of interest in the field of Seascape Genomics (Liggins et al. 2019). Also, clarifying those patterns is essential to predict the impact of environmental changes on marine populations, providing conservation guidance for preventing biodiversity loss (Zamudio et al. 2016; Wee et al. 2019; Selmoni et al. 2020).

Human-induced impacts on coastal environments, such as water pollution, introduction of invasive species, and climate change, can have major ecological consequences, including biodiversity and habitat losses (Lu et al. 2018; He & Silliman 2019; Pyšek et al. 2020). Macroalgae habitats are particularly susceptible and have been facing reductions over the last decades (Gorman et al. 2020). As seaweed beds play a major role as ecosystem engineers, forming new habitat and providing multiple resources for marine species (e.g. food, protection against predators and stressful environmental conditions, and sites for reproduction and spawning) (Christie et al. 2009; Cacabelos et al. 2010; Fulton et al. 2020), such losses affect coastal biodiversity at many levels (Roberts et al. 2008; Mayer-Pinto et al. 2020; Mancuso et al. 2021).

Among seaweed-associated invertebrate assemblages, amphipods stand out as one of the most numerous and diverse groups living in those habitats (Leite & Turra 2003; Tanaka & Leite 2003; Leite et al. 2021; Longo et al. 2021). These organisms comprise both free-living and tube-building species (Tanaka & Leite 2003; Jacobucci et al. 2009) with a great variety of feeding habits (Jacobucci et al. 2009; Guerra-García et al. 2014). These organisms also present direct development (i.e. they lack a planktonic phase) (Väinölä et al. 2007). Due to these features, amphipods are expected to have a limited dispersal potential, which could result in highly structured populations (Sherman et al. 2008), as has been demonstrated in previous studies (Baird et al. 2012; Walters et al. 2022; however see Tanaka & Leite 2004; Peres et al. 2019). Amphipod dispersal ability may vary according to growth stage, life habit (Bueno & Leite 2019) and it may also depend on external structures, like rafting macroalgae, that seems like a major hypothesis for explaining longer distances dispersal (Thiel & Gutow 2004; Haye et al. 2012; Peres et al. 2019). However, the mechanisms underlying amphipod dispersal and the distinct displacement potentials among different species remains to be further enlightened. Thus, studies on population genomics and seascape genomics, including different molecular markers are crucial for unraveling their dynamics and contributing for the conservation of those animals and the habitats they live on.

This study aims to give a first contribution to understand the patterns of genetic structuring and dispersal potential of the highly representative macroalgae-associated amphipod *Hyale niger* (Haswell, 1879). Particularly, we (1) investigate the genetic differentiation and describe the demographic history of *H. niger* populations in a fine spatial scale of dozens of kilometers, and (2) evaluate the relative contributions of geographic distance, environmental distance, and morphological changes for the genetic structuring of populations. We expect that *H. niger* presents highly structured populations and limited dispersal potential, even in a small

spatial scale, due to its direct development and lack of a planktonic larval phase. Moreover, we expect geographic distance to be the predominant factor modulating genetic variation, because environmental traits among populations at this fine scale are relatively similar.

Material and Methods

Sample collection

We selected eight localities along the São Paulo coast, in southeastern Brazil (Figure 1). During the austral summer of 2018, we randomly sampled thirteen individuals of the predominant macroalga species in the infralittoral zone. Algae fronds were wrapped in a 0.2-mm-mesh bag to prevent loss of the associated fauna and subsequently thawed and washed in seawater to remove associated fauna. For SNP analyses, one individual of the amphipod *Hyale niger* was obtained for each algal sample, except for the samples where no individuals were found. For COI analyses, from five randomly selected algal samples from each locality, we collected five individuals of *H. niger*, totalizing a maximum of 25 specimens per site. Amphipods were immediately preserved in absolute ethanol and stored in -14ºC for subsequent genetic analyses. Separately, six samples of the predominant macroalga species were randomly collected in each locality for the estimation of macroalgae wet weight, which we considered as a proxy for habitat quantification.

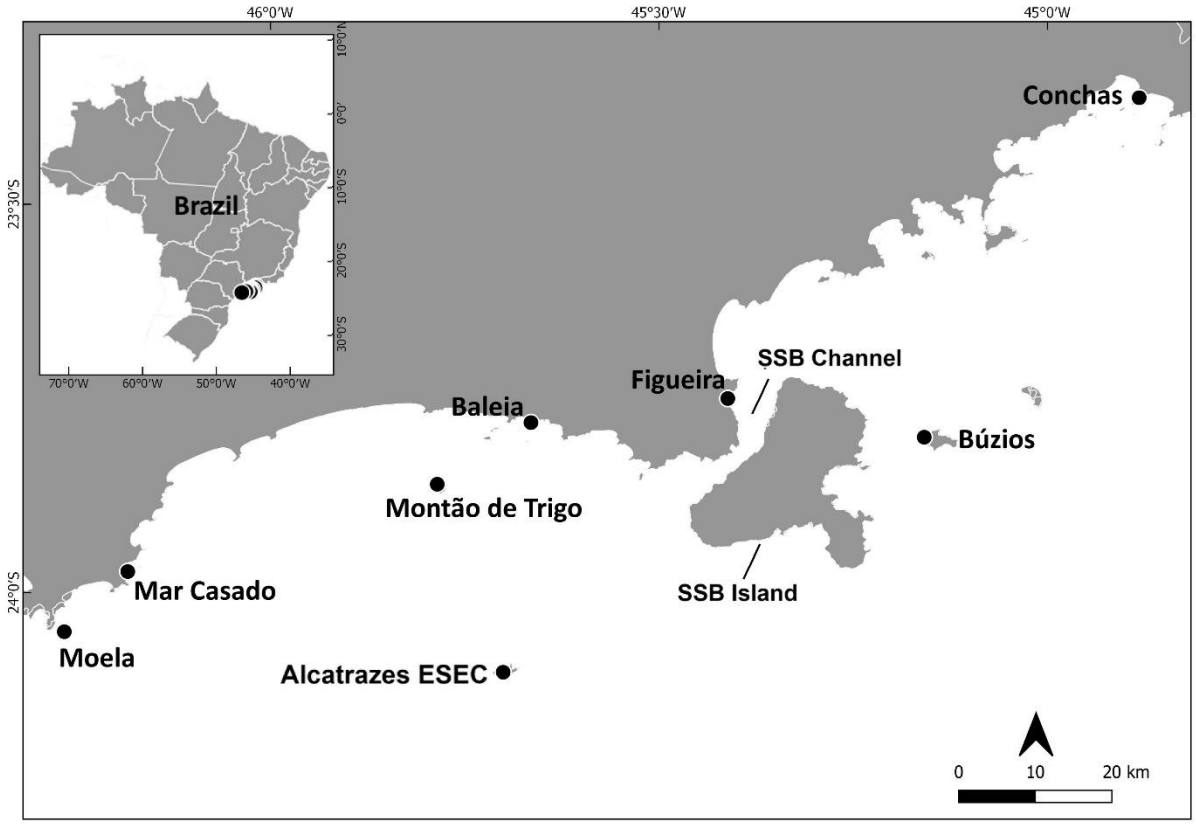


Figure 1. Map of the study area. SSB – São Sebastião.

Molecular biology procedures

We extracted genomic DNA of *H. niger* with DNeasy Blood & Tissue Kit (QIAGEN), following the manufacturer's protocol for insects. To amplify the mitochondrial gene cytochrome C oxidase I (COI), we carried out PCR using the universal primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994). PCR reactions were performed in a final volume of 20µl, containing 2.25ng DNA, 0.2µM each primer, 0.1µM each dNTP, 2X PCR buffer, 1.5µM $MgCl_2$, 0.8 unit Taq polymerase, and 20µg Bovine Serum Albumin. PCR amplifications were conducted following the conditions: 95°C for 4min, 10 x (97°C for 45s, 45ºC for 1min (touchdown with a 0.5°C reduction per cycle), 72°C for 1min and 30s), 35 x (97°C for 45s, 40°C for 1min, 72°C for 1min and 30s) and 72°C for 10min. Amplification products were purified by a standard polyethylene glycol (PEG) precipitation protocol and double sequenced using BigDye Terminator v3.1 (Applied Biosystems) in a ABI3500 automated sequencer (Applied Biosystems). Sequences were edited using software ChromasPro v. 2.1.9 (Technelysium Pty Ltd) and compared with GeneBank database through BLAST (Altschul et al. 1990). COI sequences were checked for stop codons after translating with the invertebrate mitochondrial code and determining correct reading frame in GENEIOUS version 2021.2.2 (https://www.geneious.com).

To obtain, validate and genotype SNPs we constructed and sequenced MIG-seq ("Multiplexed Inter simple sequence repeat – ISSR – Genotyping by Sequencing") libraries, as described by Suyama & Matsuki (2015). Shortly, hundreds to thousands of ISSR loci were selectively amplified using eight pairs of 12 base di- and trinucleotide microsatellites to drastically reduce genome complexity. SNP identification and selection was performed following Suyama and Matsuki (2015). The first 14 bases (12 nucleotides of the microsatellite used to construct the MIG-seq libraries, and two bases of first PCR primers) of read 2 were removed using FASTX-Toolkit (http://hannonlab.cshl.edu/fastx_toolkit/), which was also used to filter reads by quality (Phred Q score = 30 for at least 40% of the read bases). The filtered reads were then used as input for STACKS 1.15 (Catchen et al. 2011) for *de novo* assembly. We removed sequences with more than 30% missing data using the VCFtools v.0.1.12b (Danecek et al. 2011) and retained only biallelic SNPs, high quality sequences for downstream analysis.

Genetic analysis

COI data

We quantified the genetic diversity of *H. niger* populations by haplotype diversity (*h*) and nucleotide diversity (π) (Nei 1987) using 'pegas' package (Paradis 2010), in software R (R Core Team 2021). The pairwise F_{ST} among samples was estimated with ARLEQUIN 3.5 (Excoffier et al. 2010). The genetic structure of populations was evaluated by analysis of molecular variance (AMOVA) also using ARLEQUIN and we tested three hypotheses: (1) considering two hierarchical levels: (i) individuals from different samples within the same site, and (ii) individuals from different sites; (2) including the difference among genetic groups identified using COI data; and (3) including the difference among genetic groups indicated with SNP data. We considered a significant departure from a random distribution and the maximum variance among groups (ΦCT) as the criteria for determining the best hypothesized arrangement. The relationship among COI haplotypes was investigated through the construction of a minimum spanning network using software PopART v.4.8.4 (Leigh & Bryant, 2015).

To investigate deviations from neutrality, mismatch distribution computations and neutrality tests were performed using ARLEQUIN 3.5 (Excoffier & Lischer 2010). The sum of the squares deviation (SSD) and the raggedness index (*r*) were used as estimators of mismatch distribution, and Tajima's D (Tajima 1989) test and Fu's Fs test (Fu 1997) were used as neutrality tests. As a demographic parameter, we calculated Tau, which represents the time since expansion expressed in units of mutational time (Rogers 1995). Tau values were transformed to estimate the real time since expansion (*t* in generations) with the equation t = Tau/2u (Rogers & Harpending 1992), where u = μ x time of one generation x length of segment. u is the mutation rate for the whole sequence studied and μ is the mutation rate for COI. The mutation rates of COI gene was estimated as 1.9% per million years and a generation time of one month was considered for *H. niger* (Campbell et al. 2020).

We also used the Bayesian coalescent approach implemented in BEAST 1.7.4 (Drummond et al. 2005) within the CIPRES portal (Miller & Pfeiffer 2010) to infer historical demography. This procedure was used for: (1) individuals from all localities; (2) two genetic groups identified with COI data separately. We used the Bayesian skyline plot model (Drummond et al. 2006) assuming a piecewise constant model with ten coalescent intervals; Markov-Chain-Monte-Carlo simulations were run under the HKY+G model with four gamma categories using a strict molecular clock (Drummond et al. 2006). We used the divergence rate of the COI region (1.9% per million years) and ran six independent runs with 30 million iterations each. Tracer 1.5 (Drummond & Rambaut 2007) was used to assess convergence of

runs and the Effective Sample Size (ESS) of each parameter. To obtain an adequate effective sample size (ESS ≥200), the six independent runs performed for each simulation were combined using the Logcombiner utility of the BEAST 1.7.4 package. The resulting file was used to estimate population size change through time, that was visualized by the Bayesian skyline plot computed with Tracer 1.5.

SNP data

Initially, two different methods for the detection of loci putatively under selection and based on population differentiation (F_{ST} outliers) were performed, considering each sampling site as a population: FDIST (Fagundes et al. 2007), implemented in the LOSITAN software (Antao et al. 2008); Bayesian method of population differentiation implemented in the BAYESCAN 2.1 software (Foll and Gaggiotti 2008). Complementarily, we used PCADAPT (Luu et al. 2017) to detect signs of natural selection without any prior information of grouping of individuals. We considered as loci putatively under selection if all three methods indicated that a given locus is not neutral, a conservative approach due to the high rates of false positives given by F_{ST} outliers methods (Bierne et al. 2013; Francois et al. 2016). Only three non-neutral loci were detected and disregarded in downstream analyses.

For the estimation of genetic diversity of *H. niger* in each locality, we calculated the alellic richness (*Ar*), the observed heterozygosity (*Ho*), and the gene diversity (*Hs*) using 'hierfstat' package (Goudet 2005), and the proportion of heterozygous loci (*PHt*) with 'genehet' (Coulon 2010) package in software R. The pairwise F_{ST} among sampling sites was also calculated in 'hierfstat' package.

The genetic structure among populations was investigated with STRUCTURE v.2.3.4 (Pritchard et al. 2000), in which the number of populations (K) was allowed to vary from 1 to 11. We performed 20 runs for each K, with a burn-in period of 50,000 followed by 1,000,000 MCMC iterations. The most likely number of genetic groups was selected based on ΔK *ad hoc* statistic (Evanno et al., 2005) using the program STRUCTURE HARVESTER (Earl & von Holdt 2012). To identify the optimal alignment of inferred clusters across different values of K, we used the software CLUMPAK (Kopelman et al. 2015), and the graphic for the best K value was built with the 'Distruct' application also implemented in CLUMPAK. Also, we carried out Discriminant analysis of principal components (DAPC, Jombart et al., 2010) to describe the genetic structure of our data in 'adegenet' package (Jombart 2008). We considered the clusters identified with STRUCTURE as prior information while the best number of principal components (PCs) was selected according to the α-score function in 'adegenet'. Finally, the genetic structure of populations was also tested by an analysis of molecular variance

(AMOVA) in software ARLEQUIN. Three different AMOVA hypotheses were tested: (1) considering individuals from different sites; (2) including the difference among genetic groups indicated by COI data; and (3) including the difference among genetic groups indicated by SNP data.

Morphometric analysis

To investigate the relationship between morphological variations and genetic differentiation among populations of *H. niger*, we used as a proxy measurement of the outer surface of the right gnathopod 2 propodus of adult males, under a geometric morphometric framework (Zelditch et al. 2004). The posterior gnathopod is a rigid and thus well-preserved structure in amphipods, that has been associated with relevant behavioral features such as reproduction, copulation, and stabilization onto host macroalgae (Appadoo & Mayers 2003; Hume et al. 2005; Nahavandi et al. 2011). The association of morphology of this structure with genetic variation has also already been studied for other amphipod species (Peres et al. 2019).

Individuals used for morphometric analysis were the same used for genetic analysis of COI data (except when we used female individuals due to the lack of enough males, or when right gnathopod 2 of males was absent, in which cases those individuals were removed from the morphometric approach). Images were acquired using a Zeiss AxioCam camera and AxioVision software v.4.8 (Carl Zeiss). Nine landmarks were selected (Supplementary material 1) and digitized using the software tpsDig version 2.30 (Adams et al. 2004), and general Procrustes analysis (GPA) was used to quantify shape and size variation, by using a least-squared algorithm to align homologous landmarks, removing information unrelated to shape (Rohlf & Slice 1990). The GPA and most statistical analyses were carried out using the MorphoJ software package, version 1.06d (Klingenberg 2011). A principal components analysis (PCA) was carried out to identify and account for the redundancy of the variation/covariation matrix of the GPA shape coordinates, besides displaying the major shape variation features. To evaluate the variation in shape and size of propodus between insular and coastal populations (which was the main trend observed in the PCA analysis), a Procrustes ANOVA and a Centroid Size (the square-root of the summed squared distances between all landmarks, Zelditch et al. 2012) ANOVA, respectively, were performed in R software using 'geomorph' package (Adams et al. 2004). To test the separation between insular and coastal populations, we performed a linear discriminant analysis (LDA). In MorphoJ, we also obtained the Procrustes distance matrix, a pairwise comparison of the shape among populations from different localities, which was used in the association tests with genetic distance. To study the relationship between the variation of geometric shape and size of the propodus of male

gnathopods 2 in *H. niger*, we performed a multivariate regression analysis of the shape variables and centroid size. Finally, as we observed a similar coastal-insular pattern for both *H. niger* morphology and macroalgae wet weight, we performed a linear regression analysis between these two variables using the mean values obtained at each site.

Geographic and Environmental distances

The pairwise geographic distances among localities were obtained though the calculation of Euclidean distance between pairs of localities considering the geographic coordinates (WGS-84 world coordinate system) of each site. To investigate the effect of environmental differences on genetic differentiation among *H. niger* populations, we used the macroalgae wet weight measures we collected in this study and 19 environmental variables for each sampling locality, including 10 oceanographic variables from BioOracle online database (Tyberghein et al. 2012; Assis et al. 2017) and 9 oceanographic variables from MARSPEC online database (Sbrocco & Barber 2013). Variables were obtained with the package 'sdmpredictors' (Bosch et al. 2017) and highly correlated variables ($r > 0.7$) were previously removed with the function *removeCollinearity* from package 'virtualspecies' (Leroy et al. 2016) in software R. With this environmental matrix, we performed a principal components analysis (PCA), and with the mean of the scores for the first three principal components (which retained > 70% of the total variance of environmental data) we calculated the Euclidean distances between pairs of populations.

Association tests

To investigate the relationship between genetic distances for both COI and SNP markers, and geographical, environmental, and morphometric factors, we initially conducted simple Mantel tests to assess correlations between geographic, environmental, and morphometric distances with genetic differentiation. Then, partial Mantel tests (Smouse et al. 1986) were performed to evaluate the effect of each factor when conditioned to another factor as a covariate (Legendre 1993). Both Mantel tests were conducted using the 'ecodist' package (Goslee & Urban 2007), with 10000 permutations. Finally, we also conducted a multiple matrix regression with randomization (MMRR) using the *MMRR* function in R with 10000 permutations (Wang 2013), to estimate the independent effects of each predictor variable on genetic differentiation. Since environmental factor was suggested as the main effect affecting genetic variation, we performed a MMRR analysis and partial Mantel tests for each

environmental variable separately, considering geographic distance as a covariable, to identify the most important environmental features to modulate genetic structuring of *H. niger*.

Results

Genetic analysis

Fragments of COI gene with 584 bp in length were obtained from 169 individuals of *Hyale niger* and 91 haplotypes were identified, which presented 89 polymorphic sites, with 48 singletons and no *indels*. As for SNP data, a total of 513 biallellic SNPs were retained after bioinformatics efforts for reads filtering, quality control and removal of the three loci pointed as putatively under selection. For each locality, the numbers of haplotypes, haplotype diversity (h) and nucleotide diversity (π) for COI data, and the number of individuals, allelic richness (Ar), observed heterozygosity (H_O), gene diversity (Hs) and proportion of heterozygous loci (PHt) for SNP data are presented in Table 1. Haplotype diversity was, in general, high for all populations, ranging from 0.7879 in Moela to 0.9819 in Montão de Trigo. As for nucleotide diversity, higher values were found for the populations of Alcatrazes, Búzios and Conchas, which presented π higher than 0.0070; while the lowest values were found for the Moela, Mar Casado, Baleia and Figueira populations, with π lower than 0.0045. Genetic diversity parameters did not show expressive variation among populations from different localities, as illustrated by the lack of significant differences in PHt (ANOVA, F = 0.838, P = 0.56).

Table 1. Genetic diversity parameters of the eight populations of *H. niger* based on COI and SNP markers. *h*: nucleotide diversity; π: haplotype diversity; *Ar*: alellic richness; *Ho*: observed heterozygosity; *Hs*: gene diversity; *PHt*: proportion of heterozygous loci.

Site	COI					SNP				
	N	Number of haplotypes	Private haplotypes	Genetic Diversity		N	Genetic diversity			
				h	π		*Ar*	*Ho*	*Hs*	*PHt*
Búzios	22	22	12	0.9481	0.0085	9	1.2736	0.1579	0.1363	0.8822 ± 0.0050
Conchas	20	20	10	0.9526	0.0072	6	1.2881	0.1684	0.1409	0.8844 ± 0.0034
Alcatrazes	21	21	9	0.9643	0.0086	9	1.2767	0.1621	0.1376	0.8793 ± 0.0038
Figueira	19	19	10	0.8905	0.0044	13	1.2897	0.1699	0.1445	0.8748 ± 0.0070
Montão de Trigo	24	24	17	0.9819	0.0067	12	1.2721	0.1567	0.1360	0.8884 ± 0.0053
Baleia	19	19	9	0.9240	0.0043	10	1.2812	0.1621	0.1403	0.8805 ± 0.0070
Mar Casado	22	22	10	0.9221	0.0038	9	1.2932	0.1707	0.1461	0.8754 ± 0.0031
Moela	22	22	7	0.7879	0.0028	6	1.2882	0.1704	0.1438	0.8771 ± 0.0040

Pairwise F_{ST} for COI indicated the formation of two main genetic groups from all localities: one with the populations from Alcatrazes, Búzios and Conchas, and the other with the remaining populations (Figure 2a, upper panel). As for SNP data, the pairwise F_{ST} analysis showed that even though the separation of Alcatrazes, Búzios and Conchas from the remaining populations is also true, the latter may be further divided in three main groups: one with the individuals from Baleia and Montão de Trigo, another formed by individuals from Mar Casado and Moela, and the last one with individuals from Figueira (Figure 2a, bottom panel). The Bayesian STRUCTURE assignment analysis confirmed this pattern, with formation of these four distinct clusters (K = 4, Figure 2b, Supplementary material 2), and the scatter plot from DAPC analysis considering K = 4 reinforced this result (Figure 2c). AMOVA results for both COI and SNP data revealed that most of the total variance lies within localities and supported the distinct genetic grouping revealed by each marker (Table 2).

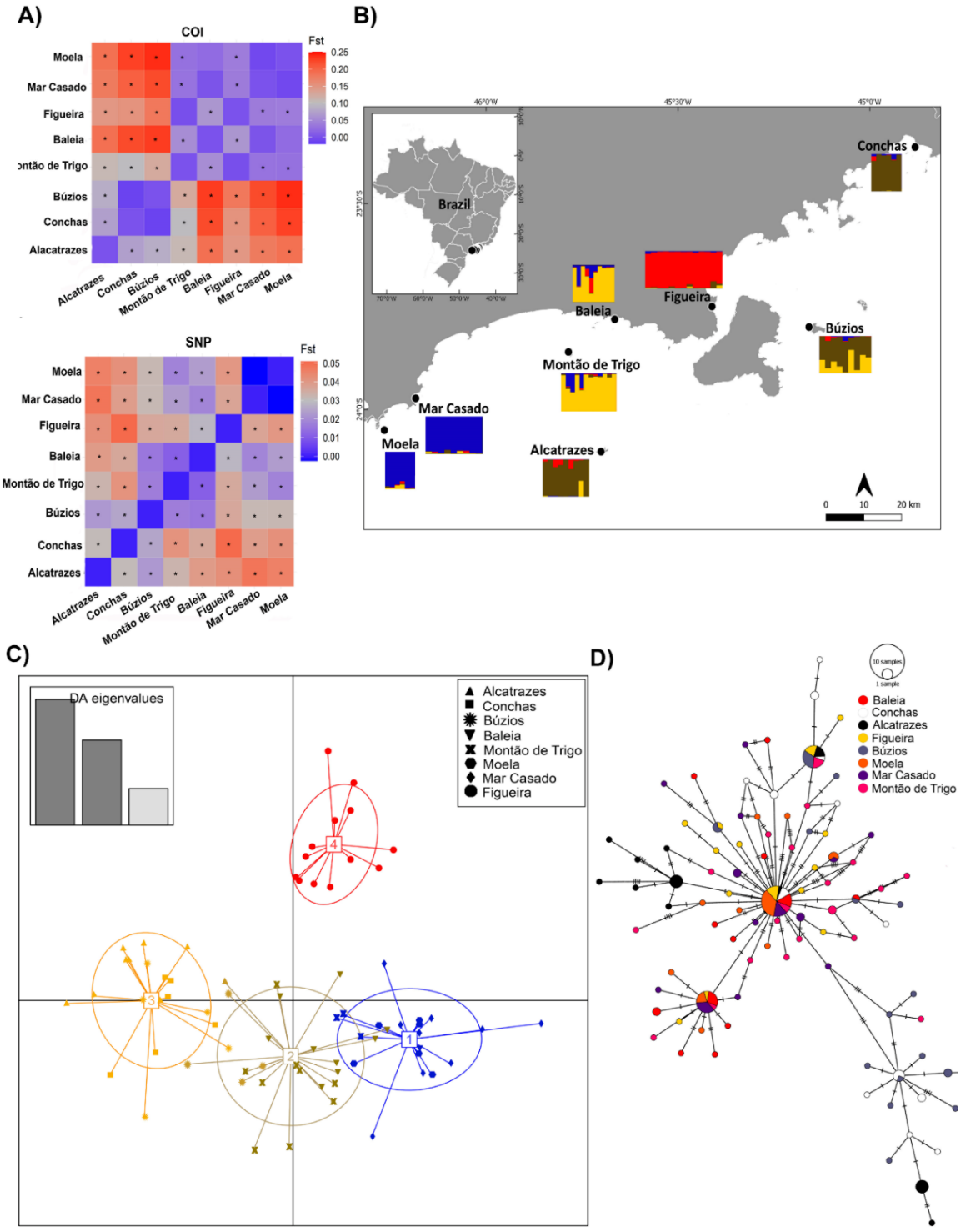


Figure 2. Population genetic structure of *Hyale niger*. A: heatmap of the pairwise F_{ST} among populations from the eight sampled locations (upper: COI markers, bottom: SNP markers, * indicates statistically significant genetic differentiation). B: Map showing each locality and respective population assignment based on STRUCTURE analysis considering 513 SNPs

and K = 4.. C: Scatterplot for the Discriminant Analysis of Principal Components (DAPC) for *H. niger* individuals, considering the two first principal coordinates and K = 4. D: Minimum spanning network based on the COI haplotypes. Each circle represents a haplotype, the area of the circle in proportional to the number of individuals with each haplotype. Different colors represent the different sampling areas.

Table 2. Analysis of Molecular Variance (AMOVA) for COI and SNP markers, testing for the differences among sites (AMOVA 1), between the two genetic groups indicated by COI markers (AMOVA 2) and among the four genetic groups indicated by SNP markers (AMOVA 3). Values in bold indicate statistically significant results.

Source of Variation	**COI**				**SNP**			
	Variance components	*Fixation index*	*% variation*	*P-value*	*Variance components*	*Fixation index*	*% variation*	*P-value*
AMOVA 1 (per site)								
Among sites	0.23434	0.11975	11.98	**< 0.0001**	0.90472	0.06593	6.59	**< 0.0001**
Among fronds within site	0.04807	0.02791	2.46	0.1711	-	-	-	-
Within fronds (COI) / Within sites (SNP)	1.67442	0.14432	85.57	**< 0.0001**	12.81865	-	93.41	-
AMOVA 2 (two main genetic groups)								
Among groups	0.33103	0.15683	15.68	**0.0176**	0.17727	0.01284	1.28	0.0718
Among sites within groups	0.06528	0.03668	3.09	**< 0.0001**	0.81512	0.05979	5.9	**< 0.0001**
Within sites	1.71448	0.18775	81.22	**< 0.0001**	12.81865	0.07185	92.81	**< 0.0001**
AMOVA 3 (four main genetic groups)								
Among groups	0.18145	0.09189	9.19	0.0596	0.52747	0.03821	3.82	**0.0013**
Among sites within groups	0.09153	0.13825	4.64	**< 0.0001**	0.45791	0.03449	3.32	**< 0.0001**
Within sites	1.70156	0.05105	86.18	**< 0.0001**	12.81865	0.07138	92.86	**< 0.0001**

The minimum spanning network for COI data presented a star-shape configuration with three haplotypes shared by most populations, from which most of the other exclusive haplotypes diverged by one or two mutations (Figure 2d). The central and most abundant haplotype was shared by all populations except Búzios. Even though there is not a clear geographical pattern in the haplotype network structure, it is noteworthy that most haplotypes from Alcatrazes were derived from one main local haplotype, and that some haplotypes from Búzios, Conchas and Alcatrazes presented a common exclusive diversification path.

The mismatch distribution obtained from COI data for all populations did not differ significantly from a sudden expansion model (Table 3). As for neutrality tests, Fu's Fs was significant and negative for all populations, also indicating the occurrence of a sudden expansion, whereas Tajima's D was negative and significant for all populations except Alcatrazes, Conchas and Búzios (Table 3). A Bayesian Skyline Plot was constructed considering (i) all *H. niger* individuals from São Paulo coast sampled in this study, (ii) individuals from Alcatrazes, Búzios and Conchas separately, and (iii) individuals from the remaining sampling sites separately. Mismatch distribution indicate that *Hyale niger* populations from Alcatrazes, Búzios and Conchas originated earlier than remaining populations (Table 3). This result is consistent with the results from the Bayesian Skyline Plots (Figure 3), which indicate that overall *H. niger* populations from São Paulo coast experienced a recent demographic expansion event around 180,000 generations ago, however when we consider the two main COI genetic groups, populations from Alcatrazes, Búzios and Conchas also emerged around 180,000 generations, while the remaining populations expanded later, around 150,000 generations ago, which corresponds to approximately 15,000 and 12,500 years ago, respectively, considering the short generation time of approximately 1 month of *H. niger* (Campbell et al. 2020).

Table 3. Mismatch distribution and Neutrality Tests analysis calculated for populations o *H. niger*. Values in bold indicate non-significant results (did not differ from sudden expansion model). Tau = expansion parameter. *Generation time for *H. niger* ~ 1 month.

	Mismatch distribution							**Neutrality Tests**			
Populations	SSD	*P-value SSD*	*Raggedness (r)*	*P-value r*	*Tau*	*t (in generations)*	*t (in years)**	*Tajima's D*	*P-value*	*Fu's Fs*	*P-value*
Baleia	**0.00114756**	0.909	**0.03423276**	0.747	2.623	118195.7462	9849.645518	**-2.05804**	0.0068	**-25.6725**	< 0.0001
Conchas	**0.01005559**	0.722	**0.01603878**	0.947	5.99	269917.0872	22493.0906	-0.01529	0.5448	**-21.4467**	< 0.0001
Alcatrazes	**0.01409992**	0.7	**0.02773243**	0.749	8.139	366753.7851	30562.81543	-0.81151	0.2107	**-20.948**	< 0.0001
Figueira	**0.01121728**	0.182	**0.06220717**	0.246	2.859	128830.2091	10735.85076	**-1.7889**	0.0198	**-25.4734**	< 0.0001
Búzios	**0.03003859**	0.074	**0.06405427**	0.095	6.279	282939.7981	23578.31651	-1.03124	0.1538	**-22.6472**	< 0.0001
Moela	**0.0018155**	0.821	**0.04660707**	0.71	1.471	66285.1478	5523.762317	**-2.05614**	0.0057	**-27.5709**	< 0.0001
Mar Casado	**0.00388671**	0.563	**0.06191788**	0.357	2.188	98594.08796	8216.173997	**-2.00479**	0.0061	**-26.8736**	< 0.0001
Montão de Trigo	**0.00250877**	0.619	**0.02834226**	0.461	3.918	176550.1081	14712.50901	**-2.12203**	0.0041	**-25.9297**	< 0.0001

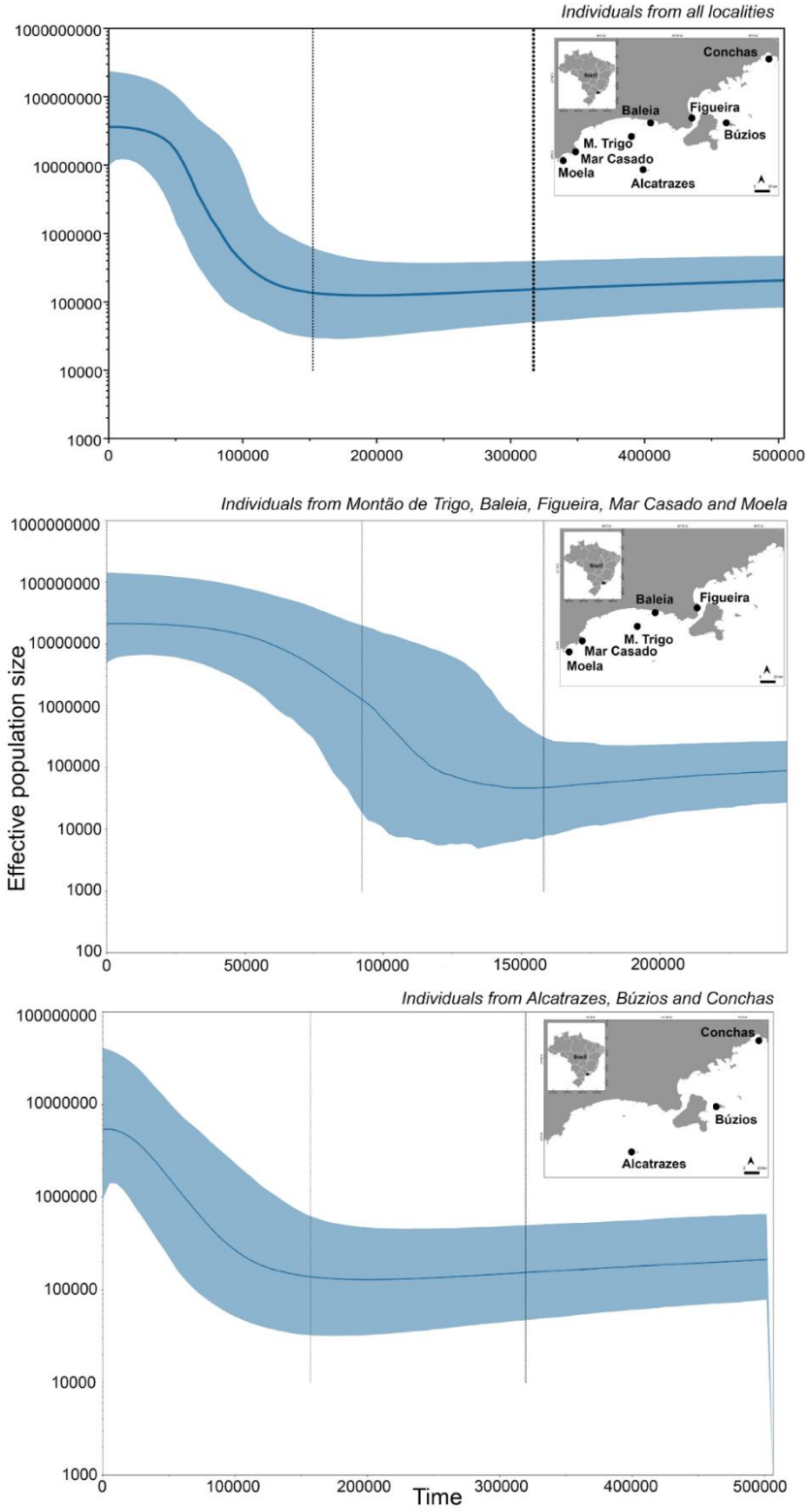


Figure 3. Demographic history of *H. niger* estimated using Bayesian skyline plots from COI sequences, considering all individuals and separately individuals from each of the two main genetic groups. Upper: individuals from all localities; middle: individuals from Montão de Trigo, Baleia, Figueira, Mar Casado and Moela; bottom: individuals from Alcatrazes, Búzios and Conchas.

Morphometric analysis

The PCA analysis for the geometric morphometrics of the propodus shape of *Hyale niger* revealed no clear differentiation among populations from different sites (Figure 4A). However, one may observe a slight morphological separation of individuals from insular and coastal areas (Figure 4B). This trend becomes more evident with the results of the linear discriminant analysis, which resulted in a significant differentiation between coastal and insular individuals (Figure 5A). Propodus shape of coastal individuals are generally more rectangular and with a larger insertion of the propodus on the carpus (Figure 5A). Both Procrustes ANOVA for shape variation and Centroid Size ANOVA for size variation unveiled significant coastal-insular differentiation (Centroid Size, $F = 27.52$, $P < 0.001$; Procrustes, $F = 3.7379$, $P = 0.011$; Figure 5B). The morphological variation in *H. niger* populations revealed to be size related, as the regression analysis showed a positive and significant linear relationship between shape and size of the propodus of gnathopod II, with coastal individuals presenting larger propodus of gnathopod in general (Figure 5C). Coastal areas overall also presented macroalgae beds with larger fronds (ANOVA, $F = 8.6446$, $P = 0.0052$, Figure 5D), and a positive relationship was found between the mean frond wet weight and the mean centroid size of *H. niger* propodus of gnathopod II from each locality (Regression Analysis, $F = 28.99$, Adjusted $R^2 = 0.799$, $P = 0.0017$, Figure 5E), indicating that the larger algal fronds in coastal areas allow the establishment of individuals with larger gnathopods, which results in morphological differentiation among populations.

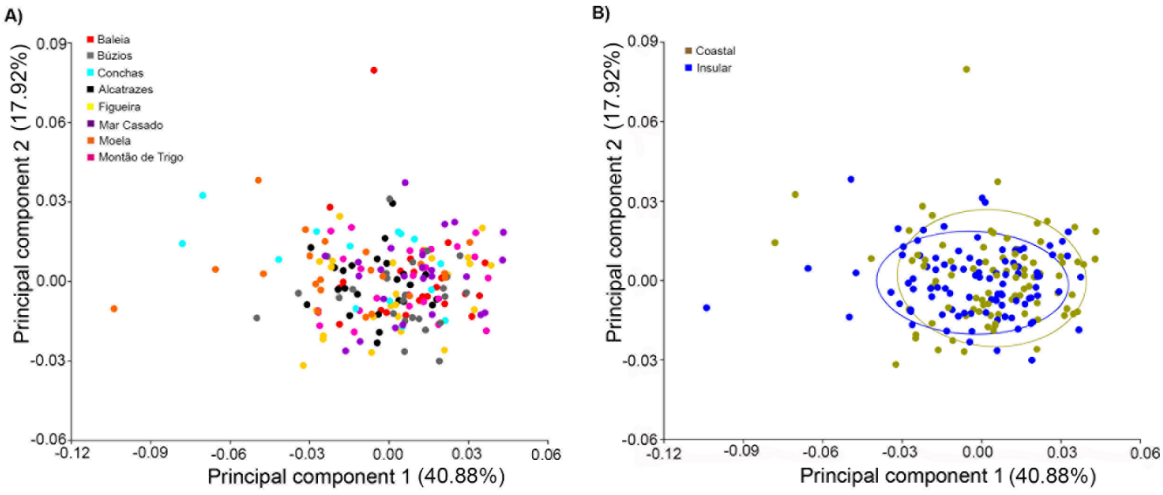


Figure 4. Scatterplot of the first and second principal components of the principal components analysis (PCA) of geometric morphometric data of the *Hyale niger* propodus of gnathopod II. A: individuals divided by site. B: individuals divided by position (coastal or insular area).

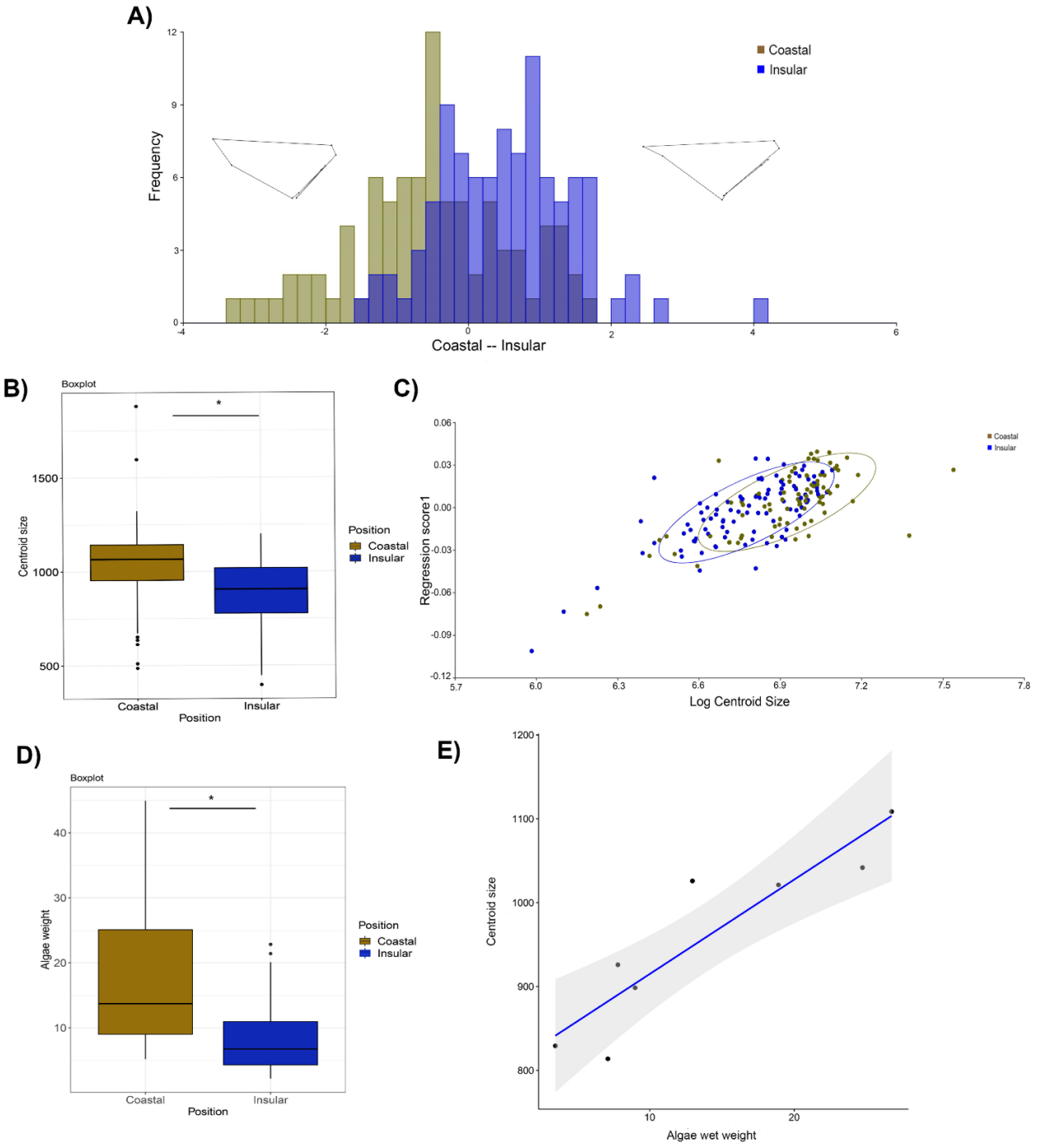


Figure 5. A: Linear Discriminant Analysis (LDA) of geometric morphometric data of the *Hyale niger* propodus of gnathopod II from coastal and insular sites. B: difference in centroid size of gnathopods from insular and coastal individuals (ANOVA, F = 27.52, P < 0.001). C: Relationship between the regression score, representing the shape variation among individuals, and centroid size. D: difference in algae wet weight from insular and coastal macroalgae beds (ANOVA, F = 8.6446, P = 0.0052). E: Relationship between the mean centroid size of gnathopods of amphipods and macroalgae wet weight. For B and D, solid horizontal lines

indicate median, boxes indicate first and third quartiles, * indicates statistically significant difference.

Environmental distances

After removal of the highly correlated variables (r > 0.7), 19 variables were retained and used for the environmental PCA. The first three axes of the PCA, which retained more than 80% of the data variance, were used for calculation of environmental distances. Environmental variance among samples was explained mainly by variations in iron range, dissolved oxygen range, phosphate mean (PC1) and algae wet weight (PC2) (Figure 6).

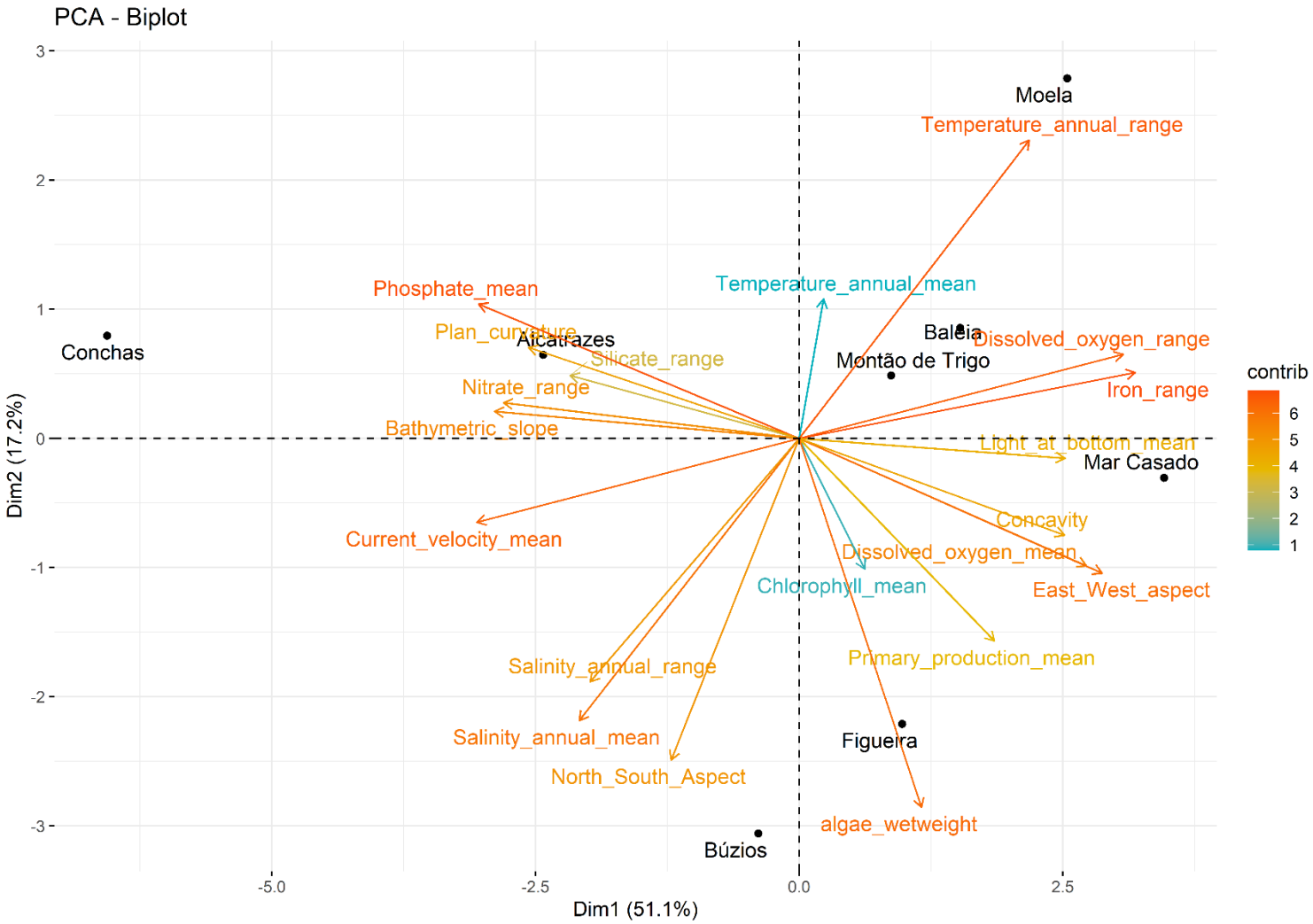


Figure 6. Locations of populations of *Hyale niger* in a bidimensional projection of the principal components analysis used to calculate the environmental distance. The color gradient represents the contribution of each environmental variable to principal components PC1 (Dim1) and PC2 (Dim2).

Association tests

For both COI and SNP markers, results of the association tests were very similar. The simple Mantle tests showed that genetic distances among *H. niger* populations were significantly and positively correlated with geographical and environmental distances, but not with morphometric distance (Table 4, Figure 7). When controlling for the other two variables in the Partial Mantel tests, the effect of environmental distance remained strong and significant, whereas the effect of geographical distance became non-significant when controlled for environmental effect (Table 5). In addition, all models from the multivariate regression analysis that considered as the predictor effect the combination of the environmental distance with one or both the other predictor variables were also significant (Table 5). The model that excluded the effect of environmental distance was not significant.

Table 4. Simple and partial Mantel tests between geographical, environmental, and morphometric distances with genetic distances (for both COI and SNP data) of *H. niger* populations.

Seascape feature	**Controlled**	**COI**		**SNP**	
		r	*P-value*	*r*	*P-value*
Geographical distance	-	**0.4242**	**0.0331**	**0.4075**	**0.0359**
Environment distance	-	**0.5208**	**0.0066**	**0.5394**	**0.0043**
Morphometric distance	-	-0.07646	0.6403	-0.07832	0.597
Geographical distance	Environment distance	0.07998	0.3297	0.02931	0.41
Geographical distance	Morphometric distance	**0.445**	**0.0317**	**0.4284**	**0.0295**
Environment distance	Geographical distance	0.3421	0.0603	0.3878	0.1094
Environment distance	Morphometric distance	**0.5791**	**0.0035**	**0.5995**	**< 0.0001**
Morphometric distance	Geographical distance	-0.1666	0.7745	-0.1641	0.726
Morphometric distance	Environment distance	-0.3055	0.9452	-0.3196	0.9457

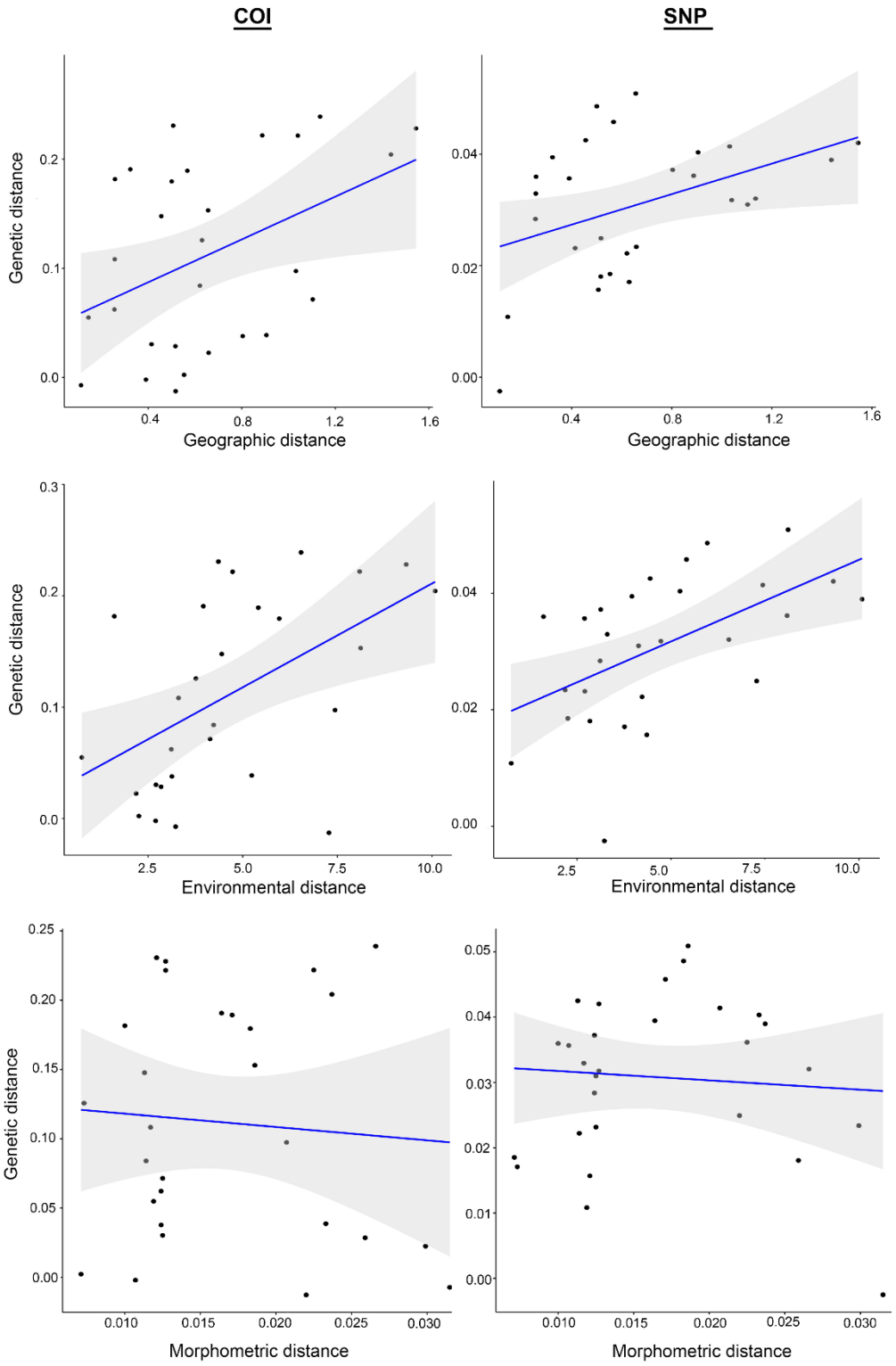


Figure 7. Bivariate relationships between geographic, environmental, and morphometric distances with genetic distan
for *Hyale niger*. Correlations of genetic distance with geographical and environmental distances were signific
according to Mantel test results. Left panels: COI data; right panels: SNP data.

Table 5. Regression coefficient (ß), coefficient of determination (R^2) and significance (P) of the multiple matrix regression with randomization analysis in the association between a combination of geographical distance, environmental, and morphometric distances with genetic distance (COI and SNP data) of *Hyale niger*.

	Combination of variables	β geographical	P-value	β environment	P-value	β morphometry	P-value	R^2	P-value
COI	*Dgeo + Denv*	0.098	0.6294	0.449	0.1008	-	-	0.276	**0.0405**
	Dgeo + Dmorfo	0.45	0.0294	-	-	-0.153	0.3586	0.203	0.0768
	Denv + Dmorfo	-	-	0.611	0.0049	-0.276	0.1089	0.339	**0.0224**
	Dgeo + Denv + Dmorfo	0.061	0.7549	0.565	0.0625	-0.271	0.1273	0.341	**0.0449**
SNP	*Dgeo + Denv*	0.035	0.7256	0.513	0.044	-	-	0.291	**0.019**
	Dgeo + Dmorfo	0.433	0.0375	-	-	-0.152	0.5148	0.203	0.0768
	Denv + Dmorfo	-	-	0.633	0.0021	-0.285	0.1458	0.363	**0.0103**
	Dgeo + Denv + Dmorfo	-0.003	0.9864	0.635	0.0217	-0.285	0.1706	0.363	**0.0213**

Since environmental distance was the most important effect explaining genetic variations, we also analyzed the correlation between each environmental variable and the genetic distance, for both COI and SNP data (Table 6). Variations in light at sea bottom, nitrate concentration and silicate concentration were significantly correlated with genetic distances for both molecular markers (Table 6).

Table 6. Multiple matrix regression with randomization (MMRR) analysis and partial Mantel test for the associations between the environmental variables of sampling sites and the genetic distances (COI and SNP data) of *Hyale niger*. Significant results are shown in bold.

	COI				SNP			
Environmental variable	MMRR		Partial Mantel Test		MMRR		Partial Mantel Test	
	β	*P-value*	*r*	*P-value*	*β*	*P-value*	*r*	*P-value*
Chlorophyll_mean	-0.101	0.5077	-0.1116	0.6536	0.172	0.193	-0.0838	0.5567
Current_velocity_mean	-0.135	0.6529	-0.08719	0.5774	0.216	0.0771	0.2451	0.2601
Dissolved_oxygen_mean	0.177	0.2908	0.1859	0.1768	**0.283**	**0.0387**	0.3743	0.0982
Dissolved_oxygen_range	0.232	0.4652	0.1485	0.2839	0.191	0.1161	0.1734	0.282
Iron_range	0.425	0.0791	0.3681	0.0557	**0.425**	**4.50E-03**	**0.5569**	**0.0179**
Phosphate_mean	0.188	0.2471	0.1949	0.1451	**0.339**	**0.0178**	0.455	0.063
Light_at_bottom_mean	**0.515**	**0.0215**	**0.569**	**0.0226**	**0.286**	**0.0159**	**0.3797**	**0.0089**
Nitrate_range	**0.457**	**0.027**	**0.5013**	**0.0243**	**0.363**	**0.0121**	**0.4863**	**0.0159**
Primary_production_mean	0.084	0.62	0.09161	0.2924	0.186	0.1473	0.1545	0.2762
Silicate_range	**0.366**	**0.0394**	**0.4029**	**0.0323**	**0.313**	**0.0231**	**0.4196**	**0.0403**
East_West_aspect	-0.03	0.8706	-0.03056	0.5482	0.227	0.0906	0.271	0.1763
North_South_Aspect	-0.066	0.6911	0.07275	0.2599	0.227	0.0554	-0.2709	0.9459
Plan_curvature	0.192	0.2259	0.2082	0.1515	0.246	0.0745	0.3099	0.1165
Bathymetric_slope	-0.052	0.8084	-0.04481	0.3958	0.181	0.1356	0.134	0.2953
Concavity	-0.23	0.3031	-0.2172	0.8288	0.168	0.1956	-0.0503	0.5167
Salinity_annual_mean	0.028	0.9111	0.0242	0.3702	0.172	0.1908	-0.0818	0.6036
Salinity_annual_range	-0.501	0.0549	-0.3717	0.9989	0.2	0.1391	-0.203	0.8024
Temperature_annual_mean	0.25	0.1546	0.2737	0.0962	**0.277**	**0.0399**	0.3656	0.1127
Temperature_annual_range	**0.497**	**0.0271**	**0.5132**	**0.0283**	0.171	0.1219	0.0742	0.3352
algae wet weight	0.198	0.062	-0.1499	0.7671	0.167	0.1319	0.0365	0.4005

Discussion

In this study, we observed that *Hyale niger* populations presented genetic structure even at a fine spatial scale, with the formation of two and four genetic groups for COI and SNP data, respectively. Unexpectedly, isolation by environment and not isolation by distance best explained the patterns of genetic differentiation, for both molecular markers. Morphometric analysis showed a differentiation between coastal and insular populations, however there was no relation with genetic differences, suggesting distinct modulator factors for genetic and morphological variations. To our best knowledge, this is the first evaluation on the genetic structure of the conspicuous seaweed-associated marine amphipod *H. niger* and the first simultaneous investigation on the effects of geographic distance, environmental factors, and morphological features on the genetic differentiation of a marine amphipod, considering both genomic and mtDNA information.

Our findings indicated that *H. niger* population expansion along São Paulo coast begun around 15,000 years ago, following the Last Glacial Maximum (LGM), when there was a retraction of continental glaciers with a consequent sea level rise and sea temperature rise, which is known to have favored the population expansion of marine species (Naro-Maciel et al. 2011; Ludt & Rocha 2015; Díaz et al. 2018) and may have allowed the colonization and survival of *H. niger* populations in the region. Interestingly, even in our narrow spatial scale, *H. niger* presented and earlier expansion process in Alcatrazes, Búzios and Conchas, one of the two genetic groups revealed by COI data. With the progressive sea level rise after LGM, it is possible that areas more distant to the shore and with deeper bathymetry such as Alzatrazes and Búzios were suitable earlier for the recruitment and establishment of macroalgae. Shifted distribution of habitat-forming seaweed during past climate-changing events are known to have an important role for the structure and diversity of marine species (Fraser 2016), especially for direct development seaweed-associated amphipods like *H. niger* (Thiel & Gutow 2004; Flynn et al. 2009). Complementarily, we hypothesize that the first colonizers came from northern lower latitude waters going southwards, following the general trend of range poleward expansion of marine species (Ávila et al. 2018), dispersing mainly through the Brazil Coast circulation, and thus initially colonizing upper northern regions of São Paulo coast like Conchas shore. Also, the more depositional and productive areas of São Paulo Bight like near Cape Frio (northwards, closer to Conchas shore) and southeast of São Sebastião Island (closer to Búzios island and Alcatrazes archipelago) (Mahiques et al. 2002; Mahiques et al. 2010) may have favored the establishment and growth of macroalgae species (Airoldi & Cinelli 1997; Lanari &

Coutinho 2014), thus forming suitable habitat for *H. niger* populations expansion initially in those three areas.

The lower values of nucleotide diversity (π) in Figueira, Baleia, Mar Casado and Moela populations can be considered low-medium levels of genetic diversity according to the classification proposed by Goodall-Copestake et al. (2012) for *cox* genes in animals, in contrast with the high levels found in Alcatrazes, Búzios and Conchas populations. This difference may be explained by the demographic history of *H. niger*, in which we expect that genetic diversity would be lower in the areas where the amphipod presented a later demographic expansion after LGM, thus experiencing stronger and more recent bottlenecks, which could result in lower values of currently genetic diversity (Nei et al. 1975). Also, non-mutually-exclusively, we do not disregard the impacts of anthropogenic activities. Even though the association of anthropogenic impacts and lower genetic diversity is complex and not consistent across taxa (Millette et al. 2020), lower genetic diversity due to higher human-induced impact has been demonstrated for different animal groups (Nehemia & Kochzius 2017; Hamamoto et al. 2021; Getelina et al. 2022), including amphipods (Ungherese et al. 2010; Chung et al. 2011; Švara et al. 2022). In line with this explanation, nucleotide diversity based on COI gene has been shown to be an effective proxy for a first evaluation of the conservation status of animal species (Petit-Marty et al. 2021). Therefore, the lower nucleotide diversity of *H. niger* in Figueira, Baleia, Mar Casado, Moela and Montão de Trigo could be due to their high proximity to urbanized regions, in special the highly anthropized areas of the São Sebastião Channel (Turra et al. 2017; Duleba et al. 2018) and Baixada Santista (Oliveira 2009; Silva-Oscar-Júnior et al. 2019), in contrast with the more isolated Conchas, Búzios and Alcatrazes, the latter being a highly preserved marine protected area (Rolim et al. 2019; Karlovic et al. 2021).

Unlike COI data, SNPs-based genetic data showed similar genetic diversity among localities and higher resolution of the genetic structure, with the formation of four genetic groups. Incongruency in the results between mtDNA and nDNA or genome-wide DNA has already been reported (e.g. Galaska et al. 2017; Hirano et al. 2019; Nowland et al. 2019; Yang et al. 2020; Yamazaki et al. 2022) and is generally related to different inheritance patterns of mtDNA and nDNA, in which the former seems to lose ancestral polymorphism faster than nDNA (Funk & Omland 2003; Toews & Brelsford 2012; Hirano et al. 2019). Mitochondrial-specific traits such as frequent introgressions and incomplete lineage sorting may also bias the investigation of genetic structuring of populations (Ballard & Whitlock 2004; Yamazaki et al. 2022). Therefore, the combined interpretation of mtDNA and nDNA-based analyses provide a more complete comprehension of genetic organization (Teske et al. 2018; Yamazaki et al.

2022), at different scales, allowing the detection of broader and finer spatial genetic structure (Heylar et al. 2011; Nowland et al. 2019). In our study, the genetic group revealed by COI data formed by Alcatrazes, Búzios and Conchas was also recovered by SNP data, however the second genetic group indicated by mtDNA may be subdivided according to SNPs analysis: (i) Mar Casado and Moela; (ii) Baleia and Montão de Trigo; and (iii) Figueira.

The genetic divergence for both COI and SNP data were significantly influenced by geographic distances and environmental distances among localities. Environmental variability and geographic distances are frequently correlated; thus, Isolation by Distance (IBD) and Isolation by Environment (IBE) are not mutually exclusive and sometimes can produce similar patterns (Manthey & Moyle 2015), which is the case in this study. Our data showed that actually both factors were important for modulating genetic structure of *H. niger*, as has already been registered for other species (Deli et al. 2018; Nielsen et al. 2020; Nikolakis et al. 2022). Even though IBD alone was sufficient to explain the genetic variation, MMRR results evidenced that environmental variability was most relevant for explaining genetic divergence, which agrees with multiple studies, that identified IBE as the best predictor of genetic variations in different species (e.g., Lee & Mitchell-Olds 2011; Rodríguez-Zárate et al. 2018; Jiang et al. 2019; da Silva et al. 2021; Frish et al. 2021).

The key environmental factors involved in the genetic structuring of *H. niger* populations were mainly related to nutrient concentrations, such as nitrate and silicate concentrations, which were particularly higher in Alcatrazes, Conchas and Búzios. Our main hypothesis is that nutrient inputs in those areas are due to upwelling formation, particularly in Cabo Frio region in São Paulo coast. In this area, especially during warmer months, the dominant NE winds favor the transport to offshore of the Coastal Water (CW), allowing the penetration of the deeper cold and nutrient-rich South Atlantic Central Water (SACW) in shallower areas of the inner shelf (Castelao & Barth 2006; Yamashita et al. 2016). These recent upwelled and nutrient-rich waters occupy a large portion of the South Brazil Bright northern sector shelf and are preferentially advected southwestward, reaching southern São Sebastião island (Lorenzzetti & Gaeta 1996; Castelao & Barth 2006; Calil et al. 2021). In Ubatuba region, upwelling of SACW waters is also responsible for nutrient enrichment of some areas, together with some sediment resuspension events due to physical disturbances of wave action, which are most effective in the bays oriented in S-SE direction, which is the case of the bay where Conchas shore is located into (Quintana et al. 2015). Intrusion of SACW in shallow waters increasing nutrient availability and thus productivity are also known to happen close to São

Sebastião island (Calil et al. 2021) and in Alcatrazes archipelago (Karlovic et al. 2021), which would explain higher nutrient levels in Búzios and Alcatrazes, respectively.

Increasing nutrient availability in the environment may result in higher nutrient uptake by macroalgae species (Alquezar et al. 2013; Li et al. 2019; Ohtake et al. 2020; Lapointe et al. 2021), thus increasing their nutrient content, which could positively affect fitness, performance, and reproductive potential of herbivore seaweed-associated amphipods (Kraufvelin et al. 2006; Duarte et al. 2010; Sudo & Yoshida 2021), like *H. niger*. Macroalgae from nutrient-rich environments presented a higher nutritional level, increasing the performance of the marine herbivore amphipod *Gammarus locusta* Kraufvelin et al. (2006) . Accordingly, our results suggest that environmental limitations in nutrient contents of macroalgae within areas with restricted nutrient concentrations could be limiting the distribution and fitness of *H. niger* populations along São Paulo coast, thus contributing for the formation of genetic groups. However, as the relationship between nutrient availability, macroalgae and amphipods' fitness may be weak (Machado et al. 2018) , studies that investigate how macroalgae nutrient contents may affect the fitness of *H. niger* should be further explored in future work for testing this hypothesis.

Another possibility to explain our findings based on genetic information is that São Sebastião island could be acting as a genetic barrier and that gene flow through the São Sebastião Channel (SSC) would be reduced, influencing the genetic structure of *H. niger*, especially if we consider the higher resolution of SNP data. The SSC is approximately 25km long and has two openings of 6-7km wide, with a narrowing of nearly 2km wide in its central part (Pires-Vanin et al. 2013). Hydrodynamics in SSC is highly variable in direction and speed through the year, but generally wind blows from northeast and promotes southwest currents, however when there is a cold front and temperature drops, the wind direction reverses and promotes northeast currents (Fo 1990; Birocchi et al. 2021). In our study, *H. niger* southwest from the São Sebastião island could be assigned to two groups, one formed by the two populations from Baixada Santista (Moela and Mar Casado), and the other formed by the populations from the geographically close Baleia and Montão de Trigo island. The third group is formed by Figueira population, which despite being geographically close to these two last areas, is the only site located within the SSC, and that genetically differentiated from all remaining populations, an indicative of a limited gene flow through the channel. In that case, populations from Alcatrazes and Búzios, which are located south to São Sebastião island and farther from São Sebastião coast, would have a stronger connection to the northern localities like Conchas shore, because the gene flow around São Sebastião island would be facilitated,

thus justifying the fourth genetic group, composed by Alcatrazes, Búzios and Conchas. Future investigation considering the water circulation patterns among localities, including differences in the resistance to gene flow, might provide a more complete and realistic understanding on the patterns of genetic structuring in the studied area.

As for morphological variation, the geometric morphometry of the propodus of gnathopod II of males indicated that the differentiation observed between coastal and insular individuals was not associated with genetic variation. Zamudio et al. (2016) reports that the existence of clustered phenotypes that are not associated to a parallel genetic differentiation may reflect a pattern of phenotypic plasticity. Previous studies have already reported the lack of relationship between phenotypic and genotypic variation (Silva & Paula 2008; Madeira et al. 2012; Paolucci et al. 2014; Vendrami et al. 2017) and in those cases, morphological differentiation was also associated to phenotypic plasticity due to environmental variation (Miner et al. 2005; Silva & Paula 2008; Vendrami et al. 2017). Peres et al. (2019), studying the seaweed-associated amphipod *Cymadusa filosa*, also found a disassociation between genetic variation and morphometric divergence of gnathopod II, argued that such mismatch could be due to phenotypic plasticity in response to different environmental conditions, such as chemical water characteristics and wave action. Similarly, our results indicate that morphometric variation may be explained by phenotypic plasticity. Although environmental distance was not a good predictor for morphological divergence, the variation in macroalgae wet weight presented a strong and significant relationship with morphometric trait, in which coastal localities presented larger macroalgae fronds that carried amphipod populations with larger and morphologically distinct gnathopod II than insular populations. Cothran & Jeyasingh (2010) showed that amphipods from the genus *Hyalella* presented allometric variation in the morphometry of gnathopod II, with smaller and more variable gnathopods in response to food stress, and that this was particularly accentuated in males, in which this feature is sexually selected. Therefore, our findings suggest that the smaller gnathopods of *H. niger* in insular areas, where quantity of algae (and thus food availability for herbivore species) is lower, may be due to food stress in those areas. Such explanation may be experimentally tested in future studies.

In conclusion, our data showed that, even at a fine spatial scale, the amphipod *Hyale niger* presented structured populations and that both historical and current processes are likely involved in shaping its genetic structure. We also demonstrated that isolation by environment (IBE) is the current predominant factor modulating genetic variation, and that nutrient concentrations in seawater seem most relevant for explaining genetic structure. In addition, our

data indicated that morphological variations in gnathopod II structure of males are not genetic-related and are probably plastic due to variations in the size of macroalgae fronds. *Hyale niger* is one of the most conspicuous species in macroalgae habitats (Bueno et al. 2017; Bueno et al. 2019; Ferreira et al. 2019; Machado et al. 2019; Leite et al. 2021) and alterations on its populations are highly responsible for changes observed in seaweed-associated invertebrate diversity and composition (Bueno et al. 2019; Machado et al. 2019; Leite et al. 2021). Therefore, understanding how *H. niger* populations are structured at genetic and phenotypic levels and unveiling the modulating factors underlying those patterns are fundamental for better understanding the dynamics of seaweed-invertebrate associations. Such information provide solid evidence for the establishment of conservation measures for those habitats, which have been threatened over the last decades (Takolander et al. 2017; Capdevilla et al. 2019; Gorman et al. 2020), despite their extreme importance for marine coastal environments (Christie et al. 2009; Macreadie et al. 2017; Duffy et al. 2019).

References

Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: ten years of progress following the 'revolution'. Italian Journal of Zoology, 71(1), 5-16.

D'Aloia, C. C., Bogdanowicz, S. M., Francis, R. K., Majoris, J. E., Harrison, R. G., & Buston, P. M. (2015). Patterns, causes, and consequences of marine larval dispersal. Proceedings of the National Academy of Sciences, 112(45), 13940-13945.

Airoldi, L., & Cinelli, F. (1997). Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. Journal of Experimental Marine Biology and Ecology, 215(2), 269-288.

Alquezar, R., Glendenning, L., & Costanzo, S. (2013). The use of the brown macroalgae, Sargassum flavicans, as a potential bioindicator of industrial nutrient enrichment. Marine pollution bulletin, 77(1-2), 140-146.

Altschul, S. F.; Gish, W.; Miller, W.; Myers, E. W.; Lipman, D. J. (1990). Basic local alignment search tool. Journal of Molecular Biology, 215(3): 403-410.

Antao, T., Lopes, A., Lopes, R. J., Beja-Pereira, A., & Luikart, G. (2008). LOSITAN: a workbench to detect molecular adaptation based on a F ST-outlier method. BMC bioinformatics, 9(1), 1-5.

Appadoo, C., & Myers, A. A. (2003). Observations on the tube-building behaviour of the marine amphipod Cymadusa filosa Savigny (Crustacea: Ampithoidae). Journal of Natural History, 37(18), 2151-2164.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018). Bio-ORACLE v2. 0: Extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography, 27(3), 277-284.

Ávila, S. P., Cordeiro, R., Madeira, P., Silva, L., Medeiros, A., Rebelo, A. C., Melo, C., Neto, A. I., Haroun, R., Monteiro, A., Rijsdijk, K., & Johnson, M. E. (2018). Global change impacts on large-scale biogeographic patterns of marine organisms on Atlantic oceanic islands. Marine Pollution Bulletin, 126, 101-112.

Baird, H. P., Miller, K. J., & Stark, J. S. (2012). Genetic population structure in the Antarctic benthos: insights from the widespread amphipod, *Orchomenella franklini*. PloS one, 7(3), e34363.

Ballard, J. W. O. & Whitlock, M. C. The incomplete natural history of mitochondria. Mol. Ecol. 13, 729–744 (2004).

Bierne, N., Roze, D., & Welch, J. J. (2013). Pervasive selection or is it…? Why are FST outliers sometimes so frequent?.

Birocchi, P., Dottori, M., Costa, C. D. G. R., & Leite, J. R. B. (2021). Study of three domestic sewage submarine outfall plumes through the use of numerical modeling in the São Sebastião channel, São Paulo state, Brazil. Regional Studies in Marine Science, 42, 101647.

Bosch, S., Tyberghein, L., & De Clerck, O. (2017). sdmpredictors: an R package for species distribution modelling predictor datasets. Marine Species Distributions: From data to predictive models, 49.

Bradburd, G. S., Ralph, P. L., & Coop, G. M. (2013). Disentangling the effects of geographic and ecological isolation on genetic differentiation. Evolution, 67(11), 3258-3273.

Bueno, M., Dias, G. M., & Leite, F. P. (2017). The importance of shore height and host identity for amphipod assemblages. Marine Biology Research, 13(8), 870-877.

Bueno, M., Flores, A. A. V., & Leite, F. P. P. (2019). Seasonal dynamics of amphipod assemblages in intertidal coralline algal mats on two Brazilian shores. Bulletin of Marine Science, 95(1), 83-100.

Bueno, M., & Leite, F. P. P. (2019). Age and life style affect macroalgae colonization by amphipods in shallow marine environments. Journal of Experimental Marine Biology and Ecology, 514, 59-66.

Buston, P. M., & D'Aloia, C. C. (2013). Marine ecology: reaping the benefits of local dispersal. Current Biology, 23(9), R351-R353.

Burton, R. S. (2009). Molecular markers, natural history, and conservation of marine animals. BioScience, 59(10), 831-840.

Cacabelos, E., Olabarria, C., Incera, M., & Troncoso, J. S. (2010). Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. Estuarine, coastal and shelf science, 89(1), 43-52.

Calil, P. H., Suzuki, N., Baschek, B., & da Silveira, I. C. (2021). Filaments, fronts and eddies in the Cabo Frio coastal upwelling system, Brazil. Fluids, 6(2), 54.

Campbell, H., Ledet, J., Poore, A., Harianto, J., & Byrne, M. (2020). Resilience of the amphipod Hyale niger and its algal host *Sargassum linearifolium* to heatwave conditions. Marine Biology, 167(6), 1-9.

Capdevila, P., Hereu, B., Salguero-Gómez, R., Rovira, G. L., Medrano, A., Cebrian, E., Garrabou, J., Kersting, D. K., & Linares, C. (2019). Warming impacts on early life stages increase the vulnerability and delay the population recovery of a long-lived habitat-forming macroalga. Journal of Ecology, 107(3), 1129-1140.

Castelao, R. M., & Barth, J. A. (2006). Upwelling around Cabo Frio, Brazil: The importance of wind stress curl. Geophysical Research Letters, 33(3).

Catchen, J. M., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. H. (2011). Stacks: building and genotyping loci de novo from short-read sequences. G3: Genes| genomes| genetics, 1(3), 171-182.

Christie, H., Norderhaug, K. M., & Fredriksen, S. (2009). Macrophytes as habitat for fauna. Marine Ecology Progress Series, 396, 221-233.

Christie, M. R., Tissot, B. N., Albins, M. A., Beets, J. P., Jia, Y., Ortiz, D. M., Thompson, S. E., & Hixon, M. A. (2010). Larval connectivity in an effective network of marine protected areas. PloS one, 5(12), e15715.

Chung, P. P., Hyne, R. V., Mann, R. M., & Ballard, J. W. O. (2011). Temporal and geographical genetic variation in the amphipod *Melita plumulosa* (Crustacea: Melitidae): Link of a localized change in haplotype frequencies to a chemical spill. Chemosphere, 82(7), 1050-1055.

Cothran, R. D., & Jeyasingh, P. D. (2010). Condition dependence of a sexually selected trait in a crustacean species complex: importance of the ecological context. Evolution: International Journal of Organic Evolution, 64(9), 2535-2546.

Coulon, A. (2010). GENHET: an easy-to-use R function to estimate individual heterozygosity. Molecular Ecology Resources, 10(1), 167-169.

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., Handsaker, R. E., Lunter, G., Marth, G. T., Sherry, S T., McVean, G., Durbin, R., & 1000 Genomes Project Analysis Group. (2011). The variant call format and VCFtools. Bioinformatics, 27(15), 2156-2158.

Deli, T., Pfaller, M., & Schubart, C. D. (2018). Phylogeography of the littoral prawn species *Palaemon elegans* (Crustacea: Caridea: Palaemonidae) across the Mediterranean Sea unveils disparate patterns of population genetic structure and demographic history in the two sympatric genetic types II and III. Marine Biodiversity, 48(4), 1979-2001.

Díaz, A., Gerard, K., González-Wevar, C., Maturana, C., Féral, J. P., David, B., Saucède, T., & Poulin, E. (2018). Genetic structure and demographic inference of the regular sea urchin *Sterechinus neumayeri* (Meissner, 1900) in the Southern Ocean: The role of the last glaciation. PloS one, 13(6), e0197611.

Duarte, C., Navarro, J. M., Acuña, K., & Gómez, I. (2010). Feeding preferences of the sandhopper *Orchestoidea tuberculata*: the importance of algal traits. Hydrobiologia, 651(1), 291-303.

Duleba, W., Teodoro, A. C., Debenay, J. P., Alves Martins, M. V., Gubitoso, S., Pregnolato, L. A., Lerena, L. M., Prada, S. M., & Bevilacqua, J. E. (2018). Environmental impact of the largest petroleum terminal in SE Brazil: A multiproxy analysis based on sediment geochemistry and living benthic foraminifera. PLoS One, 13(2), e0191446.

Drummond, A. J., Ho, S. Y. W., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. PLoS biology, 4(5), e88.

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. BMC evolutionary biology, 7(1), 1-8.

Drummond, A. J., Rambaut, A., Shapiro, B. E. T. H., & Pybus, O. G. (2005). Bayesian coalescent inference of past population dynamics from molecular sequences. Molecular Biology and Evolution, 22(5), 1185-1192.

Earl, D. A., & VonHoldt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources, 4(2), 359-361.

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology, 14(8), 2611-2620.

Excoffier, L. & H.E. L. Lischer (2010) Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources. 10: 564-567.

Foll, M., & Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics, 180(2), 977-993.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome C oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3, 294–299

Fagundes, N. J., Ray, N., Beaumont, M., Neuenschwander, S., Salzano, F. M., Bonatto, S. L., & Excoffier, L. (2007). Statistical evaluation of alternative models of human evolution. Proceedings of the National Academy of Sciences, 104(45), 17614-17619.

Ferreira, D. R. J., Dena-Silva, S. A., Güth, A. Z., Bueno, M., & Leite, F. P. P. (2019). Temporal variation in peracarid assemblages inhabiting *Caulerpa racemosa* in two Brazilian rocky shores. Marine Biodiversity, 49(3), 1253-1260.

Flynn, M. N., Pereira, W. R. L. S., Pires, R. C., & Valerio-Berardo, M. T. (2009). Population dynamics of *Hyale nigra* (Haswell, 1879)(Amphipoda, Hyalidae) associated to *Bryocladia thyrsigera* (J. Agardh) at Peruibe beach, Itanhaém (SP), southeastern Brazil. Nauplius, 17(1), 1-8.

Fo, B. M. C. (1990). Wind driven currents in the Channel of São Sebastião: winter, 1979. Boletim do Instituto Oceanográfico, 38, 111-132.

Fulton, C. J., Berkström, C., Wilson, S. K., Abesamis, R. A., Bradley, M., Åkerlund, C., Barrett, L. T., Bucol, A. A., Chacin, D. H., Chong-Seng, K. M., Coker, D. J., Depczynski, M., Eggersten, M., Ellis, D., Evans, R. D, Graham, N. A. J., Hoey, A. S., Holmes, T. H., Kulbicki, M., Leung, P. T. Y., Lam, P. K. S., van Lier, J., Matis, P. A., Noble, M. M., Pérez-Matus, A., Piggott, C., Radford, B. T., Tano, S., & Tinkler, P. (2020). Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes. Fish and Fisheries, 21(4), 700-717.

François, O., Martins, H., Caye, K., & Schoville, S. D. (2016). Controlling false discoveries in genome scans for selection. Molecular Ecology, 25(2), 454-469.

Fraser, C. I. (2016). Change in Southern Hemisphere intertidal communities through climate cycles: the role of dispersing algae. In Seaweed Phylogeography (pp. 131-143). Springer, Dordrecht.

Frisch, D., Lejeusne, C., Hayashi, M., Bidwell, M. T., Sánchez-Fontenla, J., & Green, A. J. (2021). Brine chemistry matters: Isolation by environment and by distance explain population genetic structure of *Artemia franciscana* in saline lakes. Freshwater Biology, 66(8), 1546-1559.

Funk, D. J., & Omland, K. E. (2003). Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics, 34, 397–423.

Galaska, M. P., Sands, C. J., Santos, S. R., Mahon, A. R., & Halanych, K. M. (2017). Geographic structure in the Southern Ocean circumpolar brittle star *Ophionotus victoriae* (Ophiuridae) revealed from mt DNA and single-nucleotide polymorphism data. Ecology and Evolution, 7(2), 475-485.

Getelina, M. A., Schwantes, J. B., Graichen, D. A. S., & Schuch, A. P. (2022). Influence of anthropogenic pressure on the genetic diversity and chromosomal instability of an endangered forest-specialist anuran. Hydrobiologia, 1-13.

Goodall-Copestake, W. P., Tarling, G. A., & Murphy, E. (2012). On the comparison of population-level estimates of haplotype and nucleotide diversity: a case study using the gene cox1 in animals. Heredity, 109(1), 50-56.

Gorman, D., Horta, P., Flores, A. A., Turra, A., Berchez, F. A. D. S., Batista, M. B., Lopes Filho, E. S., Melo, M. S., Ignacio, B. L., Carneiro, I. M., Villaça, R. C., & Széchy, M. T. M. (2020). Decadal losses of canopy-forming algae along the warm temperate coastline of Brazil. Global Change Biology, 26(3), 1446-1457.

Goslee, S. C., & Urban, D. L. (2007). The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software, 22, 1-19.

Goudet, J. (2005). Hierfstat, a package for R to compute and test hierarchical F-statistics. Molecular Ecology Notes, 5(1), 184-186.

Guerra-García, J. M., De Figueroa, J. T., Navarro-Barranco, C., Ros, M., Sánchez-Moyano, J. E., & Moreira, J. (2014). Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula. Journal of Sea Research, 85, 508-517.

Hamamoto, K., Soliman, T., Poliseno, A., Fernandez-Silva, I., & Reimer, J. D. (2021). Higher Genetic Diversity of the Common Sea Cucumber *Holothuria* (*Halodeima*) *atra* in Marine Protected Areas of the Central and Southern Ryukyu Islands. Frontiers in Conservation Science, 53.

Haye, P. A., Varela, A. I., & Thiel, M. (2012). Genetic signatures of rafting dispersal in algal-dwelling brooders *Limnoria* spp. (Isopoda) along the SE Pacific (Chile). Marine Ecology Progress Series, 455, 111-122.

He, Q., & Silliman, B. R. (2019). Climate change, human impacts, and coastal ecosystems in the Anthropocene. Current Biology, 29(19), R1021-R1035.

Helyar, S. J., Hemmer-Hansen, J., Bekkevold, D., Taylor, M. I., Ogden, R., Limborg, M. T., Cariani, A., Maes, G. E., Diopere, E., Carvalho, G. R., & Nielsen, E. E. (2011). Application of SNPs for population genetics of nonmodel organisms: new opportunities and challenges. Molecular Ecology Resources, 11, 123-136.

Heyden, S., Beger, M., Toonen, R. J., Herwerden, L., Juinio-Meñez, M. A., Ravago-Gotanco, R., Fauvelot, C., Bernardi, G., (2014). The application of genetics to marine management and conservation: examples from the Indo-Pacific. Bulletin of Marine Science, 90(1), 123-158.

Hirano, T., Saito, T., Tsunamoto, Y., Koseki, J., Ye, B., Do, V. T., Miura, O., Suyama, Y., & Chiba, S. (2019). Enigmatic incongruence between mtDNA and nDNA revealed by multi-locus phylogenomic analyses in freshwater snails. Scientific Reports, 9(1), 1-13.

Hume, K. D., Elwood, R. W., Dick, J. T., & Morrison, J. (2005). Sexual dimorphism in amphipods: the role of male posterior gnathopods revealed in *Gammarus pulex*. Behavioral Ecology and Sociobiology, 58(3), 264-269.

Jacobucci, G. B., Tanaka, M. O., & Leite, F. P. P. (2009). Temporal variation of amphipod assemblages associated with *Sargassum filipendula* (Phaeophyta) and its epiphytes in a subtropical shore. Aquatic Ecology, 43(4), 1031-1040.

Jiang, S., Luo, M. X., Gao, R. H., Zhang, W., Yang, Y. Z., Li, Y. J., & Liao, P. C. (2019). Isolation-by-environment as a driver of genetic differentiation among populations of the only broad-leaved evergreen shrub *Ammopiptanthus mongolicus* in Asian temperate deserts. Scientific reports, 9(1), 1-14.

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24: 1403–1405.

Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genetics, 11(1), 1-15.

Karlovic, T. C., Gomes, R. R., Paiva, P. C., Babcock, E. A., & Dias, J. F. (2021). Functionality and Effectiveness of Marine Protected Areas in Southeastern Brazilian Waters for Demersal Elasmobranchs. Frontiers in Marine Science, 1204.

Klingenberg, C. P. (2011). MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources, 11(2), 353-357.

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. Molecular Ecology Resources, 15(5), 1179-1191.

Kraufvelin, P., Salovius, S., Christie, H., Moy, F. E., Karez, R., & Pedersen, M. F. (2006). Eutrophication-induced changes in benthic algae affect the behaviour and fitness of the marine amphipod *Gammarus locusta*. Aquatic Botany, 84(3), 199-209.

Lanari, M. D. O., & Coutinho, R. (2014). Reciprocal causality between marine macroalgal diversity and productivity in an upwelling area. Oikos, 123(5), 630-640.

Lapointe, B. E., Brewton, R. A., Herren, L. W., Wang, M., Hu, C., Mcgillicuddy, D. J., Lindell, S., Hernandez, F. J, & Morton, P. L. (2021). Nutrient content and stoichiometry of pelagic *Sargassum* reflects increasing nitrogen availability in the Atlantic Basin. Nature Communications, 12(1), 1-10.

Lee, C. R., & Mitchell-Olds, T. (2011). Quantifying effects of environmental and geographical factors on patterns of genetic differentiation. Molecular Ecology, 20(22), 4631-4642.

Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm?. Ecology, 74(6), 1659-1673.

Leigh, J. W., & Bryant, D. (2015). popart: full-feature software for haplotype network construction. Methods in Ecology and Evolution, 6(9), 1110-1116.

Leite, F. P., Bottcher, C., Lewinsohn, I. D., Siqueira, S. G., Mansur, K. F., Longo, P. A., & Vieira, E. A. (2021). Asymmetric effects of changes in the habitat-forming algae Sargassum on different associated mobile faunas along São Paulo coast, Brazil. Marine Ecology, 42(3), e12649.

Leite, F. P. P., & Turra, A. (2003). Temporal variation in Sargassum biomass, Hypnea epiphytism and associated fauna. Brazilian Archives of Biology and Technology, 46(4), 665-671.

Leroy, B., Meynard, C. N., Bellard, C., & Courchamp, F. (2016). virtualspecies, an R package to generate virtual species distributions. Ecography, 39(6), 599-607

Levin, L. A. (2006). Recent progress in understanding larval dispersal: new directions and digressions. Integrative and comparative biology, 46(3), 282-297.

Li, H., Zhang, Y., Chen, J., Zheng, X., Liu, F., & Jiao, N. (2019). Nitrogen uptake and assimilation preferences of the main green tide alga Ulva prolifera in the Yellow Sea, China. Journal of Applied Phycology, 31(1), 625-635.

Liggins, L., Treml, E. A., & Riginos, C. (2019). Seascape genomics: contextualizing adaptive and neutral genomic variation in the ocean environment. In Population genomics: Marine organisms (pp. 171-218). Springer, Cham.

Longo, P. A. D. S., Mansur, K. F. R., Siqueira, S. G. L., Passos, F. D., & Leite, F. P. P. (2021). *Sargassum*-associated gastropod and amphipod assemblages in relation to metal pollution in a semi-enclosed bay. Aquatic Ecology, 55(2), 623-646.

Lorenzzetti, J. A., & Gaeta, S. A. (1996). The Cape Frio Upwelling Effect over the South Brazil Blight Northern Sector Shelf Waters: a Study Using AVHRR Images. International Archives of Photogrammetry and Remote Sensing, 31, 448-453.

Lu, Y., Yuan, J., Lu, X., Su, C., Zhang, Y., Wang, C., Cao, X., Li, Q., Su, J., Ittekkot, V., Garbutt, R. A., Bush, S., Fletcher, S., Wagey, T., Kachur, A., & Sweijd, N. (2018). Major threats of pollution and climate change to global coastal ecosystems and enhanced management for sustainability. Environmental Pollution, 239, 670-680.

Ludt, W. B., & Rocha, L. A. (2015). Shifting seas: The impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. Journal of Biogeography, 42(1), 25-38.

Luu, K., Bazin, E., & Blum, M. G. (2017). pcadapt: an R package to perform genome scans for selection based on principal component analysis. Molecular Ecology Resources, 17(1), 67-77.

Machado, G. B., Ferreira, A. P., Bueno, M., Siqueira, S. G., & Leite, F. P. (2019). Effects of macroalgal host identity and predation on an amphipod assemblage from a subtropical rocky shore. Hydrobiologia, 836(1), 65-81.

Machado, G. B., Leite, F. P., & Sotka, E. E. (2018). Nutrition of marine mesograzers: integrating feeding behavior, nutrient intake and performance of an herbivorous amphipod. PeerJ, 6, e5929.

Macreadie, P. I., Jarvis, J., Trevathan-Tackett, S. M., & Bellgrove, A. (2017). Seagrasses and macroalgae: importance, vulnerability and impacts. Climate Change Impacts on Fisheries and Aquaculture: A Global Analysis (Wiley-Blackwell), 729-770.

Madeira, C., Alves, M. J., Mesquita, N., Silva, S. E., & Paula, J. (2012). Tracing geographical patterns of population differentiation in a widespread mangrove gastropod:

genetic and geometric morphometrics surveys along the eastern African coast. Biological Journal of the Linnean Society, 107(3), 647-663.

Magris, R. A., Treml, E. A., Pressey, R. L., & Weeks, R. (2016). Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography, 39(7), 649-664.

Mahiques, M. M. D., da Silveira, I. C. A., & Sousa, S. H. D. M., & Rodrigues, M. (2002). Post-LGM sedimentation on the outer shelf–upper slope of the northernmost part of the São Paulo Bight, southeastern Brazil. Marine Geology, 181(4), 387-400.

Mahiques, M. M. D., Sousa, S. H. D. M., Furtado, V. V., Tessler, M. G., Toledo, F. A. D. L., Burone, L., Figueira, R. C. L., Klein, D. A., Martins, C. C., & Alves, D. P. V. (2010). The Southern Brazilian shelf: general characteristics, quaternary evolution and sediment distribution. Brazilian Journal of Oceanography, 58(spe2), 25-34.

Mancuso, F. P., Milazzo, M., & Chemello, R. (2021). Decreasing in patch-size of *Cystoseira* forests reduces the diversity of their associated molluscan assemblage in Mediterranean rocky reefs. Estuarine, Coastal and Shelf Science, 250, 107163.

Manthey, J. D., & Moyle, R. G. (2015). Isolation by environment in White-breasted Nuthatches (*Sitta carolinensis*) of the Madrean Archipelago sky islands: A landscape genomics approach. Molecular Ecology, 24(14), 3628-3638.

Mayer-Pinto, M., Ledet, J., Crowe, T. P., & Johnston, E. L. (2020). Sublethal effects of contaminants on marine habitat-forming species: a review and meta-analysis. Biological Reviews, 95(6), 1554-1573.

Miller, M., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES science gateway for inference of large phylogenetic trees, p 11572–8. In Proceedings of the Gateway Computing Environments Workshop (GCE). Institute of Electrical and Electronics Engineers, Piscataway, NJ. http://dx. doi. org/10.1109/GCE.

Millette, K. L., Fugère, V., Debyser, C., Greiner, A., Chain, F. J., & Gonzalez, A. (2020). No consistent effects of humans on animal genetic diversity worldwide. Ecology letters, 23(1), 55-67.

Miner, B. G., Sultan, S. E., Morgan, S. G., Padilla, D. K., & Relyea, R. A. (2005). Ecological consequences of phenotypic plasticity. Trends in Ecology & Evolution, 20(12), 685-692.

Nahavandi, N., Plath, M., Tiedemann, R., & Mirzajani, A. R. (2011). Sexual and natural selection on morphological traits in a marine amphipod, *Pontogammarus maeoticus* (Sowinsky, 1894). Marine Biology Research, 7(2), 135-146.

Naro-Maciel, E., Reid, B., Holmes, K. E., Brumbaugh, D. R., Martin, M., & DeSalle, R. (2011). Mitochondrial DNA sequence variation in spiny lobsters: population expansion, panmixia, and divergence. Marine Biology, 158(9), 2027-2041.

Nehemia, A., & Kochzius, M. (2017). Reduced genetic diversity and alteration of gene flow in a fiddler crab due to mangrove degradation. PLoS One, 12(8), e0182987.

Nei M. 1987. Molecular evolutionary genetics. New York: Columbia University Press.

Nei, M., Maruyama, T., & Chakraborty, R. (1975). The bottleneck effect and genetic variability in populations. Evolution, 1-10.

Nielsen, E. S., Henriques, R., Beger, M., Toonen, R. J., & Von der Heyden, S. (2020). Multi-model seascape genomics identifies distinct environmental drivers of selection among sympatric marine species. BMC Evolutionary Biology, 20(1), 1-17.

Nikolakis, Z. L., Orton, R. W., & Crother, B. I. (2022). Fine-scale population structure within an Eastern Nearctic snake complex (*Pituophis melanoleucus*). Zoologica Scripta, 51(2), 133-146.

Nowland, S. J., Silva, C. N., Southgate, P. C., & Strugnell, J. M. (2019). Mitochondrial and nuclear genetic analyses of the tropical black-lip rock oyster (*Saccostrea echinata*) reveals population subdivision and informs sustainable aquaculture development. BMC Genomics, 20(1), 1-14.

Ohtake, M., Nishihara, G. N., Inoue, Y., Tsuchiya, K., & Toda, T. (2020). Phosphorus demand and uptake during growth and maturation of the brown alga *Sargassum macrocarpum*. Phycological Research, 68(4), 277-289.

Oliveira, R. D. (2009). Ambiente costeiro–fragilidades e impactos relacionados a ação antrópica: o cenário da baixada santista no estado de São Paulo/Brasil. Encontro Latino Americano De Geógrafos, XII.

Paolucci, E. M., Sardiña, P., Sylvester, F., Perepelizin, P. V., Zhan, A., Ghabooli, S., Cristescu, M. E., Oliveira, M D., & MacIsaac, H. J. (2014). Morphological and genetic variability in an alien invasive mussel across an environmental gradient in South America. Limnology and Oceanography, 59(2), 400-412.

Paradis, E. (2010). "pegas: an R package for population genetics with an integrated–modular approach." Bioinformatics, 26: 419-420

Peres, P. A., Azevedo-Silva, M., Andrade, S. C., & Leite, F. P. (2019). Is there host-associated differentiation in marine herbivorous amphipods?. Biological Journal of the Linnean Society, 126(4), 885-898.

Pessanha, A. L. M., Sales, N. S., da Silva Lima, C. S., Clark, F. J. K., de Lima, L. G., de Lima, D. E. P. C., & Brito, G. J. S. (2021). The occurrence of fish species in multiple habitat types in a tropical estuary: Environmental drivers and the importance of connectivity. Estuarine, Coastal and Shelf Science, 262, 107604.

Petit-Marty, N., Vázquez-Luis, M., & Hendriks, I. E. (2021). Use of the nucleotide diversity in COI mitochondrial gene as an early diagnostic of conservation status of animal species. Conservation Letters, 14(1), e12756.

Pires-Vanin, A. M. S., Arasaki, E., & Muniz, P. (2013). Spatial pattern of benthic macrofauna in a sub-tropical shelf, São Sebastião Channel, southeastern Brazil. Latin American Journal of Aquatic Research, 41(1), 42-56.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. Genetics, 155(2), 945-959.

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., Kleunen, M., Vilá, M., Wingfield, M. J., & Richardson, D. M. (2020). Scientists' warning on invasive alien species. Biological Reviews, 95(6), 1511-1534.

Quintana, C. O., Bernardino, A. F., de Moraes, P. C., Valdemarsen, T., & Sumida, P. Y. (2015). Effects of coastal upwelling on the structure of macrofaunal communities in SE Brazil. Journal of Marine Systems, 143, 120-129.

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

Roberts, D. A., Johnston, E. L., & Poore, A. G. (2008). Contamination of marine biogenic habitats and effects upon associated epifauna. Marine Pollution Bulletin, 56(6), 1057-1065.

Rodríguez-Zárate, C. J., Sandoval-Castillo, J., van Sebille, E., Keane, R. G., Rocha-Olivares, A., Urteaga, J., & Beheregaray, L. B. (2018). Isolation by environment in the highly mobile olive ridley turtle (*Lepidochelys olivacea*) in the eastern Pacific. Proceedings of the Royal Society B: Biological Sciences, 285(1878), 20180264.

Rogers, A. R. (1995). Genetic evidence for a Pleistocene population explosion. Evolution, 49(4), 608-615.

Rohlf, F. J., & Slice, D. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic biology, 39(1), 40-59.

Rolim, F. A., Langlois, T., Rodrigues, P. F., Bond, T., Motta, F. S., Neves, L. M., & Gadig, O. B. (2019). Network of small no-take marine reserves reveals greater abundance and body size of fisheries target species. PLoS One, 14(1), e0204970.

Sbrocco, E. J., & Barber, P. H. (2013). MARSPEC: ocean climate layers for marine spatial ecology: Ecological Archives E094-086. Ecology, 94(4), 979-979.

Selmoni, O., Rochat, E., Lecellier, G., Berteaux-Lecellier, V., & Joost, S. (2020). Seascape genomics as a new tool to empower coral reef conservation strategies: An example on north-western Pacific *Acropora digitifera*. Evolutionary Applications, 13(8), 1923-1938.

Sexton, J. P., Hangartner, S. B., & Hoffmann, A. A. (2014). Genetic isolation by environment or distance: which pattern of gene flow is most common?. Evolution, 68(1), 1-15.

Sherman, C. D., Hunt, A., & Ayre, D. J. (2008). Is life history a barrier to dispersal? Contrasting patterns of genetic differentiation along an oceanographically complex coast. Biological Journal of the Linnean Society, 95(1), 106-116.

Silva, I. C., & Paula, J. (2008). Is there a better chela to use for geometric morphometric differentiation in brachyuran crabs? A case study using *Pachygrapsus marmoratus* and *Carcinus maenas*. Journal of the Marine Biological Association of the United Kingdom, 88(5), 941-953.

Da Silva, M. F., Cruz, M. V., Vidal Júnior, J. D. D., Zucchi, M. I., Mori, G. M., & De Souza, A. P. (2021). Geographical and environmental contributions to genomic divergence in mangrove forests. Biological Journal of the Linnean Society, 132(3), 573-589.

Silva Oscar Júnior, A. C. D., Oliveira Santos, B. B. D., Hosokawa, E. K., Araújo, P. P. D., & Carriço, J. M. (2019). Land use change dynamics in the metropolitan region of Baixada Santista MRBS (SP): between development and environmental impacts. In Climate Change in Santos Brazil: Projections, Impacts and Adaptation Options (pp. 177-199). Springer, Cham.

Smouse, P. E., Long, J. C., & Sokal, R. R. (1986). Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Systematic zoology, 35(4), 627-632.

Sudo, H., & Yoshida, G. (2021). Effects of a reduction in algal nitrogen content on survival, growth, and reproduction of an herbivorous amphipod. Journal of Experimental Marine Biology and Ecology, 539, 151543.

Suyama, Y., & Matsuki, Y. (2015). MIG-seq: an effective PCR-based method for genome-wide single-nucleotide polymorphism genotyping using the next-generation sequencing platform. Scientific Reports, 5(1), 1-12.

Švara, V., Michalski, S. G., Krauss, M., Schulze, T., Geuchen, S., Brack, W., & Luckenbach, T. (2022). Reduced genetic diversity of freshwater amphipods in rivers with increased levels of anthropogenic organic micropollutants. Evolutionary Applications.

Takolander, A., Cabeza, M., & Leskinen, E. (2017). Climate change can cause complex responses in Baltic Sea macroalgae: A systematic review. Journal of Sea Research, 123, 16-29.

Tanaka, M. O., & Leite, F. P. (2003). Spatial scaling in the distribution of macrofauna associated with Sargassum stenophyllum (Mertens) Martius: analyses of faunal groups, gammarid life habits, and assemblage structure. Journal of Experimental Marine Biology and Ecology, 293(1), 1-22.

Tanaka, M. O., & Leite, F. P. (2004). Distance effects on short-term recolonization of Sargassum stenophyllum by mobile epifauna, with an analysis of gammarid life habits. Journal of the Marine Biological Association of the United Kingdom, 84(5), 901-910.

Teske, P. R., Golla, T. R., Sandoval-Castillo, J., Emami-Khoyi, A., Van der Lingen, C. D., Von der Heyden, S., Chiazzari, B., van Vuuren, B. J., & Beheregaray, L. B. (2018). Mitochondrial DNA is unsuitable to test for isolation by distance. Scientific Reports, 8(1), 1-9.

Thiel, M., & Gutow, L. (2004). The ecology of rafting in the marine environment. I. The floating substrata. Oceanography and Marine Biology: an annual review, 42, 181-264.

Thiel, M., & Gutow, L. (2005). The ecology of rafting in the marine environment. II. The rafting organisms and community. In Oceanography and Marine Biology (pp. 289-428). CRC Press.

Toews, D. P. L., & Brelsford, A. (2012). The biogeography of mitochondrial and nuclear discordance in animals. Molecular Ecology 21, 3907–3930.

Turra, A., Amaral, A. C. Z., Ciotti, A., Wongtschowski, C. L. R., Schaeffer-Novelli, Y., Marques, A. C., Siegle, E., Sinisgalli, P. A. A., dos Santos, C. R., & Carmo, A. B. (2017). Environmental impact assessment under an ecosystem approach: the São Sebastião harbor expansion project. Ambiente & Sociedade, 20, 155-176.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global Ecology and Biogeography, 21(2), 272-281.

Ungherese, G., Mengoni, A., Somigli, S., Baroni, D., Focardi, S., & Ugolini, A. (2010). Relationship between heavy metals pollution and genetic diversity in Mediterranean populations of the sandhopper *Talitrus saltator* (Montagu) (Crustacea, Amphipoda). Environmental Pollution, 158(5), 1638-1643.

Väinölä, R., Witt, J. D. S., Grabowski, M., Bradbury, J. H., Jazdzewski, K., & Sket, B. (2007). Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. In Freshwater animal diversity assessment (pp. 241-255). Springer, Dordrecht.

Vendrami, D. L., Telesca, L., Weigand, H., Weiss, M., Fawcett, K., Lehman, K., Clark, M. S., Leese, F., McMinn, C., Moore, H., & Hoffman, J. I. (2017). RAD sequencing resolves fine-scale population structure in a benthic invertebrate: implications for understanding phenotypic plasticity. Royal Society Open Science, 4(2), 160548.

Walters, A. D., Trujillo, D. A., & Berg, D. J. (2022). Micro-endemic species of snails and amphipods show population genetic structure across very small geographic ranges. Heredity, 1-13.

Wang, I. J. (2013). Examining the full effects of landscape heterogeneity on spatial genetic variation: a multiple matrix regression approach for quantifying geographic and ecological isolation. Evolution, 67(12), 3403-3411.

Wang, I. J., & Bradburd, G. S. (2014). Isolation by environment. Molecular Ecology, 23(23), 5649-5662.

Wee, A. K., Mori, G. M., Lira, C. F., Núñez-Farfán, J., Takayama, K., Faulks, L., Shi, S., Tsuda, Y., Suyama, Y., Yamamoto, T., Iwasaki, T., Nagano, Y., Wang, Z., Watanabe, S., & Kajita, T. (2019). The integration and application of genomic information in mangrove conservation. Conservation Biology, 33(1), 206.

Wright, S. (1943). Isolation by distance. Genetics, 28(2), 114.

Xuereb, A., D'Aloia, C. C., Daigle, R. M., Andrello, M., Dalongeville, A., Manel, S., Mouillot, D., Guichard, F., Côté, I. M., Curtis, J. M. R., Bernatchez, L., & Fortin, M. J. (2019). Marine conservation and marine protected areas. In Population genomics: marine organisms (pp. 423-446). Springer, Cham.

Yamashita, C., Nagai, R. H., Martins, M. V. A., Vicente, T. M., e Sousa, S. D. M., Frontalini, F., Palóczy, A., Mahiques, M. M., Godoi, S. S., Montoya-Montes, I., & Figueira, R. C. L. (2016). On the interplay between hydrodynamics, bottom morphology, sedimentary processes and benthic foraminifera assemblages in the São Paulo Bight (Brazil, SW Atlantic). Journal of Sedimentary Environments, 1(3), 326-347.

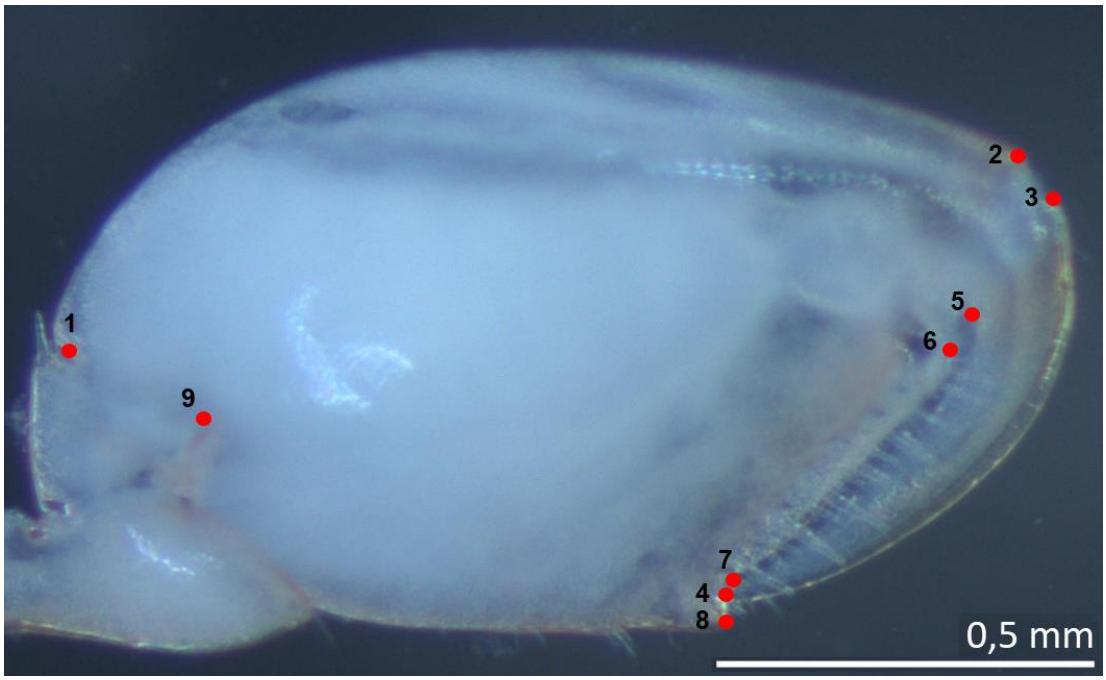
Yamazaki, D., Ito, S., Miura, O., Sasaki, T., & Chiba, S. (2022). High-throughput SNPs dataset reveal restricted population connectivity of marine gastropod within the narrow distribution range of peripheral oceanic islands. Scientific reports, 12(1), 1-11.

Yang, N., Dong, Z., Chen, A., Yin, Y., Li, X., & Chu, D. (2020). Migration of Sogatella furcifera between the Greater Mekong Subregion and northern China revealed by mtDNA and SNP. BMC Evolutionary Biology, 20(1), 1-10.

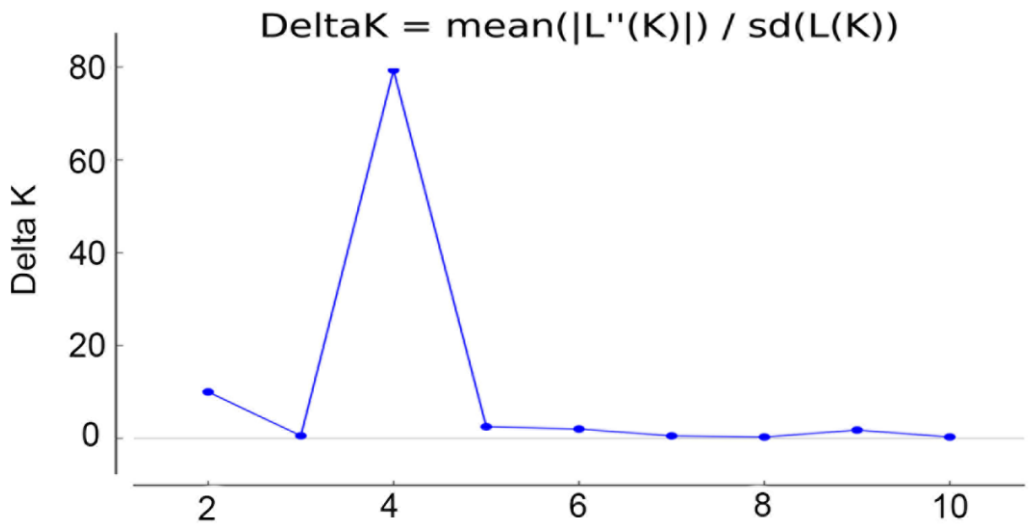
Zamudio, K. R., Bell, R. C., & Mason, N. A. (2016). Phenotypes in phylogeography: Species' traits, environmental variation, and vertebrate diversification. Proceedings of the National Academy of Sciences, 113(29), 8041-8048.

Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2012). Geometric morphometrics for biologists: a primer. academic press.

Supplementary 1 – Microphotograph of the male propodus of gnathopod 2, showing the position of the nine landmarks used in morphometric analysis.



Supplementary 2 - K = 4 inferred by STRUCTURE HARVESTER for the genetic assignment based on 513 SNPs



CHAPTER 2: MULTISPECIES POPULATION GENOMICS AND COMMUNITY VARIATIONS OF SEAWEED-ASSOCIATED INVERTEBRATES UNVEIL INDEPENDENT RESPONSES ACROSS BIODIVERSITY LEVELS

Pedro A. S. Longo; Marianne Azevedo-Silva; Karine F. R. Mansur; André G. Madeira; Shun K. Hirota; Anete P. de Souza; Joseph Harari; Yoshihisa Suyama; Gustavo M. Mori; Fosca P. P. Leite

Introduction

Biodiversity is the variety of life across all levels of organization Colwell et al. (2009), and it can be expressed in two fundamental levels: the genetic diversity and species diversity (Vellend 2003; Hughes et al. 2008; Lamy et al. 2017). Both levels have traditionally been treated independently, however it has been shown that intra and interspecific variations may be driven by parallel processes and thus be correlated, potentially presenting effects on different ecological scales (Vellend 2003, 2005; Vellend & Geber 2005; Witham et al. 2006; Hughes et al. 2008; Lamy et al. 2017). These studies are in the field of Community Genetics (Agrawal 2003), which usually aims to investigate the existence of "species-genetic diversity correlations" (SGDC), quantifying the relationship between genetic diversity variations of one or more focal species and the species diversity of the community in which they are inserted in (Vellend 2003, 2005; Vellend & Geber 2005; Lamy et al. 2013, Papadopoulou et al. 2011). These investigations usually try to understand how different factors like habitat structure, spatial heterogeneity and environmental features modulate biological diversity in its different levels (Witham et al. 2006; Hughes et al. 2008; Laroche et al. 2015).

Unravelling how those modulating factors can affect genetic structure and SGDC patterns of marine populations is one of the main goals of Seascape Genomic, a progression of Seascape Genetics (Selkoe et al. 2016a) and derived from Landscape Genomics, applied for marine habitats, which are usually very dynamic in space and time, highly influenced by water currents where species present complex life histories, relatively high dispersal potentials and large effective population sizes (Riginos et al. 2016; Liggins et al. 2019).

Understanding the patterns of genetic structure and species distribution in marine realm is a complex process, due to the wide extension of ocean waters and the influence of water currents, which promote connectivity among distant localities (Oleksiak 2018). Therefore, to unravel genetic and species variability, it is important to comprehend not only the historical processes and geographic features that may have generated current patterns of biodiversity distribution, but also consider how relevant biotic features of different species, like

relevant life history traits, morphological variations and responses to environmental gradients may generate those patterns (Papadopoulou & Knowles 2016).

Dispersal is a fundamental process that leads to the movement of species across localities and ultimately is responsible for the patterns of spatial structure and connectivity in metapopulations of a species (Clobert et al. 2004). Most of marine benthic species present an elevated dispersal capacity through water currents, mainly due to the existence of a pelagic larval phase. However, species with direct development are not uncommon and are traditionally expected to present a more restricted dispersal ability and lower rates of individuals exchange among subpopulations (Wares et al. 2001; Foggo et al. 2007; Cowen & Sponaugle 2009). Besides larval duration, dispersal potential in marine species may also be modulated by other factors like environmental conditions and historical processes, which are all determinant features for generating the patterns of species distribution and spatial structuring of their populations (Pringle & Wares 2007; Jolly et al. 2009).

Documenting dispersal events in marine environment is rather challenging and information on larval and species movements in the literature is scarce (Christie et al. 2010). In this context, genetic studies raise as an essential alternative and have been extensively explored for better understanding patterns of dispersal and connectivity in the marine realm (Heyden et al. 2014). Over the past decades, the use of molecular tools, together with the advances in sequencing technology (with the rise of multiple methods of next-sequencing techniques, Davey et al. 2011; Levy & Myers 2016) applied for population genomics studies have been of extreme importance for investigating the structure and dynamics of marine populations, generating crucial guideline information for the development of conservation measures for marine biodiversity (Chatzigeorgiou et al. 2014; Heyden et al. 2014). Associated to population genomics approaches, the use of biophysical models of dispersal can be of great contribution for comprehending how these complex dynamics of marine species may be influenced by seascape features (Jahnke & Jonsson 2022) which, in turn, can be fundamental for the conservation planning of marine habitats (Selkoe et al. 2016a, Selkoe et al. 2016b). However, different species may be distinctly affected by seascape features depending on their particular life histories (Boström et al. 2011), and understanding those species-specific particularities is crucial for establishing effective conservation measures for marine coastal habitats (Palumbi 2003; Boström et al. 2011).

Seaweed beds constitute an important and highly productive marine coastal habitat, presenting a worldwide distribution and allowing a great diversity of species to thrive by living in association to macroalgae fronds, where they benefit from multiple resources, such as food,

refuge against predators and higher environmental stability (Roberts et al. 2008; Christie et al. 2009; Cacabelos et al. 2010). However, they are also highly susceptible and therefore threatened by the recent overall increase of anthropogenic impacts on coastal areas over the last decades, raising the importance to discuss conservation of those habitats (Roberts et al. 2008; Gorman et al. 2020; Mayer-Pinto et al. 2020).

The goal of this study is to unveil the predominant factors that modulate variations in seaweed-associated invertebrate community and in populations of four focal species from a discrete community. We developed a study integrating information from Population Genomics in a multispecies approach, to better understand intra- and interspecies dynamics in seaweed habits. Specifically, we first aim to compare if species with different types of dispersal will have differences in their genetic structure in a fine spatial scale of dozens of kilometers. We expect that species with a planktonic larval phase (the bivalve *Pinctada imbricata* Röding, 1798 and the gastropod *Costoanachis sertulariarum* (d'Orbigny, 1839)) will present lower or no genetic structure, in contrast to direct developer species with parental care and no planktonic phase (the amphipods *Hyale niger* (Haswell, 1879) and *Cymadusa filosa* Savigny, 1816). Secondly, we want to investigate if the genetic variation of some key species and variations in the whole seaweed-associated invertebrate assemblages are modulated by similar factors. To answer that, we will consider as potential modulating factors the geographic distance, the environmental dissimilarities, and the dispersal simulations among localities. Finally, we tested whether there is correlation between the two levels of biological organization (genetic and community) in marine invertebrates living in macroalgae habitats.

Material and Methods

Sample collection

Samples were taken in 12 localities along the São Paulo coast, in southeastern Brazil, with different conservation status (Table 1, Figure 1), during the austral summer of 2018. For genetic analysis, at each locality, thirteen individuals of the predominant macroalga species were randomly collected in the infralittoral zone, where algae fronds were wrapped in a 0.2-mm-mesh bag to prevent loss of the associated fauna. Fronds were thawed and washed in seawater to remove associated fauna, and one individual of each of the four invertebrate species studied was obtained from each algal sample, except for the samples where no individuals were found. Specimens were immediately preserved in absolute ethanol under -14ºC and used in the subsequent genetic analysis. For community analysis, samples were taken in all localities except in Moela and Cibratel. At each locality, four fronds of the predominant macroalga species were randomly collected in the infralittoral zone, where algae fronds were wrapped in a 0.2-mm-mesh bag to prevent loss of the associated fauna, and then preserved at -14ºC. In the laboratory, fronds were thawed and carefully washed three times in distilled water to remove the associated fauna, which was preserved in 70% ethanol. All the macrofauna retained by the 0.2-mm-mesh bag was considered. The fauna was sorted under a stereomicroscope of 6:1 zoom factor combined with a S1.0 9 plan apochromat objective; invertebrates were separated for identification to species level (or the lowest possible taxonomic level).

Table 1. Sampling localities, conservation status of the area, number of individuals of each species collected for genetic analysis. * Indicates sites samples for community analysis were also taken.

Site	**Conservation Status**	**Genetic**			
		Hyale niger	*Cymadusa filosa*	*Pinctada imbricata*	*Costoanachis sertulariarum*
Lamberto*	Unprotected	0	4	9	11
Conchas*	Partial Protection	6	4	8	1
Búzios*	Partial Protection	9	10	5	0
Palmas*	Full Protection	0	0	10	2
Figueira*	Unprotected	13	4	3	4
Baleia*	Partial Protection	10	9	10	13
Montão de Trigo*	Partial Protection	12	9	13	6
Alcatrazes ESEC*	Full Protection	9	9	4	0
Alcatrazes Refuge*	Full Protection	7	6	4	0
Mar Casado*	Partial Protection	9	6	7	9
Moela	Partial Protection	6	0	0	0
Cibratel	Partial Protection	3	0	0	0

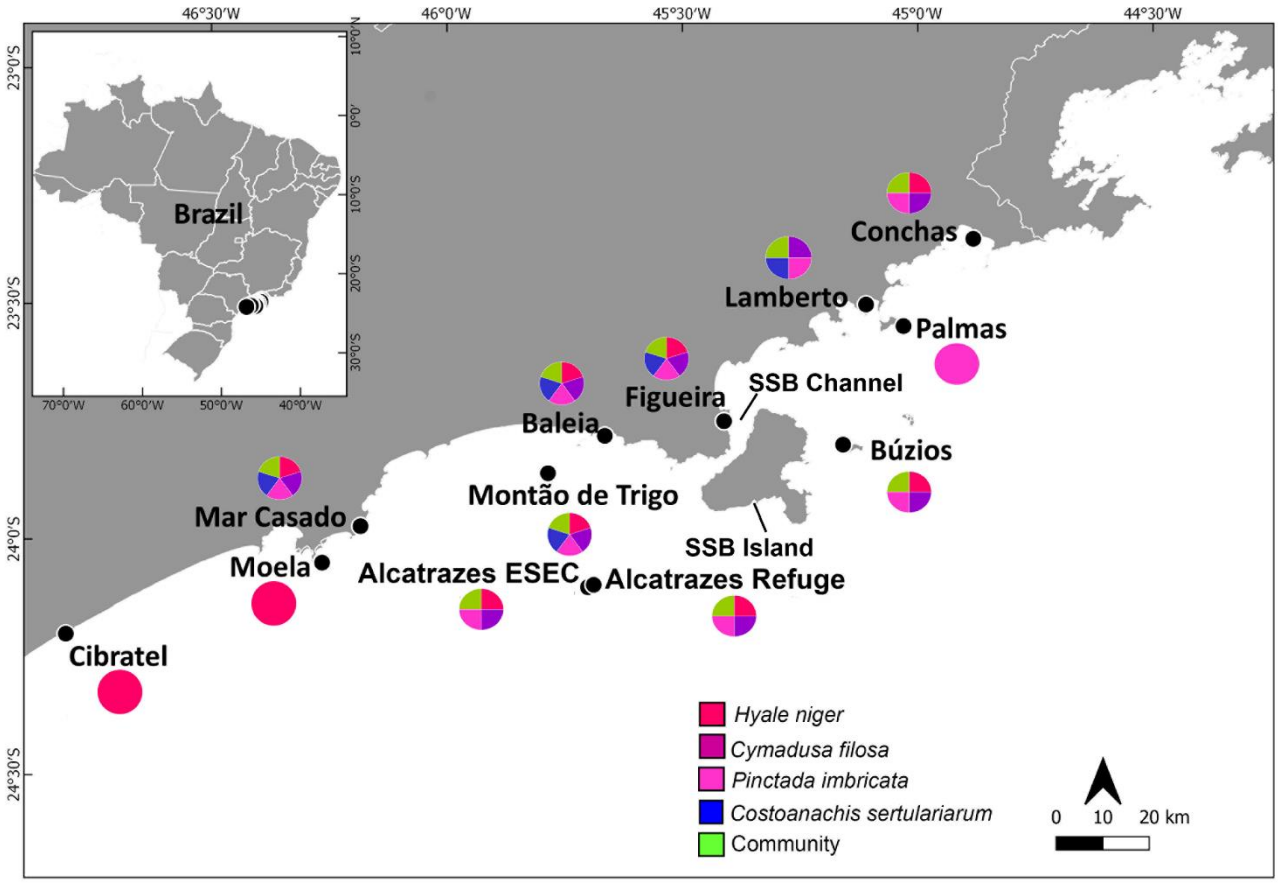


Figure 1. Map of the study area, and indication of which samples were taken in each area. SSB Island – São Sebastião Island; SSB Channel – São Sebastião Channel.

DNA extraction

Genomic DNA was extracted from whole individuals of *H. niger*, *C. filosa*, *P. imbricata* and *C. sertulariarum*. For *H. niger*, DNA was extracted with DNeasy Blood & Tissue Kit (QIAGEN), following the manufacturer's protocol for insects. For *C. filosa*, we used the protocol for DNA extraction described by Aljanabi & Martinez (1997). Briefly, individuals were immersed in a buffer containing 10mM Tris-HCl, 2mM EDTA and 400mM NaCl and then macerated in a TissueLyser (QIAGEN). 40µL of sodium dodecyl sulfate (SDS, 20% solution) and 8µL of Proteinase K (20ng.mL^{-1}) were added and samples were incubated for one hour at 60°C. Afterwards, 300µL of NaCl 5M was added and samples were centrifuged at 13000rpm for 30 minutes. The supernatant was recovered and precipitated in cold isopropanol, then samples were incubated for one hour at -20ºC. Finally, samples were washed in two successive baths in absolute and 70% ethanol, respectively, and then dried and resuspended in 100µL TED solution (3mM Tris-HCl and 0.2mM EDTA). For both molluscan species, DNA extraction was based on the protocol described by Sokolov (2000): individuals were immersed

in 200µL buffer solution (50mM Tris-HCl, 10mM EDTA and 100mM NaCl), and macerated in a TissueLyser (QIAGEN). Then, we added 725µL of the buffer, 50µL of SDS 20%, and 15µL of Proteinase K (20ng.mL^{-1}). Samples were incubated for one hour at 55ºC, then we added 100µL saturated KCl and incubated them for 5 minutes in ice. Afterwards, samples were centrifuged at 13000rpm for 15 minutes, supernatant was recovered, and we added 450µL Phenol – chloroform – isoamyl alcohol mixture (5:24:1), centrifugated samples at 13000 for 15minutes, and then supernatant was recovered. This step was performed twice. DNA samples were then precipitated in cold isopropanol, incubated for 10 minutes in room temperature, and centrifuged for more 20 minutes at 13000rpm. Pellets were then washed in two successive baths with 70% cold ethanol, completely dried and resuspended in TED buffer.

MIG-seq library preparation and sequencing

The obtention, validation and genotyping of SNPs were performed through the MIG-seq ("multiplexed ISSR genotyping by sequencing") technique (Suyama & Matsuki 2015). Shortly, hundreds to thousands of ISSR loci were selectively amplified using eight pairs of 12 base di- and trinucleotide microsatellites. The first 14 bases (12 nucleotides of the microsatellite used to construct the MIG-seq libraries, and two bases of first PCR primers) of read 2 were removed using FASTX-Toolkit (http://hannonlab.cshl.edu/fastx_toolkit/), which was also used to filter reads by quality (Phred Q score = 30 for at least 40% of the read bases). The filtered reads were then used as input for STACKS 1.15 (Catchen et al. 2011) for *de novo* assembly. Only biallelic SNPs were maintained and sequences with high quality were used for analysis, with the removal of sequences with more than 30% missing data (35% was allowed for *C. filosa*) using the VCFtools v.0.1.12b (Danecek et al. 2011).

Particle dispersal model

Simulations of the three-dimensional coastal circulation were performed through the Delft3D Flow Hydrodynamic Module (Deltares 2019). This module calculates flows and transports resulting from the action of meteorological forces, density and tides, in a coastal domain covered by a computational grid. In the present work, a regular Arakawa C type grid was used, between 23ºS and 25.5ºs and between 43ºW and 47ºW, with 1196 points parallel to the coast, 410 points perpendicular to the coast, horizontal spacing of 400 m and 8 vertical sigma levels equally spaced; the maximum depth of the modeled region is 160 m. The model uses the Navier-Stokes equations, based on mass, momentum, heat, and salt conservation laws, resolved by the finite difference method. Thus, the model computes the sea level, east, north, and vertical components of the currents, and temperature, salinity, and seawater density, in three-dimensional standard.

The hydrodynamic model was processed from the specification of surface meteorological forces and boundary conditions at the open boundaries of the grid. As for the meteorological forces, the model runs considered wind at the surface, atmospheric pressure reduced at sea level, total cloud cover, relative humidity at the surface and air temperature at the surface; these variables were extracted from the Global CFSv2 atmospheric model, with a time resolution of one hour (Saha et al. 2011). Regarding lateral boundary conditions, tide fluctuations were provided by the global TPXO tidal model (Egbert et al. 1994) and mean sea level oscillations, currents, temperature, and salinity (3D standard), with daily temporal resolution, were extracted from Copernicus Marine Environment Monitoring Service (CMEMS) GAFP0124 Model (Lellouche et al. 2016; Nouel 2018).

The implemented hydrodynamic model, with the mentioned boundary conditions, has been routinely used in oceanographic studies of the São Paulo State coastal region, such as the forecast of storm surges (Ruiz et al 2021) and the study of the dispersion of effluent plumes (Yang et al 2019).

For the purposes of this work, the hydrodynamic model has been processed for the São Paulo coast from January 2017 until May 2018, providing hourly surface currents for the particle dispersion model. This model renews in time the positions of particles in the ocean, through the mathematical relationship:

Renewed position = starting position + speed * time interval

This expression is used with the ocean currents computed at the grid points by the hydrodynamic model being interpolated to the exact positions of the particles. With the successive calculations of particle positions, their trajectories over time are determined. This type of modeling has been extensively used in many dispersion studies, such as the modeling of plastic trajectories in coastal areas (Gorman et al 2020).

In the present study, 12 geographical positions were selected, in which 100 particles were launched at the beginning of each simulation month, to determine the trajectories of the particles throughout each month. By analyzing the particle trajectories, it was then possible to determine the estimated dispersal among localities on the São Paulo coast.

To calculate particle dispersals, we considered a 2km buffer around each geographic coordinate. Both sites from Alcatrazes (ESEC and Refuge) are too close from each other, so their geographic buffers overlapped, thus we considered only Alcatrazes Refuge in the analysis.

Two different matrices were constructed from the results of particle dispersal model: (1) the asymmetric dispersal rate, which was calculated from the proportion of particles

that reached a particular locality that was originated from each of the remaining sites; and (2) the rate of particle exchange between each pair of localities, which was calculated as the sum of the number of particles released from site "x" that reached site "y" and the number of particles released from "y" that reached "x", divided by the total number of particles released from "x" and "y". The first measure is hereafter considered as an estimation of asymmetric dispersal among localities, whilst the second one as a symmetric measure of dispersal distance among pairs of localities. We also estimated the level of connectivity of each locality, which was considered as the number of particles reaching each site that came from other localities divided by the total number of particles released from other localities.

Genetic analysis

Initially, three different methods for the detection of loci putatively under selection and based on population differentiation (F_{ST} outliers) were performed, considering each sampling site as a population: FDIST (Fagundes et al. 2007), implemented in the LOSITAN software (Antao et al. 2008); Bayesian method of population differentiation implemented in the BAYESCAN 2.1 software (Foll and Gaggiotti 2008); and F_{ST} outliers detection with the function 'qvalue' of the package PCADAPT (Luu et al. 2017) in software R. We considered as loci putatively under selection if all three methods indicated that a given locus was not neutral, a conservative approach due to the high rates of false positives given by F_{ST} outliers methods (Bierne et al. 2013; Francois et al. 2016). Three loci for *H. niger* and two loci for *C. filosa* were detected as outliers and were not considered in downstream analyses. To estimate the genetic diversity of the studied species in each locality, we calculated the allelic richness (*Ar*), the observed heterozygosity (*Ho*), and the gene diversity (*Hs*) using 'hierfstat' package (Goudet 2005) in R.

We inferred the genetic structure of our focus species using different approaches. The pairwise F_{ST} among populations from different localities were estimated in 'hierfstat' package (Goudet 2005). Also, individuals were assigned to populations using STRUCTURE v.2.3.4 (Pritchard et al. 2000) Bayesian method, in which the number of populations (K) was allowed to vary from 1 to 11. The program performed 20 runs for each value of K, with a burn-in period of 50,000 followed by 1,000,000 MCMC iterations. The most likely number of genetic groups was selected based on ΔK *ad hoc* statistics using the program STRUCTURE HARVESTER (Earl & von Holdt 2012). To identify the optimal alignment of inferred clusters across different values of K, we used the software CLUMPAK (Kopelman et al. 2015), which was also used to build the most likely K with the "Distruct" application.

Recent asymmetric migration rates among pairs of sampling localities were estimated using BayesAss 3.04 (Wilson & Rannala 2003), implemented in BA3-SNPs (Mussmann et al. 2019), which uses a Bayesian MCMC approach and multilocus genotypes to estimate migration rates over the last several generations. For *H. niger*, final mixing parameters for allele frequencies, inbreeding coefficients, and migration rates were 0.4, 0.2, and 0.1, respectively. For the other three species, mixing parameters could not reach optimal acceptance according to Wilson & Rannala (2003), so they were set to 1.0, the maximum value. The final analysis was completed using 10,000,000 MCMC iterations with 6,000,000 iterations discarded as burn-in. Migration rates and 95% credible intervals (calculated as migration rate ± 1.96*standard deviation) were estimated, and values of migration rates can be considered statistically significant if 95% credible intervals are higher than zero (Wilson & Rannala 2003).

Community analysis

Species diversity of seaweed-associated invertebrate assemblages was compared among localities using a combined individual-based interpolation and extrapolation approach (Colwell et al. 2012), based on the first three Hill numbers (species richness for q = 0, Shannon diversity for q = 1 and Simpson diversity for q = 2) (Chao et al. 2014). Rarefactions were performed with 400 bootstrap resamplings, using the iNEXT package in R software (Hsieh et al. 2016). Results were considered statistically significant ($\alpha = 0.05$) when 95% confidence intervals did not overlap. We also constructed a dissimilarity matrix among assemblages of each pair of sampling localities, using the Sørensen index of beta diversity as a measure dissimilarity (Baselga 2010).

Assemblage structure among localities was compared using a permutational analysis of variance (PERMANOVA, Anderson 2001). This analysis was based on a Bray–Curtis similarity matrix constructed from the mean densities of invertebrate species (log (X + 1) transformed) with 9,999 permutations. To evaluate the homogeneity of dispersal among groups, a PERMDISP procedure was performed using the similarity matrix. Pairwise comparisons were performed for significant effects, and the species that most contributed to the differences found were indicated by a SIMPER analysis (Clarke 1993). Differences in assemblage structure were viewed using the constrained ordination technique CAP (Canonical Analysis of Principal Coordinates), using the CAP classification success rate and CAP traceQ_m'HQ_m statistics, and were performed with 9,999 permutations using the Bray-Curtis similarity matrices.

Association tests

The pairwise geographic distances among localities were obtained though the calculation of Euclidean distance between pairs of localities considering the geographic coordinates (WGS-84) of each site. To investigate the effect of environmental differences on genetic differentiation among populations, we selected 19 environmental variables for each sampling locality, including 10 oceanographic variables from BioOracle online database (Tyberghein et al. 2012; Assis et al. 2017) and 9 oceanographic variables from MARSPEC online database (Sbrocco & Barber 2013). Oceanographic variables were obtained with the package 'sdmpredictors' (Bosch et al. 2017) and highly correlated variables ($r > 0.7$) were removed with the function *removeCollinearity* from package 'virtualspecies' (Leroy et al. 2016) in R. Afterwards, we ran BIOENV analyses using the program primer v. 6 (PRIMER-E Ltd, Lutton, UK) to identify which environmental variables were most correlated with the pairwise genetic distance matrix based on FST of each species. With those variables, we calculated the Euclidean distances between pairs of localities, which was used as a measure of environmental distance.

To test for the relationship between (1) genetic distances of each invertebrate species and geographical, environmental, and dispersal distances among localities; (2) asymmetric migration rates among populations of each species and asymmetric dispersal estimations among localities; (3) beta diversity of invertebrate assemblages and geographical, environmental, and dispersal distances among localities; and (4) genetic distance among populations of each species and beta diversity among invertebrate assemblages of each site, we conducted a multiple matrix regression with randomization (MMRR) analysis using the *MMRR* function in R with 10000 permutations (Wang 2013), to estimate the independent effects of each predictor variable, separately and together, on genetic differentiation.

To check for the association between genetic diversity of the four species and species diversity of invertebrate assemblages (α-SGDC), we also calculated the Spearman's rank correlation coefficient. As the three genetic diversity indexes considered in this study were highly correlated among each other, we selected *Ar* and checked for its correlation with species diversity. As a proxy for species diversity, we calculated the non-parametric Chao-1 species richness estimator, which is based on the proportion between the number of species collected once ("singletons") and the number of species collected twice ("doubletons") (Chao 1984).

When significant species-genetic diversity correlations (α-SGDC) were found, we investigated the effects of habitat size, environmental variables, and connectivity level of each

site, on the α-SGDC, by performing regression analysis, considering as response variables the Chao-1 species richness estimator and *Ar* (see supplementary material 1 for further details).

Results

Oceanographic modelling

Our dispersal estimations were obtained using the particle dispersal models and consist in the fraction of particles released in a particular locality that reached each of the further localities. This was represented in an asymmetric transport matrix (supplementary 2) and in Figure 2. We observed that, even though there is a slight connection among all localities, some main stronger patterns of dispersal are evident, mainly connecting the areas further southwards (Moela, Mar Casado, Baleia and Montão de Trigo) and areas located northwards from São Sebastião island (Búzios, Lamberto, Palmas and Conchas). Alcatrazes, which is located south of São Sebastião island however at 45km offshore, and Figueira, which is positioned inside the São Sebastião Channel, both received mainly from areas southwards and from Búzios, but sent particles only northwards. Cibratel was the most isolated locality in our sampling design.

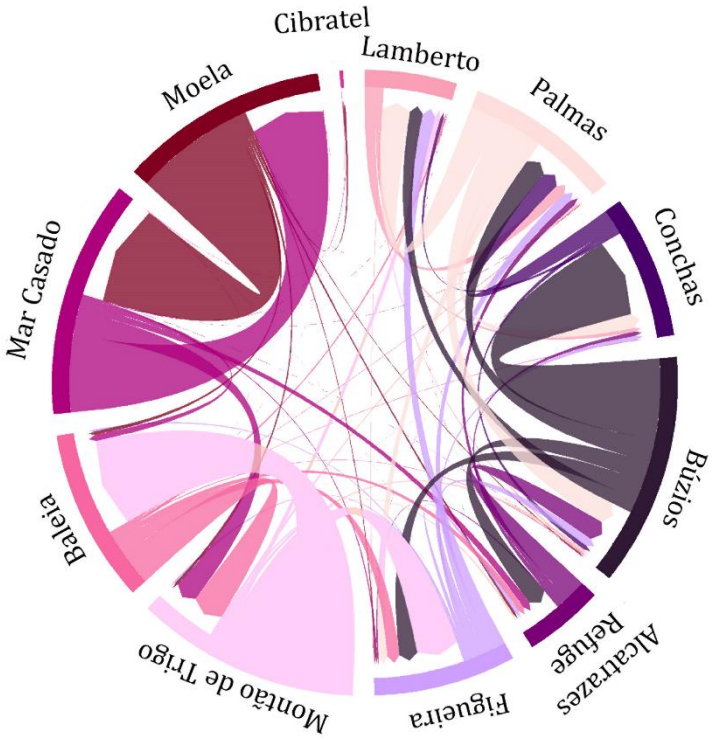


Figure 2. Graphic representation of the bilateral particle dispersal model.

Genetic analysis

After bioinformatics efforts for reads filtering, quality control and removal of loci putatively under selection, we retained a total of 513, 148, 328 and 248 biallelic SNPs for *Hyale*

niger, *Cymadusa filosa*, *Pinctada imbricata* and *Costoanachis sertulariarum*, respectively. Across the 12 sampling locations along São Paulo coast, each species was present at 5–10 sites. Genetic diversity estimates varied considerably between species and samples (Table 2). For *H. niger*, 84 individuals were sampled from 10 different sampling localities. The average allelic richness varied from 1.1338 (Alcatrazes Refuge) to 1.1477 (Mar Casado) and mean parameters of heterozygosity (*Ho* and *Hs*) were higher in Mar Casado (1.1707 and 1.1461, respectively) and lower in Alcatrazes Refuge (1.1520 and 1.1288, respectively). Overall, genetic diversity was highest in Mar Casado, Moela and Figueira, and lowest in Alcatrazes (especially in Refuge), Búzios and Cibratel.

For *C. filosa*, a total of 61 individuals were collected in 9 different sampling localities. In general, values of genetic diversity were higher than values of *H. niger*. Genetic diversity was overall highest in Alcatrazes ESEC and Búzios, and lowest in Baleia, Figueira and Lamberto.

Diversity values for molluscan species were rather similar than values of amphipods. For *P. imbricata*, 73 individuals were collected in 10 different sites. *Ar*, *Ho* and *Hs* were highest in Figueira (1.1406, 0.1512 and 0.1369, respectively) and lowest in Baleia (1.1208, 0.1364 and 0.1197, respectively). For *C. sertulariarum*, we collected 43 specimens from 5 localities. Genetic diversity was higher in Figueira (Ar: 1.997, Ho: 0.2217, Hs: 0.2003) and lower in Montão de Trigo (Ar: 1.1568, Ho: 0.1780, Hs: 0.1537).

Table 2. Genetic diversity of the populations of *Hyale niger*, *Cymadusa filosa*, *Pinctada imbricata* and *Costoana sertulariarum* based on SNP markers. *Ar*: alellic richness; H_O: observed heterozygosity; H_S: gene diversity.

Site	*Hyale niger*				*Cymadusa filosa*				*Pinctada imbricata*				*Costoanachis sertulariarum*			
	N	**Genetic diversity**			**N**	**Genetic diversity**			**N**	**Genetic diversity**			**N**	**Genetic diversity**		
		Ar	*Ho*	*Hs*		*Ar*	*Ho*	*Hs*		*Ar*	*Ho*	*Hs*		*Ar*	*Ho*	*Hs*
Baleia	10	1.1416	0.1621	0.1403	9	1.1849	0.2205	0.1820	10	1.1208	0.1364	0.1197	13	1.1720	0.1995	0.1706
Búzios	9	1.1378	0.1579	0.1363	10	1.2439	0.2975	0.2403	5	1.1320	0.1509	0.1292	0	-	-	-
Cibratel	3	1.1429	0.1567	0.1282	0	-	-	-	0	-	-	-	0	-	-	-
Conchas	6	1.1439	0.1684	0.1409	4	1.2255	0.2649	0.2191	8	1.1277	0.1455	0.1260	<3	-	-	-
Alcatrazes ESEC	9	1.1393	0.1621	0.1376	9	1.2443	0.2939	0.2403	4	1.1307	0.1463	0.1259	0	-	-	-
Alcatrazes Refuge	7	1.1338	0.1520	0.1288	6	1.2137	0.2537	0.2078	4	1.1329	0.1443	0.1229	0	-	-	-
Figueira	13	1.1457	0.1699	0.1445	4	1.2073	0.2420	0.2001	3	1.1406	0.1512	0.1369	4	1.1997	0.2217	0.2003
Lamberto		-	-	-	4	1.2095	0.2387	0.1967	9	1.1255	0.1421	0.1243	11	1.1642	0.1904	0.1625
Mar Casado	9	1.1477	0.1707	0.1461	6	1.2252	0.2604	0.2227	7	1.1295	0.1463	0.1276	9	1.1662	0.1930	0.1639
Moela	6	1.1466	0.1704	0.1438	0	-	-	-	0	-	-	-	0	-	-	-
Montão de Trigo	12	1.1371	0.1567	0.1360	9	1.2238	0.2736	0.2202	13	1.1323	0.1502	0.1315	6	1.1568	0.1780	0.1537
Palmas		-	-	-	0	-	-	-	10	1.1310	0.1488	0.1298	<3	-	-	-

The pairwise F_{ST} and the Bayesian STRUCTURE assignment analysis indicated that both amphipod species, with a direct development, presented structured populations, whilst molluscan species, with a pelagic larva, had no observable genetic structure (Figure 3). Among amphipods, *C. filosa* presented lower genetic structure, with the formation of two genetic

clusters (STRUCTURE, k = 2, Figure 3B), one composed by Búzios and both Alcatrazes populations, and the other by the remaining populations, whereas for *H. niger* we found three genetic clusters (STRUCTURE, k = 3, Figure 3B): the first one included populations from Alcatrazes (ESEC and Refuge), Búzios and Conchas; the second group was formed by Baleia, Montão de Trigo, Moela and Mar Casado; while Figueira individuals formed a third separated genetic cluster, along with the three individuals from Cibratel.

Estimations of migration rates among pairs of populations were in general low ($m < 0.01$) for all species, however some punctual signs of recent gene flow could be observed (Figure 4). For *H. niger*, current migration could be inferred among populations from the same genetic cluster, such as from Alcatrazes Refuge into Alcatrazes ESEC, from Conchas into Búzios and from Moela into Mar Casado (Figure 4A). For *C. filosa*, signs of current migration could be observed from Búzios and Alcatrazes Refuge into Alcatrazes ESEC, and from Lamberto, Conchas, Figueira, Montão de Trigo and Mar Casado into Baleia (Figure 4B). For *P. imbricata*, the higher migration rates were observed from all localities into Palmas (Figure 4C). For *C. sertulariarum*, higher migration rates were found from all localities into Baleia (Figure 4D).

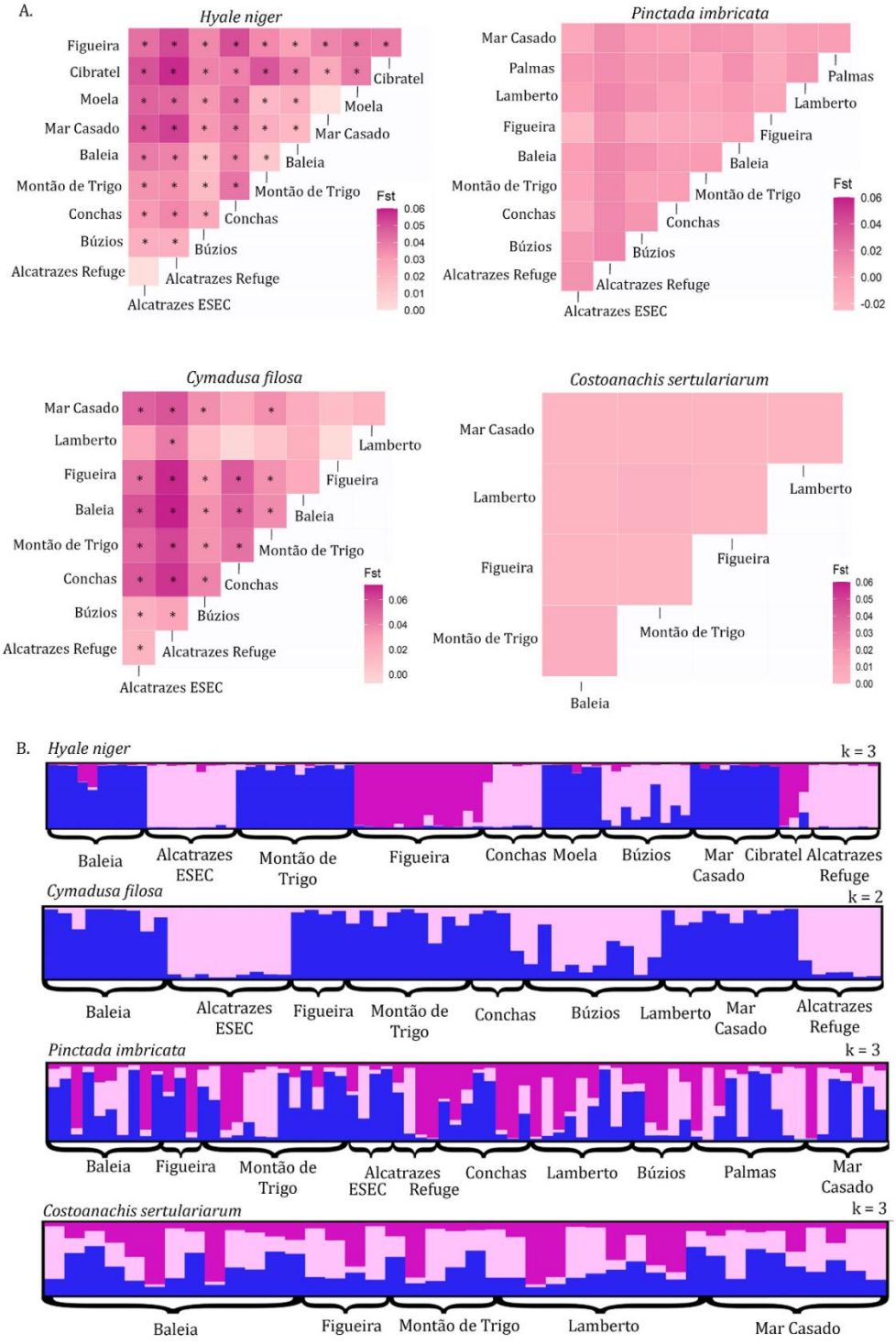


Figure 3. Genetic structure of the amphipods *Hyale niger*, *Cymadusa filosa*, the bivalve *Pinctada imbricata* and the gastropod *Costoanachis sertulariarum* along sampling stations in São Paulo coast. **A:** heatmaps of the pairwise F_{ST} among populations of each species. * indicates statistically significant genetic differentiation. **B:** populations assignment based on STRUCTURE analysis considering 513, 148, 328 and 248 SNPs and K = 4, 3, 3 and 3, respectively, for *H. niger*, *C. filosa*, *P. imbricata* and *C. sertulariarum*. Each vertical bar is an individual and different colors indicate the different genetic clusters.

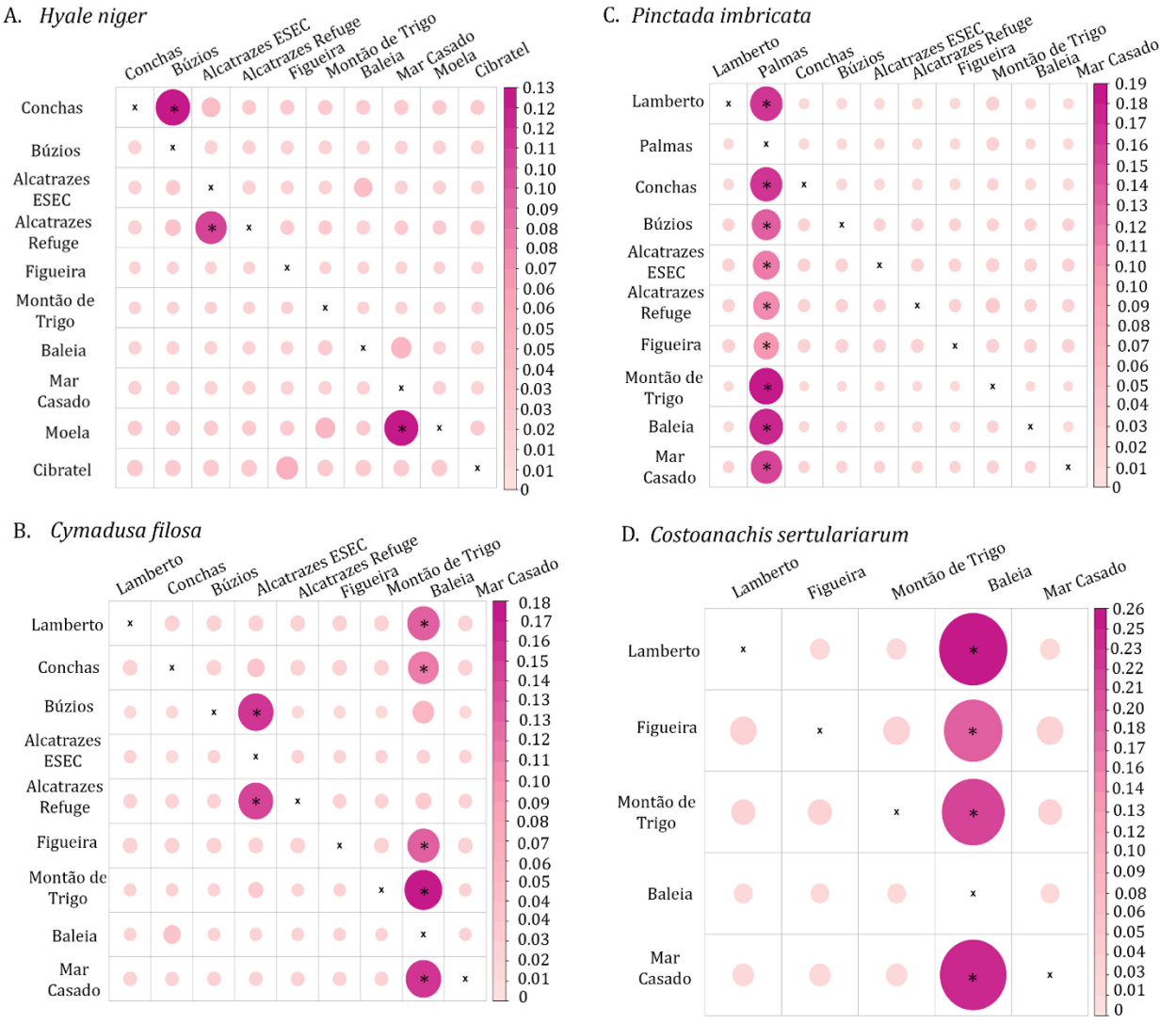


Figure 4. Migration rates estimates between pairs of sites estimated from BAYESASS. Values represent the fraction of individuals in a column population that is derived from a row population (per generation). * indicates statistically significant migration rates. **A:** *Hyale niger*; **B:** *Cymadusa filosa*; **C:** *Pinctada imbricata*; **D:** *Costoanachis sertulariarum*.

Community analysis

Species diversity of seaweed-associated invertebrate assemblages differed among localities according to the comparison of the interpolated and extrapolated rarefaction curves (based on Hill numbers q = 0, 1, 2; Figures 5ABC). It showed that species diversity (for q = 1 and q = 2, equivalent to Shannon and Simpson diversity, respectively) was significantly higher in Palmas, Conchas and Alcatrazes Refuge, respectively, and was significantly lower in Mar Casado and Lamberto, respectivelly (Figures 5BC), while species richness (q = 0, Figure 5A) was higher only in Palmas.

As for species composition, all assemblages presented significantly different invertebrate compositions except for Búzios and Alcatrazes ESEC (PERMANOVA, Pseudo-F = 9.6066, P = 0.0001, supplementary material 3). Among the species that most contributed for differences in species composition, there were the amphipods *Hyale niger* (Haswell, 1879), *Ericthonius brasiliensis* (Dana, 1853) and *Stenothoe* sp., the isopod *Janaira gracilis* Moreira & Pires, 1977, the gastropod *Bittiolum varium* (L. Pfeiffer, 1840) and the ophiuroid *Ophiothela mirabilis* Verrill, 1867 (SIMPER results, Figure 5E, Supplementary material 4). It is also noteworthy that assemblages that presented differences in species diversity, such as Palmas, Alcatrazes Refuge and Lamberto in general presented more dissimilar species composition (Figure 5D), and that changes in the relative densities of some key species like *H. niger* are essential for explaining diversity changes (Figure 5E).

Overall, *H. niger* was a very frequent species in most localities, with a relative density between 20-40%, reaching 50% in Mar Casado, where this species was most dominant, together with *B. catarinensis* and *E. brasiliensis*, resulting in a reduced species diversity (Figure 5E). Meanwhile, both in Lamberto, where invertebrate diversity was lower, and in Palmas, Conchas and Acatrazes Refuge, where diversity was higher, a similar phenomenon was observed: an expressive reduction in the relative density of *H. niger*. However, in Lamberto, in the absence of *H. niger*, we observed a strong dominance of the gastropod *B. varium*, probably causing a diversity drop in this site, whilst in the most diverse localities, the absence of *H. niger* resulted in more even assemblages, with more species represented in lower relative densities, which would explain the high species diversity (Figure 5E).

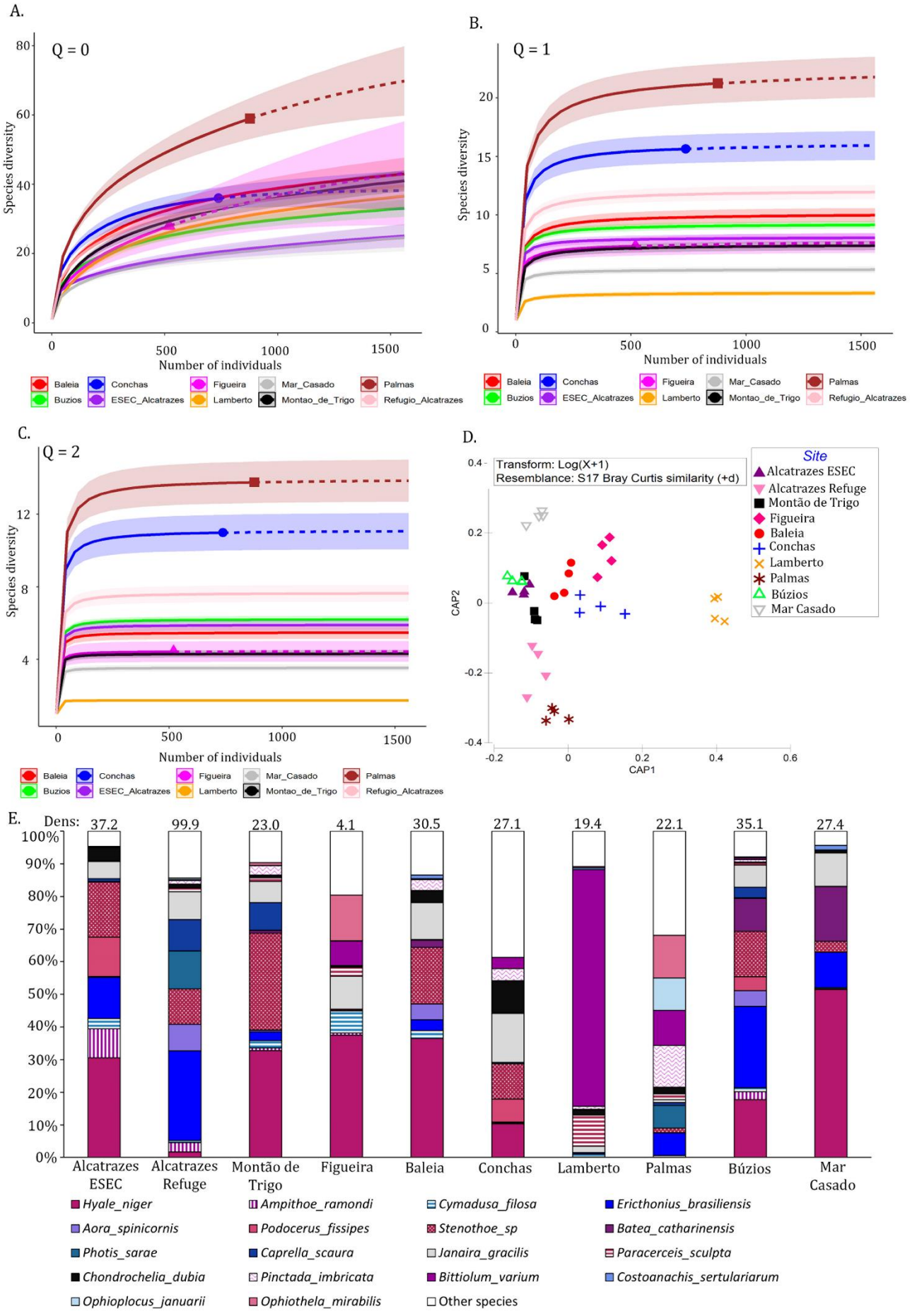

A.
Q = 0
Species diversity
Number of individuals
B.
Q = 1
Species diversity
Number of individuals
Baleia
Buzios
Conchas
ESEC_Alcatrazes
Figueira
Lamberto
Mar_Casado
Montao_de_Trigo
Palmas
Refugio_Alcatrazes
C.
Q = 2
Species diversity
Number of individuals
D.
Transform: Log(X+1)
Resemblance: S17 Bray Curtis similarity (+d)
CAP1
CAP2
Site
Alcatrazes ESEC
Alcatrazes Refuge
Montão de Trigo
Figueira
Baleia
Conchas
Lamberto
Palmas
Búzios
Mar Casado
E.
Dens:
37.2
99.9
23.0
4.1
30.5
27.1
19.4
22.1
35.1
27.4
Alcatrazes ESEC
Alcatrazes Refuge
Montão de Trigo
Figueira
Baleia
Conchas
Lamberto
Palmas
Búzios
Mar Casado
Hyale_niger
Ampithoe_ramondi
Cymadusa_filosa
Ericthonius_brasiliensis
Aora_spinicornis
Podocerus_fissipes
Stenothoe_sp
Batea_catharinensis
Photis_sarae
Caprella_scaura
Janaira_gracilis
Paracerceis_sculpta
Chondrochelia_dubia
Pinctada_imbricata
Bittiolum_varium
Costoanachis_sertulariarum
Ophioplocus_januarii
Ophiothela_mirabilis
Other species

Figure 5. Species diversity and composition for the seaweed-associated invertebrate assemblages in the sampling localities of this study. **A, B, C:** Individual-based rarefaction (solid lines) and extrapolation (dashed lines, up to triple the reference sample size, following recommendations by Colwell et al. 2012) of molluscan diversity based on Hill numbers (**A:** q = 0 ; **B:** q = 1; **C:** q = 2). **D:** CAP analysis based on Bray-Curtis similarity among invertebrate samples from the 10 localities. **E:** Relative densities of the most representative invertebrate species from the 10 sampling localities (we selected, besides the four species also includes in the genetic analysis, the four species that most contributed for pairwise differences in assemblage structure, indicated by SIMPER analysis).

Association tests

MMRR analysis showed that different factors were responsible for modulating the genetic distances among populations of each species (Table 3, Figure 6A).

For *H. niger*, both the effects of geographic distance, environmental distance and differences in water circulation significantly affected genetic differentiation, and the model considering all three variables together best explained genetic distances (Table 3). The BIOENV analysis pointed out primary productivity, silicate and iron concentrations in seawater, and sea surface temperature and salinity as the best set of environmental predictors explaining genetic variation for this species (Table 3). Likewise, there was also a significant association between asymmetric rates of gene flow and modelled dispersal for *H. niger* (MMRR, $R^2 = 0.1978$; $P = 0.0463$, Figure 6B).

For *C. filosa*, environmental distance was the only significant factor explaining genetic differentiation of populations, and BIOENV analysis pointed out primary productivity, silicate concentrations and sea surface temperature and the best variables explaining genetic variation (Table 3). Like the former amphipod, *C. filosa* also presented a significant association between rates of gene flow and particle dispersal among locations (MMRR, $R^2 = 0.1820$; $P = 0.0339$, Figure 6B).

For *P. imbricata*, only environmental distance was significant for explaining genetic distance, and exclusively when considered together with dispersal distance (Table 3). Sea surface temperature was the only predictor environmental variable pointed out by BIOENV procedure (Table 3). The relationship between particle dispersal and migration among populations, although significant, was very weak (MMRR, $R^2 = 0.0603$; $P = 0.0468$, Figure 6B).

For *C. sertulariarum*, genetic variation was very low and was not associated with by any factors considered in this study (Tables 3, MMRR, $R^2 = 0.0662$; $P = 0.3256$, Figure 6B).

At the community level, MMRR analysis indicated that environmental distance among localities was significant for explaining the patterns of pairwise beta diversity (Sorensen index) among invertebrate assemblages, and the model considering environmental distance together with geographic distance better explained community variation (Table 4, MMRR, $R^2 = 0.2185$, $P = 0.0205$; Figure 6C). The BIOENV analysis indicated light at bottom, iron concentrations and sea surface temperature as the best oceanographic variables for explaining community distances (Table 4).

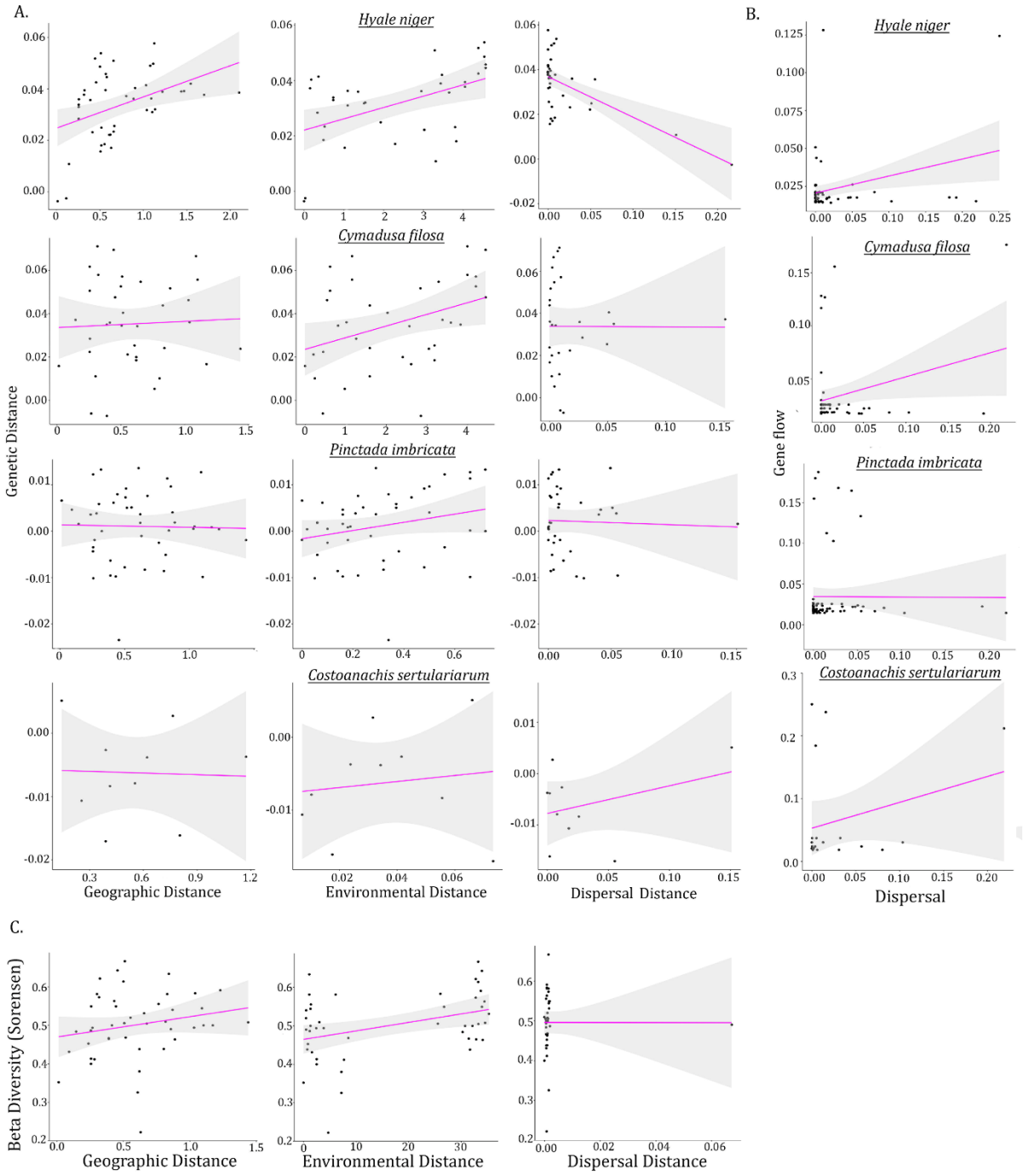


Figure 6. Multiple matrix regression with randomization (MMRR) analyses between genetic distance and combinations of geographical distance, environmental distance, and dispersal distance. **A.** the relationship between genetic distance and geographic, environmental, and dispersal distances for *H. niger*, *C. filosa*, *P. imbricata* and *C. sertulariarum*; **B.** the relationship between asymmetric rates of gene flow among populations and dispersal simulations among localities for *H. niger*, *C. filosa*, *P. imbricata* and *C. sertulariarum*; **C.** the relationship between beta diversity of seaweed-associated invertebrate assemblages and geographic, environmental, and dispersal distances.

Table 3. Results of the BIOENV analysis and regression coefficient (ß), coefficient of determination (R^2) and significance (P-value) of the multiple matrix regression with randomization analysis in the association between genetic distance and combinations of geographical distance, environmental distance, and dispersal distance of *Hyale niger*, *Cymadusa filosa*, *Pinctada imbricata* and *Costoanachis sertulariarum* populations. Bold indicates statistically significant results.

	Variables BIOENV	Combination of variables	β geographical	P-value	β environment	P-value	β dispersal	P-value	R^2	P-value
	Correlation: 0.8142292	*Dgeo*	0.408	0.0111	-	-	-	-	0.1665	**0.0111**
	Primary productivity	*Denv*	-	-	0.4927	0.0052	-	-	0.2343	**0.0052**
	Sillicate	*Ddisp*	-	-	-	-	-0.5879	0.0008	0.383	**< 0.0001**
Hyale niger	*Iron*	*Dgeo+Denv*	0.4801	0.0211	0.4965	0.0031	-	-	0.3741	**0.0023**
	Sea Surface Salinity	*Dgeo+Ddisp*	0.1526	0.3354	-	-	-0.5154	0.0045	0.4044	**0.002**
	Sea Surface Temperature	*Denv+Ddisp*	-	-	0.3137	0.0385	-0.5254	0.002	0.492	**0.0017**
		Dgeo+Denv+Ddisp	0.1454	0.5238	0.3215	0.0348	-0.4713	0.0072	0.503	**0.0039**
	Correlation: 0.5743423	*Dgeo*	0.0454	0.8099	-	-	-	-	0.0021	0.8099
	Light at bottom	*Denv*	-	-	0.2594	0.109	-	-	0.0673	0.109
	Primary productivity	*Ddisp*	-	-	-	-	-0.0048	0.9841	< 0.0001	0.9841
Cymadusa filosa	*Sea Surface Temperature*	*Dgeo+Denv*	0.047	0.8079	0.2597	0.1162	-	-	0.0695	0.3685
	Algae wet weight	*Dgeo+Ddisp*	0.0492	0.8471	-	-	0.0169	0.9407	0.0018	0.9803
		Denv+Ddisp	-	-	0.3013	0.1426	-0.0604	0.7919	0.073	0.3557
		Dgeo+Denv+Ddisp	0.0185	0.9425	0.2996	0.1489	-0.0519	0.8247	0.0732	0.6127
	Correlation: 0.2938506	*Dgeo*	-0.0023	0.8961	-	-	-	-	0.0005	0.8961
	Sea Surface Temperature	*Denv*	-	-	0.2431	0.2544	-	-	0.0591	0.2544
		Ddisp	-	-	-	-	-0.0353	0.8117	0.0015	0.8117
Pinctada imbricata		*Dgeo+Denv*	-0.0298	0.8694	0.2439	0.2643	-	-	0.06	0.4835
		Dgeo+Ddisp	-0.0374	0.8677	-	-	-0.0545	0.731	0.0028	0.9567
		Denv+Ddisp	-	-	0.629	0.0119	0.0387	0.7468	0.3813	**0.0156**
		Dgeo+Denv+Ddisp	0.0766	0.688	0.642	0.0109	0.0795	0.5199	0.3865	**0.0249**
	Correlation: 0.3919744	*Dgeo*	-0.0362	0.927	-	-	-	-	0.0013	0.927
	Phosphate	*Denv*	-	-	0.1305	0.8195	-	-	0.017	0.8195
		Ddisp	-	-	-	-	0.3432	0.4012	0.1178	0.4012
Costoanachis sertulariarum		*Dgeo+Denv*	0.0239	0.9731	0.1407	0.8095	-	-	0.0175	0.9722
		Dgeo+Ddisp	0.2967	0.5884	-	-	0.5297	0.235	0.171	0.5878
		Denv+Ddisp	-	-	-0.1771	0.7394	0.4613	0.4201	0.1352	0.7018
		Dgeo+Denv+Ddisp	0.2945	0.6362	-0.1731	0.76	0.6438	0.278	0.1877	0.8219

Table 4. Results of the BIOENV analysis and regression coefficient (ß), coefficient of determination (R^2) and significance (P-value) of the multiple matrix regression with randomization analysis in the association between beta diversity of invertebrate assemblages and combinations of geographical distance, environmental distance, and dispersal distance. Bold indicates statistically significant results.

Variables BIOENV	Combination of variables	β geographical	P-value	β environment	P-value	β waterflow	P-value	R^2	P-value
Correlation: 0.5234874	*Dgeo*	0.139	0.3359	-	-	-	-	0.0193	0.3359
Light at bottom	*Denv*	-	-	0.4526	0.0123	-	-	0.2048	**0.0123**
Iron	*Dwf*	-	-	-	-	0.1045	0.49	0.0129	0.49
Sea Surface Temperature	*Dgeo+Denv*	0.117	0.3709	0.4468	0.0145	-	-	0.2185	**0.0205**
	Dgeo+Dwf	0.105	0.498	-	-	0.0906	0.5608	0.026	0.6291
	Denv+Dwf	-	-	0.3885	0.0319	0.1774	0.2222	0.1826	0.0593
	Dgeo+Denv+Dwf	0.0498	0.7269	0.3809	0.0312	0.1694	0.2594	0.503	0.1039

Association tests: SGDCs

Hyale niger was the only species that presented significant SGDC results, with negative α-SGDC between genetic diversity and species richness (Spearman's correlation, Rho = -0.8809; P = 0.0072), and positive ß-SGDC (MMRR, R^2 = 0.3926, P < 0.0001). The other three species presented only non-significant SGDC results (P > 0.1, supplementary material 5 and 6). When checking for the influence of habitat size, environmental variables, and connectivity on α-SGDCs of *H. niger* (the only species with significant SGDC results), we found that neither factor explained invertebrate species richness, while genetic diversity was only explained by variations in connectivity (supplementary material 1).

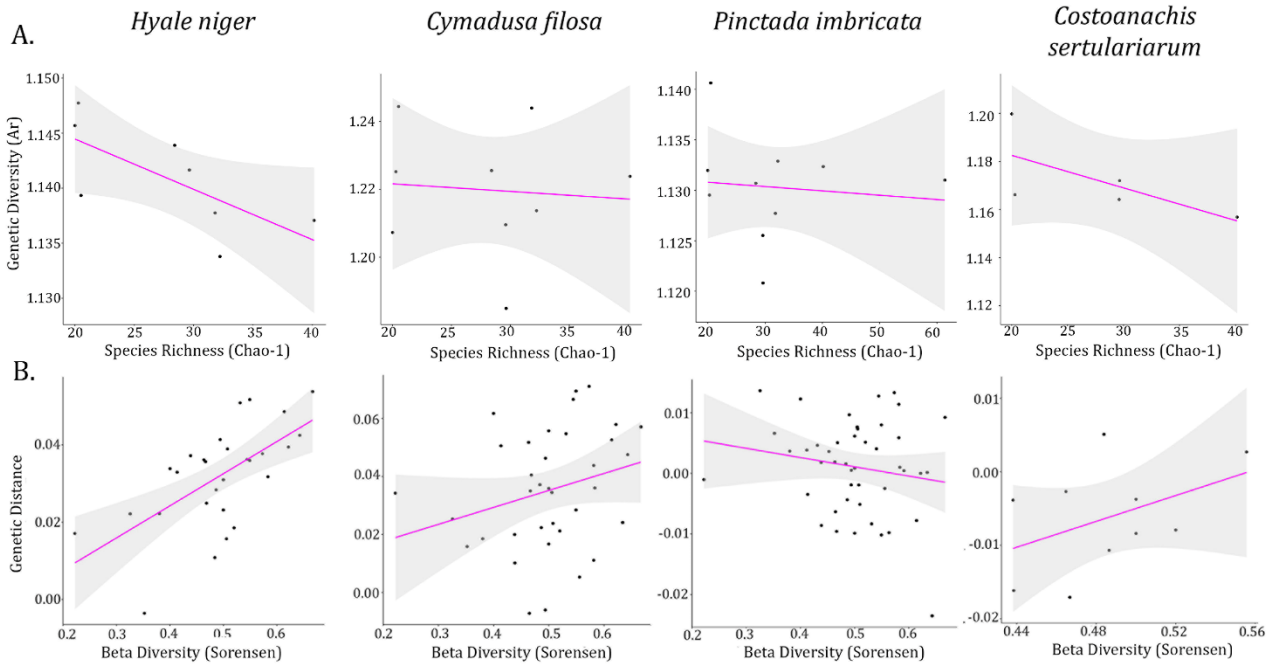


Figure 7. Graphical illustrations of **A.** the relationship between the Allelic Richness (Ar) and Species Richness (Chao-1 estimator) for *H. niger*, *C. filosa*, *P. imbricata* and *C. sertulariarum*; **B.** the relationship between the Genetic Distance (F_{ST}) and the beta diversity (Sorensen index) among localities for *H. niger*, *C. filosa*, *P. imbricata* and *C. sertulariarum*.

Discussion

To our knowledge, this is the first study that simultaneously evaluates how genetic variation of different species and the community they compose are modulated and their association, in the highly diverse and ecologically important marine seaweed habitats. Our results showed that species with a direct development and no planktonic phase presented structured populations even at a fine spatial scale, whereas mollusks, with planktonic larvae,

presented no genetic structure. Among amphipods, *Hyale niger* presented a stronger genetic structure than *Cymadusa filosa*. Overall, environmental distance was the main factor modulating genetic variation of species (especially amphipods) and invertebrate assemblages. Abiotic variables related to nutrient concentrations and productivity, such as primary productivity, silicate concentrations and light at bottom, and to temperature (sea surface temperature) best explained both genetic and community levels. However, water circulation among localities was also important for explaining genetic variation of species, especially for amphipods and particularly for *H. niger*. For this species, the association of geographic, environmental and simulated dispersal factors best explained genetic structuring. As for the associations between genetic and community levels, overall, we found only non-positive SGDC values for all species.

Genetic level

The dispersal ability of animals, which is frequently related to the type of development in marine species, is highly associated with population genetic structure (Hoskin 1997; Arndt & Smith 1998; Bohonak 1999). Previous studies have shown that species with a direct development had stronger genetic structure than species with planktonic larvae and that life history strategy was more important to explain genetic differentiation than larvae duration in the plankton, for example (Teske et al. 2007; Riginos et al. 2011). In our study, there was a clear genetic structure for the direct developer amphipods, whereas the molluscan species with pelagic larvae presented no genetic structure, confirming that pattern. Walters et al. (2022), also developing a multispecies study considering small invertebrates with different dispersal abilities at a fine spatial scale, reported that genetic structuring was influenced by a combination of dispersal potential and habitat preference of freshwater species. Noteworthy is that our spatial scale is even finer than the one in Walters et al. (2022), and even so we could observe clear genetic structures for both marine amphipods. These results reinforce the importance of including life history features and biotic information about different species, besides historical and geologic factors, building a more trait-based approach for explaining the genetic structuring patterns of populations (Papadopoulou & Knowles 2016).

Even though it is expected for amphipods to present high genetic differentiation among localities as they are direct brooders with supposed limited dispersal potential (Franz & Mohamed 1989; Palumbi 1994; Ros et al. 2020), several studies have shown that this is not necessarily true (Havermans et al. 2007; Wildish 2012; Peres et al. 2019). Peres et al. (2019) reported that there was no clear genetic structure for *C. filosa* populations in different areas along the northern coast of São Paulo. Complementarily, dispersal in this species is higher in

juveniles than in adults, and that over large spatial scales (scale of Km), it is not sex-biased and possibly occurs through rafting of floating substrates like macroalgae (Peres et al. 2021, Thiel & Gutow 2004) following a long-distance dispersal pattern rather than in stepping-stones, because there was no sign of Isolation by Distance (IBD). In our study, with a slightly larger geographic scale than Peres et al. (2019) and Peres et al. (2021), *C. filosa* presented a genetic differentiation, but with the formation of only two genetic groups, showing a lower genetic structure and probably lower dispersal potential than the other amphipod *Hyale niger*, which had a higher genetic differentiation among populations, and the formation of three genetic clusters.

Amphipods in this study present distinct life habits: while *H. niger* is a free-living, highly mobile species (Tanaka & Leite 2004), *C. filosa* is a tube-building species, using detritus, faecal pellets and macroalgae fronds for tube construction (Appadoo & Myers 2003). Bueno & Leite (2019), found that there was no difference in dispersal according to life habits for recolonization of macroalgae despite their initial expectations that free living species could disperse longer distances than tube-building. In fact, there can be a great variation in dispersal abilities among species within each category (Tanaka & Leite 2004). Our results indicate that the free-living *H. niger*, unlike the tube building *C. filosa*, probably disperse for shorter distances and discontinuously in stepping-stones, as indicated by its greater genetic structure among localities and significant signs of IBD for this species.

For both species, as for many crustacean brooders, rafting on floating macroalgae may be a plausible explanation for understanding their dispersal abilities for longer distances (Gutow & Thiel 2005; Haye et al. 2012). Rafting can be a successful dispersal mechanism for species that can survive on floating structures for extended periods (Scheltema 1977), so our main hypothesis here is that tube-building lifestyle is responsible for a better attachment of individuals to the alga, reducing dislodgement (Fenwick 1976; Moore & Eastman 2015). Also it increases protection against visual predators (Moore & Eastman 2015), which could allow *C. filosa* to stay and survive for longer periods on rafting and thus disperse continuously and for longer distances than *H. niger*.

For this species, on the other hand, other dispersal methods also reported for amphipods, like floating of individuals on water surface and passively drifting through water currents (Havermans et al. 2007; Drolet & Barbeau 2012; Peres et al. 2021), may be more important than rafting itself. Even though Bueno & Leite (2019) observed no difference in dispersal distance among life habits of these two species through drifting, our spatial scale is way larger than the one of their field experiments. So, it is possible that for the smaller and

more motile species *H. niger*, dispersal through drifting may be effective for displacement in the scale of kilometers, but not enough to equally cover the whole studied area, being higher among closer localities. It could explain the significant signs of IBD only for this species, and the significant and strong effect of water currents predicting genetic differentiation, since the model of particle dispersal considers passively drifting particles that may behave similarly to what would be a drifting amphipod.

Areas with more intense water circulation, usually geographically close from each other, such as Moela and Mar Casado, Baleia and Montão de Trigo, and Búzios and Conchas, presented lower genetic differentiation and higher migration rates of *H. niger* populations. For this species, there was the formation of a genetic cluster including all populations located southwestward from São Sebastião (SSB) Island except the two Alcatrazes sites, which are located at ~ 45km from SSB shore and were grouped in a second genetic cluster with the sites located northward from São Sebastião Island (Búzios and Conchas). Figueira formed a third separated genetic cluster. A similar pattern of genetic structuring for *H. niger* in this region was previously presented in Longo et al. (in prep.), likely because of existence of the role played by the São Sebastião (SSB) island as a barrier to movements, with limited gene flow through the São Sebastião Channel. This could contribute to the formation of separated genetic clusters for the populations southwestward from the island and close to shore, northward from the island or farther from shore, and within SSB Channel. Authors hypothesized that southwestward populations would have limited capacity for northward dispersal through the SSB channel, and that populations from the more offshore Alcatrazes island would more easily disperse in that direction moving around SSB island (Longo et al., *in prep*). In our study, we show that genetic distances of *H. niger* are in fact mostly explained by differences in water circulation pattern among localities, and that circulation through the SSB channel exists, but seems mostly unidirectional and northwards. Indeed, connections among all localities with Figueira (within SSB channel) are less expressive than connections among northward and southwestward localities, respectively, indicating that SSB island might not be an actual barrier, however it may provide limiting dispersal through SSB channel for drifting species and thus be crucial for the genetic structure of some benthic invertebrates like *H. niger*.

Another possibility to explain the clear differentiation of Figueira population of *H. niger* would be anthropogenic stress. Figueira is an unprotected area, highly urbanized, with intense boating activity, and located within SSB channel, relatively close to an oil terminal. Therefore, we cannot reject that local environmental contamination could act as a selective agent for *H. niger* populations, which had become tolerant and well-adapted to stressors like

contamination stress, explaining the formation of a distinct genetic cluster together with the high-density levels observed for this species in this locality. Environmental contamination may affect genetic structure of animal species (Guttman 1994; Zvuloni 2008; Bach & Dahllöf 2012) and rapid adaptative responses to pollutants, following the pace of environmental change, are particularly possible for small-bodied species with a short generation time (Bergland et al. 2014; Whitehead et al. 2017), as is the case of *H. niger*. However, studies testing the specific relation between contaminant concentrations and genetic variability for this species are still necessary for testing this hypothesis. Also, in this study we are considering only neutral loci so, even though selective responses may reflect on demographic patterns (Li et al. 2012), any hypothesis based on adaptive pressures should be taken with caution and further tested including the adaptive information of genomic data.

For both amphipod species, environmental differences among localities, represented mainly by nutrient-related variables and sea surface temperature, were important for explaining genetic differentiation among populations. The main genetic pattern that is coincident between these two species is the clear differentiation of Alcatrazes populations. In Alcatrazes, most nutrients concentrations such as silicate, phosphate and nitrate were higher than in the remaining localities, however iron concentration and primary productivity were lower. Following what was previously discussed in Longo et al. (in prep.), it is possible that nutrient inputs are due to upwelling formations in that area (Lorenzzetti & Gaeta 1996; Calil et al. 2021; Karlovic et al. 2021), and this might increase nutrient availability and consequently nutrient uptake by macroalgae species (Ohtake et al. 2020; Lapointe et al. 2021), increasing the fitness of associated herbivore amphipods (Kraufvelin et al. 2006; Sudo & Yoshida 2021) such as *H. niger* and *C. filosa*, contributing to the formation of their genetic clusters. However, even in an apparent nutrient-rich environment, primary productivity in Alcatrazes was lower than in the other localities. One possible explanation is that the lower levels of iron in that area could be acting as a limiting factor for local productivity since this element is essential for several photosynthetic processes and for the growth of phytoplankton elements like diatoms (Martin & Fitzwater 1988; Whitney et al. 2005). Another possibility is the presence of coherent vortices associated to the upwelling region, which can reduce primary productivity (Pasquero et al. 2005). However, further investigations on nutrient dynamics in Alcatrazes are still needed to confirm either of these hypotheses.

Our results also showed that even in a more restricted spatial scale and limited temperature gradient, variations in Sea Surface Temperature (SST) can also be important for explaining genetic differences, as was seen for *H. niger*, *C. filosa* and *P. imbricata*. A few

studies have also demonstrated that SST is a relevant feature for modulating genetic divergence in different aquatic invertebrates, including other crustaceans and mollusks, however sampling in wider temperature gradients, usually in interlatitudinal spatial scales (Banks et al. 2007; Paul et al. 2012; Wei et al. 2013; Singh et al. 2018). Considering a more extensive spatial scale in our study would probably reveal more accentuated genetic structure patterns and better elucidate the effects of SST for genetic differentiation of these species, however our results already demonstrate that even slight variations in SST may have an effect on genetic structure of seaweed-associated invertebrate species, which raises important questions about how will these species genetically respond to the future scenarios of temperature change due to climate change, for example.

Community Data

Species diversity of seaweed-associated invertebrate assemblages differed among localities and was higher in Marine Protected Areas (MPAs) like Palmas and Alcatrazes Refuge, and in sites of partial protection and more isolated from urbanized centers, like Conchas, whilst was lower in Lamberto, an unprotected area close to a state marina, and in Mar Casado, of partial protection but located within Baixada Santista, a highly urbanized region of São Paulo coast. In a recent work in the same area, we studied the species diversity and composition of peracarid and molluscan assemblages separately and found similar patterns (Mansur et al. in prep.). Specifically, we observed a lower species diversity in more impacted areas like Lamberto and found a significant association of lower diversity values and higher heavy metal concentrations in algal tissues. In this study, we explored the effect of other oceanographic variables on the diversity patterns of invertebrate assemblages, and show that environmental dissimilarities among localities, particularly alterations in iron concentration, light at bottom and SST, best explained community variations.

Localities with the more extreme diversity alterations (higher and lower values) also presented most dissimilar assemblage composition, with one major similar feature: the extremely reduced relative densities of *Hyale niger*. This species is herbivorous, can feed on both the host alga and other associated epiphytic algae (Jacobucci & Leite 2008, 2014), and can benefit from increments of seaweed biomass, increasing its density on macroalgae habitats (Leite et al. 2021). Therefore, our results suggest that variations in species diversity and composition are due to a combination of local nutrient/light limitations, macroalgae growth, anthropogenic impact, and colonization rate of northern areas, with *H. niger* as a key species driving community patterns.

Seaweed growth may be influenced by different environmental factors in marine environment, and limitations of nutrients availability and light incidence can be essential to modulate macroalgae growth and productivity in coastal areas (Davison & Pearson 1996; Viaroli et al. 2005). Among nutrients, iron is essential for chlorophyll synthesis and photosynthetic reactions (Kwon et al. 2022) and can also have a major role in nitrate utilization by macroalgae, thus in its production and growth (Viaroli et al. 2005). Likewise, light incidence is crucial for modulating photosynthetic rates of macroalgae and, consequently, their growth (Hanelt & Figueroa 2012). Hence, we hypothesize that in Palmas, Alcatrazes Refuge and Conchas, where species diversity was higher, the lower levels of iron concentration and light at bottom may have limited macroalgae growth, which is corroborated by the smaller fronds in those areas (supplementary material 1). It would lead to reduced populations of the fast-growing herbivorous amphipod *H. niger*, while many other non-herbivorous species, like the amphipods *Ericthonius brasiliensis*, *Stenothoe* sp., *Photis sarae* and *Caprella scaura*, the bivalve *Pinctada imbricata* and the ophiuroids *Ophiothela mirabilis* and *Ophioplocus januarii*, were able to thrive, resulting in species-rich and species-even assemblages in those areas.

Meanwhile, in Lamberto, despite the similarly low levels of light at bottom, probably due to elevated water turbidity in that area, iron concentrations are higher and macroalgae fronds are large, so we believe that the limiting densities of *H. niger* populations in that area could be due to anthropogenic impact, since Lamberto is located within the Saco da Ribeira, an area with high concentrations of different pollutants, such as heavy metals, hydrocarbons, and organic pollution (CETESB 2014, 2015, 2016), being probably the most contaminated area in our sampling (Mansur et al. in prep). Amphipods can be highly sensitive to marine contamination (Landrum et al. 2003; Roberts et al. 2006; Felden et al. 2008), including Hyallidae species (Goulding et al. 2017; Wu et al. 2021), and particularly for *H. niger*. There is evidence that different pollutants in sediments and/or in water affect this species (Passarelli et al. 2017, Passarelli et al. 2019), but Mansur et al. (in prep) and Longo et al. (2021) did not find a significant relationship between this species' densities and heavy metal concentrations in host algal tissue. Therefore, it is possible that pollutants othern than heavy metals limit the growth of *H. niger* populations, and that allowed the strong dominance of the opportunistic and more tolerant gastropod species *Bittiolum varium* (Longo et al. 2021), resulting in a lower species diversity in that locality.

Finally, dispersal limitations of *H. niger* for sites located northward from SSB island, as was further discussed in the previous section, may also have limited the colonization

of that species in sites like Lamberto, Palmas and Conchas, and would help explain the reduced densities of *H. niger* in those areas.

Relationship between genetic and community levels

Positive values of SGDC have been extensively reported in the literature, driven by different factors like site size, connectivity, and environmental features, which can have parallel eco-evolutionary effects on both diversity levels (Vellend 2004; Vellend & Geber 2005; Messmer et al. 2012; Kahilainen et al. 2014; Laroche et al. 2015; Fortune et al. 2016; Knott et al. 2018). Non-positive SGDC, although less frequent, have also been reported and usually indicate that species and genetic diversity are modulated by different predominant factors (Taberlet et al. 2012; Kahilainen et al. 2014 Seymour et al. 2016; Marchesini et al. 2018). Positive SGDCs have been frequently (but not exclusively) associated to discrete habitat units such as islands, forest fragments and lakes, while non-positive correlations would be more associated with more arbitrary spatial units (Taberlet et al. 2012; Vellend et al. 2014). Therefore, co-variation between species and genetic diversity is still not a consensus and thus should be tested for different systems and especially in a multi-species approach (Fourtune et al. 2016; Seymour et al. 2016; Watanabe & Monaghan 2017).

Our study is the first attempt to investigate the existence of SGDCs for seaweed-associated invertebrate assemblages. We found only non-positive α-SGDCs for all species studies, while for ß-SGDC, values were positive for *H. niger* and not significant of the remaining species. Studies on ß-SGDC of multiple-species have already indicated that stronger values can be found for focal species with low dispersive abilities (Papadopoulou et al. 2011), which is one possible reason why we have found positive and significant values for the more abundant and less dispersive amphipod *H. niger* in contrast to the other species. The positive ß-SGDC values found for *H. niger* agree with most of the recent results in the literature (Lamy et al. 2017) and are probably justified here by the strong influence of environmental variables on both genetic and species dissimilarities among localities (Fortune et al. 2016).

As for α-SGDC, only *H. niger* presented significant but negative correlations. Negative α-SGDCs can arise under different scenarios, such as when focal species has opposite responses to environmental variations than other species from the community, or when community factors like interspecific competition can affect population size and thus genetic diversity of focal species (Vellend 2005; Lamy et al. 2017). We tested for the effects of site factors (environmental variables, macroalgae frond size - which was used as a proxy of habitat

size, and connectivity) on both genetic and species diversity and found that, even though connectivity promoted genetic diversity, probably due to a higher number of immigrants in more connected areas (Lamy et al. 2013), that was not true for the whole community, as would be expected (Lamy et al. 2013; Chust et al. 2016), and none of the other factors presented any effect on either diversity levels. We argue that community factors rather than site factors might be predominant for explaining the observed negative α-SGDC. In species-richer communities, more species would be co-existing and thus competing for available resources, resulting in species with decreased niche breadth and lower effective population size due to limiting carrying capacity of the system, consequently losing genetic diversity (Vellend & Geber 2005; Silvertown & Freeland 2009; Laroche et al. 2015; Xu et al. 2016), especially for the more isolated populations (lower connectivity) (Palumbi 1994).

For future studies of *H. niger* SGDCs in macroalgal habitats we suggest that (1) this hypothesis should be further investigated, including the potential effects of biotic interactions for SGDCs; (2) the role of other potential environmental variables, such as anthropogenic disturbances, which can lead to parallel (Frey et al. 2016; Schwensow et al. 2022) and non-parallel (Wei & Jiang 2012) effects on genetic and species diversity, and other potential environmental features that can act on species interactions (Lamy et al. 2017); and (3) also include the adaptative genetic variation, which would allow a more complete investigation of the mechanisms producing SGDCs (Watanabe & Monaghan 2017; Pfeiffer et al. 2018). Even though several aspects of species-genetic diversity correlations for seaweed invertebrates remain to be studied, our results are an important indicator that those diversity levels are not positively related and then species diversity cannot be used as a surrogate for genetic diversity, or vice versa, in conservation planning of macroalgae habitats.

Final remarks

Macroalgae habitats have been facing expressive reductions over the past decades due to increasing anthropogenic impacts in coastal areas (Gorman et al. 2020). This trend is major threat for associated invertebrate species (Roberts et al. 2008; Mayer-Pinto et al. 2020; Mancuso et al. 2021) and highlight the need for effective conservation measures for preserving those habitats and their associated biodiversity. Our results bring out important aspects of seaweed-associated invertebrate biology that should be considered for planning their future conservation. In our study, not only we confirm that species with a planktonic larval phase will present lower genetic structure than direct developers, but also show that different co-existing brooder species can have different dispersal potentials and thus distinct patterns of genetic

structure and gene flow, which highlights the importance of considering multi-species approaches for establishing effective conservation measures of these habitats. We also show that, for both amphipod species, Alcatrazes populations constituted a clearly distinct genetic cluster, while for the whole invertebrate assemblage, Palmas presented the highest levels of species richness and diversity. Alcatrazes and Palmas are considered pristine areas, since they are both part of ESEC Tupinambás and Alcatrazes Archipelago Marine Refuge, two major marine protected areas (MPAs) in São Paulo coast, which elucidates the importance of existing MPAs for maintaining both species and genetic diversity of seaweed-associated fauna. And finally, we indicate that species and genetic diversity are not driven by parallel processes and one level cannot be used as a surrogate for the other in conservation planning of macroalgae habitats.

As a final conclusion of this work, we show that species with different life histories in relevant biotic features – such as the type of development in marine species – may result in differences of key ecological processes like dispersal, which in turn affect the genetic structure of species and ultimately influence the distribution of multiple species, resulting in potential effects on community parameters.

References

Agrawal, A. A. (2003). Community Genetics: New insights into community ecology by integrating population genetics. Ecology, 84: 543-544.

Aljanabi, S. M., & Martinez, I. (1997). Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. Nucleic acids research, 25(22), 4692-4693.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. Austral Ecology, 26, 32–46.

Antao, T., Lopes, A., Lopes, R. J., Beja-Pereira, A., & Luikart, G. (2008). LOSITAN: a workbench to detect molecular adaptation based on a F ST-outlier method. BMC bioinformatics, 9(1), 1-5.

Appadoo, C., & Myers, A. A. (2003). Observations on the tube-building behaviour of the marine amphipod *Cymadusa filosa* Savigny (Crustacea: Ampithoidae). Journal of Natural History, 37(18), 2151-2164.

Arndt, A., & Smith, M. J. (1998). Genetic diversity and population structure in two species of sea cucumber: differing patterns according to mode of development. Molecular Ecology, 7(8), 1053-1064.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018). Bio-ORACLE v2. 0: Extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography, 27(3), 277-284.

Bach, L., & Dahllöf, I. (2012). Local contamination in relation to population genetic diversity and resilience of an arctic marine amphipod. Aquatic Toxicology, 114, 58-66.

Banks, S. C., Piggott, M. P., Williamson, J. E., Bové, U., Holbrook, N. J., & Beheregaray, L. B. (2007). Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. Ecology, 88(12), 3055-3064.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global ecology and biogeography, 19(1), 134-143.

Bergland, A. O., Behrman, E. L., O'Brien, K. R., Schmidt, P. S., & Petrov, D. A. (2014). Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in *Drosophila*. PLoS genetics, 10(11), e1004775.

Bierne, N., Roze, D., & Welch, J. J. (2013). Pervasive selection or is it…? Why are FST outliers sometimes so frequent?.

Bohonak, A. J. (1999). Dispersal, gene flow, and population structure. The Quarterly review of biology, 74(1), 21-45.

Bosch, S., Tyberghein, L., & De Clerck, O. (2017). sdmpredictors: an R package for species distribution modelling predictor datasets. Marine Species Distributions: From data to predictive models, 49.

Boström, C., Pittman, S. J., Simenstad, C., & Kneib, R. T. (2011). Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Marine ecology progress series, 427, 191-217.

Bueno, M., & Leite, F. P. P. (2019). Age and life style affect macroalgae colonization by amphipods in shallow marine environments. Journal of Experimental Marine Biology and Ecology, 514, 59-66.

Cacabelos, E., Olabarria, C., Incera, M., & Troncoso, J. S. (2010). Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. Estuarine, coastal and shelf science, 89(1), 43-52.

Calil, P. H., Suzuki, N., Baschek, B., & da Silveira, I. C. (2021). Filaments, fronts and eddies in the Cabo Frio coastal upwelling system, Brazil. Fluids, 6(2), 54.

Catchen, J. M., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. H. (2011). Stacks: building and genotyping loci de novo from short-read sequences. G3: Genes| genomes| genetics, 1(3), 171-182.

CETESB – Companhia Ambiental do Estado de São Paulo, 2016. Qualidade das águas superficiais do estado de São Paulo. Parte 2 – Águas salinas e salobras. p 164

CETESB – Companhia Ambiental do Estado de São Paulo, 2015. Qualidade das águas superficiais do estado de São Paulo. Parte 2 – Águas salinas e salobras. p 164

CETESB – Companhia Ambiental do Estado de São Paulo, 2014. Qualidade das águas superficiais do estado de São Paulo. Parte 2 – Águas salinas e salobras. p 164

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. Scandinavian Journal of statistics, 265-270.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological monographs, 84(1), 45-67.

Chatzigeorgiou, G., Sarropoulou, E., Vasileiadou, K., Brown, C., Faulwetter, S., Kotoulas, G., & Arvanitidis, C. D. (2014). Community structure and population genetics of Eastern Mediterranean polychaetes. Frontiers in Marine Science, 1, 47.

Christie, H., Norderhaug, K. M., & Fredriksen, S. (2009). Macrophytes as habitat for fauna. Marine ecology progress series, 396, 221-233.

Christie, M. R., Tissot, B. N., Albins, M. A., Beets, J. P., Jia, Y., Ortiz, D. M., ... & Hixon, M. A. (2010). Larval connectivity in an effective network of marine protected areas. PloS one, 5(12), e15715.

Chust, G., Villarino, E., Chenuil, A., Irigoien, X., Bizsel, N., Bode, A., ... & Borja, A. (2016). Dispersal similarly shapes both population genetics and community patterns in the marine realm. Scientific reports, 6(1), 1-12.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18, 117–143.

Clobert, J., Ims, R. A., & Rousset, F. (2004). Causes, mechanisms and consequences of dispersal. In Ecology, genetics and evolution of metapopulations (pp. 307-335). Academic Press.

Colwell, R. K. (2009). Biodiversity: concepts, patterns, and measurement. The Princeton guide to ecology, 663, 257-263.

Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S. Y., Mao, C. X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of plant ecology, 5(1), 3-21.

Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. Annual review of marine science, 1(1), 443-466.

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., ... & 1000 Genomes Project Analysis Group. (2011). The variant call format and VCFtools. Bioinformatics, 27(15), 2156-2158.

Davey, J. W., Hohenlohe, P. A., Etter, P. D., Boone, J. Q., Catchen, J. M., & Blaxter, M. L. (2011). Genome-wide genetic marker discovery and genotyping using next-generation sequencing. Nature Reviews Genetics, 12(7), 499-510.

Davison, I. R., & Pearson, G. A. (1996). Stress tolerance in intertidal seaweeds. Journal of Phycology, 32(2), 197-211.

Deltares. (2019). Delft3D-FLOW User Manual: simulation of multi-dimensional hydrodynamics flows and transport phenomena, including sediments. Version 3.15 (SVN Revision 60015). Delft (Netherlands): Deltares Systems. 680p.

Drolet, D., & Barbeau, M. A. (2012). Population structure of resident, immigrant, and swimming *Corophium volutator* (Amphipoda) on an intertidal mudflat in the Bay of Fundy, Canada. Journal of sea research, 70, 1-13.

Earl, D. A., & VonHoldt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation genetics resources, 4(2), 359-361.

Egbert, G. D., Bennett, A. F., & Foreman, M. G. (1994). TOPEX/POSEIDON tides estimated using a global inverse model. Journal of Geophysical Research: Oceans, 99(C12), 24821-24852.

Fagundes, N. J., Ray, N., Beaumont, M., Neuenschwander, S., Salzano, F. M., Bonatto, S. L., & Excoffier, L. (2007). Statistical evaluation of alternative models of human evolution. Proceedings of the National Academy of Sciences, 104(45), 17614-17619.

Felten, V., Charmantier, G., Mons, R., Geffard, A., Rousselle, P., Coquery, M., Garric J., & Geffard, O. (2008). Physiological and behavioural responses of Gammarus pulex (Crustacea: Amphipoda) exposed to cadmium. Aquatic Toxicology, 86(3), 413-425.

Fenwick G.D. (1976) The effect of wave exposure on the amphipod fauna of the alga Caulerpa brownii. Journal of Experimental Marine Biology and Ecology 25, 1–18

Foggo, A., Bilton, D. T., & Rundle, S. D. (2007). Do developmental mode and dispersal shape abundance–occupancy relationships in marine macroinvertebrates?. Journal of Animal Ecology, 76(4), 695-702.

Foll, M., & Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics, 180(2), 977-993.

Fourtune, L., Paz-Vinas, I., Loot, G., Prunier, J. G., & Blanchet, S. (2016). Lessons from the fish: A multi-species analysis reveals common processes underlying similar species-genetic diversity correlations. Freshwater Biology, 61(11), 1830-1845.

François, O., Martins, H., Caye, K., & Schoville, S. D. (2016). Controlling false discoveries in genome scans for selection. Molecular ecology, 25(2), 454-469.

Franz, D. R., & Mohamed, Y. (1989). Short-distance dispersal in a fouling community amphipod crustacean, Jassa marmorata Holmes. Journal of Experimental Marine Biology and Ecology, 133(1-2), 1-13.

Frey, D., Arrigo, N., Granereau, G., Sarr, A., Felber, F., & Kozlowski, G. (2016). Parallel declines in species and genetic diversity driven by anthropogenic disturbance: a multispecies approach in a French Atlantic dune system. Evolutionary Applications, 9(3), 479-488.

Gorman, D., Gutiérrez, A. R., Turra, A., Manzano, A. B., Balthazar-Silva, D., Oliveira, N. R., & Harari, J. (2020). Predicting the dispersal and accumulation of microplastic pellets within the estuarine and coastal waters of South-Eastern Brazil using integrated rainfall data and Lagrangian particle tracking models. Frontiers in Environmental Science, 8, 559405.

Gorman, D., Horta, P., Flores, A. A., Turra, A., Berchez, F. A. D. S., Batista, M. B., ... & Széchy, M. T. M. (2020). Decadal losses of canopy-forming algae along the warm temperate coastline of Brazil. Global change biology, 26(3), 1446-1457.

Goudet, J. (2005). Hierfstat, a package for R to compute and test hierarchical F-statistics. Molecular Ecology Notes, 5(1), 184-186.

Goulding, T. A., De Orte, M. R., Szalaj, D., Basallote, M. D., DelValls, T. A., & Cesar, A. (2017). Assessment of the environmental impacts of ocean acidification (OA) and carbon capture and storage (CCS) leaks using the amphipod *Hyale youngi*. Ecotoxicology, 26(4), 521-533.

Gutow, L., & Thiel, M. (2005). The ecology of rafting in marine crustaceans.

Guttman, S. I. (1994). Population genetic structure and ecotoxicology. Environmental Health Perspectives, 102(suppl 12), 97-100.

Hanelt, D., & Figueroa, F. L. (2012). Physiological and photomorphogenic effects of light on marine macrophytes. In Seaweed biology (pp. 3-23). Springer, Berlin, Heidelberg.

Havermans, C., De Broyer, C., Mallefet, J., & Zintzen, V. (2007). Dispersal mechanisms in amphipods: a case study of Jassa herdmani (Crustacea, Amphipoda) in the North Sea. Marine Biology, 153(1), 83-89.

Haye, P. A., Varela, A. I., & Thiel, M. (2012). Genetic signatures of rafting dispersal in algal-dwelling brooders Limnoria spp.(Isopoda) along the SE Pacific (Chile). Marine Ecology Progress Series, 455, 111-122.

von der Heyden, S., Beger, M., Toonen, R. J., van Herwerden, L., Juinio-Meñez, M. A., Ravago-Gotanco, R., ... & Bernardi, G. (2014). The application of genetics to marine management and conservation: examples from the Indo-Pacific. Bulletin of Marine Science, 90(1), 123-158.

Hoskin, M. G. (1997). Effects of contrasting modes of larval development on the genetic structures of populations of three species of prosobranch gastropods. Marine Biology, 127(4), 647-656.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0. 12.

Hughes, A. R.; Inouye, B. D.; Johnson, M. T. J.; Underwood, N.; Vellend, M. (2008). Ecological consequences of genetic diversity. Ecology Letters, 11: 609-623.

Jacobucci, G. B., & Leite, F. P. P. (2008). Effect of temporal variation and size of herbivorous amphipods on consumption levels of *Sargassum filipendula* (Phaeophyta, Fucales) and their main epiphyte, *Hypnea musciformis*. Neotropical Biology and Conservation, 3, 78–85.

Jacobucci, G. B., & Leite, F. P. P. (2014). The role of epiphytic algae and different species of *Sargassum* in the distribution and feeding of herbivorous amphipods. Latin American Journal of Aquatic Research, 42, 353–363

Jahnke, M., & Jonsson, P. R. (2022). Biophysical models of dispersal contribute to seascape genetic analyses. Philosophical Transactions of the Royal Society B, 377(1846), 20210024.

Jolly, M. T., Guyard, P., Ellien, C., Gentil, F., Viard, F., Thiébaut, E., & Jollivet, D. (2009). Population genetics and hydrodynamic modeling of larval dispersal dissociate contemporary patterns of connectivity from historical expansion into European shelf seas in the polychaete Pectinaria koreni. Limnology and Oceanography, 54(6), 2089-2106.

Kahilainen, A., Puurtinen, M., & Kotiaho, J. S. (2014). Conservation implications of species–genetic diversity correlations. Global Ecology and Conservation, 2, 315-323.

Karlovic, T. C., Gomes, R. R., Paiva, P. C., Babcock, E. A., & Dias, J. F. (2021). Functionality and Effectiveness of Marine Protected Areas in Southeastern Brazilian Waters for Demersal Elasmobranchs. Frontiers in Marine Science, 1204.

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. Molecular ecology resources, 15(5), 1179-1191.

Knott, K. E., Thonig, A., Heiskanen, S., Hansen, B. W., & Banta, G. T. (2018). Seasonal variation in diversity of marine benthic invertebrates leads to a positive species-genetic diversity correlation (SGDC). Marine Ecology Progress Series, 592, 129-140.

Kwon, P. K., Kim, H. S., & Jeong, S. W. (2022). Dissolved Iron from Steel Slag with Its Chelating Agent Promotes Seaweed Growth. Sustainability, 14(9), 5498.

Lamy, T.; Jarne, P.; Laroche, F.; Pointier, J. P.; Huth, G.; Segard, A.; David, P. (2013). Variation in habitat connectivity generates positive correlations between species and genetic diversity in a metacommunity. Molecular Ecology, 22: 4445-4456.

Lamy, T.; Laroche, F.; David, P.; Massol, F.; Jarne, P. (2017). The contribution of species – genetic diversity correlations to the understanding of community assembly rules. Oikos, 000: 001-013.

Landrum, P. F., Lotufo, G. R., Gossiaux, D. C., Gedeon, M. L., & Lee, J. H. (2003). Bioaccumulation and critical body residue of PAHs in the amphipod, *Diporeia* spp.: additional evidence to support toxicity additivity for PAH mixtures. Chemosphere, 51(6), 481-489.

Lapointe, B. E., Brewton, R. A., Herren, L. W., Wang, M., Hu, C., Mcgillicuddy, D. J., ... & Morton, P. L. (2021). Nutrient content and stoichiometry of pelagic Sargassum reflects increasing nitrogen availability in the Atlantic Basin. Nature communications, 12(1), 1-10.

Laroche, F., Jarne, P., Lamy, T., David, P., & Massol, F. (2015). A neutral theory for interpreting correlations between species and genetic diversity in communities. The American Naturalist, 185(1), 59-69.

Leite, F. P., Bottcher, C., Lewinsohn, I. D., Siqueira, S. G., Mansur, K. F., Longo, P. A., & Vieira, E. A. (2021). Asymmetric effects of changes in the habitat-forming algae *Sargassum* on different associated mobile faunas along São Paulo coast, Brazil. Marine Ecology, 42(3), e12649.

Lellouche, J.M.; Legalloudec, O.; Regnier, C.; Levier, B.; Greiner, E.; Drevillon, M. (2016). Quality information document for the GLOBAL ocean sea physical analysis and forecasting products: Global_Analysis_Forecast_Phy_001_024. Technical report. Version 2.3 (Issue 1.3). Brussels (Belgium): CMEMS, 67p.

Leroy, B., Meynard, C. N., Bellard, C., & Courchamp, F. (2016). virtualspecies, an R package to generate virtual species distributions. Ecography, 39(6), 599-607

Levy, S. E., & Myers, R. M. (2016). Advancements in next-generation sequencing. Annu Rev Genomics Hum Genet, 17(1), 95-115.

Li, J., Li, H., Jakobsson, M., Li, S. E. N., SjÖDin, P. E. R., & Lascoux, M. (2012). Joint analysis of demography and selection in population genetics: where do we stand and where could we go?. Molecular ecology, 21(1), 28-44.

Liggins, L., Treml, E. A., & Riginos, C. (2019). Seascape genomics: contextualizing adaptive and neutral genomic variation in the ocean environment. In Population genomics: Marine organisms (pp. 171-218). Springer, Cham.

Longo, P. A. S., Mansur, K. F. R., Siqueira, S. G. L., Passos, F. D., & Leite, F. P. P. (2021). Sargassum-associated gastropod and amphipod assemblages in relation to metal pollution in a semi-enclosed bay. Aquatic Ecology, 55(2), 623-646.

Lorenzzetti, J. A., & Gaeta, S. A. (1996). The Cape Frio Upwelling Effect over the South Brazil Blight Northern Sector Shelf Waters: a Study Using AVHRR Images. International Archives of Photogrammetry and Remote Sensing, 31, 448-453.

Luu, K., Bazin, E., & Blum, M. G. (2017). pcadapt: an R package to perform genome scans for selection based on principal component analysis. Molecular ecology resources, 17(1), 67-77.

Mancuso, F. P., Milazzo, M., & Chemello, R. (2021). Decreasing in patch-size of *Cystoseira* forests reduces the diversity of their associated molluscan assemblage in Mediterranean rocky reefs. Estuarine, Coastal and Shelf Science, 250, 107163.

Marchesini, A., Vernesi, C., Battisti, A., & Ficetola, G. F. (2018). Deciphering the drivers of negative species–genetic diversity correlation in Alpine amphibians. Molecular ecology, 27(23), 4916-4930.

Martin, J. H., & Fitzwater, S. E. (1988). Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. Nature, 331(6154), 341-343.

Mayer-Pinto, M., Ledet, J., Crowe, T. P., & Johnston, E. L. (2020). Sublethal effects of contaminants on marine habitat-forming species: a review and meta-analysis. Biological Reviews, 95(6), 1554-1573.

Messmer, V., Jones, G. P., Munday, P. L., & Planes, S. (2012). Concordance between genetic and species diversity in coral reef fishes across the Pacific Ocean biodiversity gradient. Evolution: International Journal of Organic Evolution, 66(12), 3902-3917.

Moore, P. G., & Eastman, L. B. (2015). The tube-dwelling lifestyle in crustaceans and its relation to feeding. The natural history of the Crustacea, 2, 35-77.

Mussmann, S. M., Douglas, M. R., Chafin, T. K., & Douglas, M. E. (2019). BA3-SNPs: Contemporary migration reconfigured in BayesAss for next-generation sequence data. Methods in Ecology and Evolution, 10(10), 1808-1813.

Nouel, L. (2018). Product user manual for the GLOBAL ocean sea physical analysis and forecasting products: Global_Analysis_Forecast_Phy_001_024. Technical report. Version 3.2 (Issue 1.3). Brussels (Belgium): CMEMS, 16p.

Ohtake, M., Nishihara, G. N., Inoue, Y., Tsuchiya, K., & Toda, T. (2020). Phosphorus demand and uptake during growth and maturation of the brown alga *Sargassum macrocarpum*. Phycological Research, 68(4), 277-289.

Oleksiak, M. F. (2018). Adaptation without boundaries: population genomics in marine systems. In Population Genomics (pp. 587-612). Springer, Cham.

Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. Annual review of ecology and systematics, 547-572.

Palumbi, S. R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. Ecological Applications, 13(1): S146-S158.

Papadopoulou, A., Anastasiou, I., Spagopoulou, F., Stalimerou, M., Terzopoulou, S., Legakis, A., & Vogler, A. P. (2011). Testing the species–genetic diversity correlation in the Aegean archipelago: toward a haplotype-based macroecology?. The American Naturalist, 178(2), 241-255.

Papadopoulou, A., & Knowles, L. L. (2016). Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. Proceedings of the National Academy of Sciences, 113(29), 8018-8024.

Pasquero, C., Bracco, A., & Provenzale, A. (2005). Impact of the spatiotemporal variability of the nutrient flux on primary productivity in the ocean. Journal of Geophysical Research: Oceans, 110(C7).

Passarelli, M. C., Abessa, D., & Cesar, A. (2019). Sensitivities of two tropical epibenthic amphipodsto physical chemical variables and reference toxicants. Ecotoxicology and Environmental Contamination, 14(1), 27-33.

Passarelli, M. C., Cesar, A., & Abessa, D. M. S. (2017). Using the Amphipod Hyale nigra to Assess the Quality of Marine Sediments. Annals of Limnology and Oceanography, 2(1), 025-030.

Paul, R. J., Mertenskötter, A., Pinkhaus, O., Pirow, R., Gigengack, U., Buchen, I., ... & Zeis, B. (2012). Seasonal and interannual changes in water temperature affect the genetic

structure of a Daphnia assemblage (D. longispina complex) through genotype-specific thermal tolerances. Limnology and Oceanography, 57(2), 619-633.

Peres, P. A., Azevedo-Silva, M., Andrade, S. C., & Leite, F. P. (2019). Is there host-associated differentiation in marine herbivorous amphipods?. Biological Journal of the Linnean Society, 126(4), 885-898.

Peres, P. A., Ferreira, A. P., Machado, G. B., Azevedo-Silva, M., Siqueira, S. G., & Leite, F. P. (2021). Sex-biased dispersal depends on the spatial scale in a tube-building amphipod. Marine Ecology Progress Series, 658, 135-148.

Pfeiffer, V. W., Ford, B. M., Housset, J., McCombs, A., Blanco-Pastor, J. L., Gouin, N., ... & Bertin, A. (2018). Partitioning genetic and species diversity refines our understanding of species–genetic diversity relationships. Ecology and evolution, 8(24), 12351-12364.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. Genetics, 155(2), 945-959.

Pringle, J. M., & Wares, J. P. (2007). Going against the flow: maintenance of alongshore variation in allele frequency in a coastal ocean. Marine Ecology Progress Series, 335, 69-84.

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., & Treml, E. A. (2016). Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. Current zoology, 62(6), 581-601.

Riginos, C., Douglas, K. E., Jin, Y., Shanahan, D. F., & Treml, E. A. (2011). Effects of geography and life history traits on genetic differentiation in benthic marine fishes. Ecography, 34(4), 566-575.

Roberts, D. A., Johnston, E. L., & Poore, A. G. (2008). Contamination of marine biogenic habitats and effects upon associated epifauna. Marine Pollution Bulletin, 56(6), 1057-1065.

Roberts, D. A., Poore, A. G., & Johnston, E. L. (2006). Ecological consequences of copper contamination in macroalgae: effects on epifauna and associated herbivores. Environmental Toxicology and Chemistry: An International Journal, 25(9), 2470-2479.

Ros, M., Navarro-Barranco, C., González-Sánchez, M., Ostalé-Valriberas, E., Cervera-Currado, L., & Guerra-García, J. M. (2020). Starting the stowaway pathway: the role of dispersal behavior in the invasion success of low-mobile marine species. Biological Invasions, 22(9), 2797-2812.

Ruiz, M. S., Harari, J., Ribeiro, R. B., & Sampaio, A. F. (2021). Numerical modelling of storm tides in the Estuarine System of Santos, São Vicente and Bertioga (SP, Brazil). Regional Studies in Marine Science, 44, 101791.

Saha, S.; Moorthi, S.; Wu, X.; Wang, J.; Nadiga, S.; Tripp, P.; Behringer, D.; Hou, Y.; Chuang, H.; Iredell, M.; Ek, M.; Meng, J.; Yang, R.; Mendez, M.P.; Van Den Dool, H.; Zhang, Q.; Wang, W.; Chen, M. & Becker, E. (2011). NCEP Climate Forecast System Version 2 (CFSv2) Selected Hourly Time-Series Products. Boulder (Colorado, USA): Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory. Available in: <https://rda.ucar.edu/datasets/ds094.1/>. Accessed in 11 set. 2018.

Sbrocco, E. J., & Barber, P. H. (2013). MARSPEC: ocean climate layers for marine spatial ecology: Ecological Archives E094-086. Ecology, 94(4), 979-979.

Scheltema, R. S. (1977). Dispersal of marine Invertebrate organisms: paleobiogeographic and biostratigraphic implications. In: Kauffman, E. G., Hazel, J. E. (ed) Concepts and methods of biostratigraphy. Dowden, Hutchinson & Ross, Stroudsberg, Pennsylvannia, p. 73

Selkoe, K. A., Aloia, C. C., Crandall, E. D., Iacchei, M., Liggins, L., Puritz, J. B., ... & Toonen, R. J. (2016a). A decade of seascape genetics: contributions to basic and applied marine connectivity. Marine Ecology Progress Series, 554, 1-19.

Selkoe, K. A.; Gaggiotti, O. E.; Treml, E. A.; Wren, J. L. K.; Donovan, M. K.; Consortium, H. R. C.; Toonen, R. J. (2016b). The DNA of coral reef biodiversity: predicting and protecting genetic diversity of reef assemblages. Proceedings of the Royal Society, Biological Sciences, 283: 1-10.

Seymour, M., Seppälä, K., Mächler, E., & Altermatt, F. (2016). Lessons from the macroinvertebrates: species-genetic diversity correlations highlight important dissimilar relationships. Freshwater Biology, 61(11), 1819-1829.

Silvertown, J., Biss, P. M., & Freeland, J. (2009). Community genetics: resource addition has opposing effects on genetic and species diversity in a 150-year experiment. Ecology Letters, 12(2), 165-170.

Singh, S. P., Groeneveld, J. C., Hart-Davis, M. G., Backeberg, B. C., & Willows-Munro, S. (2018). Seascape genetics of the spiny lobster *Panulirus homarus* in the Western Indian Ocean: Understanding how oceanographic features shape the genetic structure of species with high larval dispersal potential. Ecology and evolution, 8(23), 12221-12237.

Sokolov, E. P. (2000). An improved method for DNA isolation from mucopolysaccharide-rich molluscan tissues. Journal of Molluscan Studies, 66(4), 573-575.

Sudo, H., & Yoshida, G. (2021). Effects of a reduction in algal nitrogen content on survival, growth, and reproduction of an herbivorous amphipod. Journal of Experimental Marine Biology and Ecology, 539, 151543.

Suyama, Y., & Matsuki, Y. (2015). MIG-seq: an effective PCR-based method for genome-wide single-nucleotide polymorphism genotyping using the next-generation sequencing platform. Scientific reports, 5(1), 1-12.

Taberlet, P., Zimmermann, N. E., Englisch, T., Tribsch, A., Holderegger, R., Alvarez, N., ... & IntraBioDiv Consortium. (2012). Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. Ecology Letters, 15(12), 1439-1448.

Tanaka, M. O., & Leite, F. P. (2004). Distance effects on short-term recolonization of Sargassum stenophyllum by mobile epifauna, with an analysis of gammarid life habits. Journal of the Marine Biological Association of the United Kingdom, 84(5), 901-910.

Teske, P. R., Papadopoulos, I., Zardi, G. I., McQuaid, C. D., Edkins, M. T., Griffiths, C. L., & Barker, N. P. (2007). Implications of life history for genetic structure and migration rates of southern African coastal invertebrates: planktonic, abbreviated and direct development. Marine Biology, 152(3), 697-711.

Thiel M, Gutow L. 2005. The ecology of rafting in the marine environment. I. The floating substrata. Oceanography and Marine Biology 42: 181–264.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global ecology and biogeography, 21(2), 272-281.

Vellend, M. (2003). Island biogeography of genes and species. *The American Naturalist, 162*(3), 358-365.

Vellend, M. (2004). Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. Ecology, 85(11), 3043-3055.

Vellend, M. (2005). Species diversity and genetic diversity: parallel processes and correlated patterns. The American Naturalist, 166(2): 199-215.

Vellend, M., & Geber, M. A. (2005). Connections between species diversity and genetic diversity. Ecology letters, 8(7), 767-781.

Vellend, M., Lajoie, G., Bourret, A., Múrria, C., Kembel, S. W., & Garant, D. (2014). Drawing ecological inferences from coincident patterns of population-and community-level biodiversity. Molecular Ecology, 23(12), 2890-2901.

Viaroli, P., Bartoli, M., Azzoni, R., Giordani, G., Mucchino, C., Naldi, M., ... & Taje, L. (2005). Nutrient and iron limitation to *Ulva* blooms in a eutrophic coastal lagoon (Sacca di Goro, Italy). Hydrobiologia, 550(1), 57-71.

Walters, A. D., Trujillo, D. A., & Berg, D. J. (2022). Micro-endemic species of snails and amphipods show population genetic structure across very small geographic ranges. Heredity, 128(5), 325-337.

Wang, I. J. (2013). Examining the full effects of landscape heterogeneity on spatial genetic variation: a multiple matrix regression approach for quantifying geographic and ecological isolation. Evolution, 67(12), 3403-3411.

Wares, J. P., Gaines, S., & Cunningham, C. W. (2001). A comparative study of asymmetric migration events across a marine biogeographic boundary. Evolution, 55(2), 295-306.

Watanabe, K., & Monaghan, M. T. (2017). Comparative tests of the species-genetic diversity correlation at neutral and nonneutral loci in four species of stream insect. Evolution, 71(7), 1755-1764.

Wei, X., & Jiang, M. (2012). Contrasting relationships between species diversity and genetic diversity in natural and disturbed forest tree communities. New Phytologist, 193(3), 779-786.

Wei, K., Wood, A. R., & Gardner, J. P. (2013). Seascape genetics of the New Zealand greenshell mussel: sea surface temperature explains macrogeographic scale genetic variation. Marine Ecology Progress Series, 477, 107-121.

Whitehead, A., Clark, B. W., Reid, N. M., Hahn, M. E., & Nacci, D. (2017). When evolution is the solution to pollution: Key principles, and lessons from rapid repeated adaptation of killifish (*Fundulus heteroclitus*) populations. Evolutionary applications, 10(8), 762-783.

Whitham, T. G.; Bailey, J. K.; Schweitzer, J. A.; Shuster, S. M.; Bangert, R. K.; LeRoy, C. J.; Lonsdorf, E. V.; Allan, G. J.; DiFazio, S. P.; Potts, B. M.; Fischer, D. G.; Gehring, C. A.; Lindroth, R. L.; Marks, J. C.; Hart, S. C.; Wimp, G. M.; Wooley, S. C. (2006). A framework for community and ecosystem genetics: from genes to ecosystems. Nature Reviews Genetics, 7: 510-523.

Whitehead, A., Clark, B. W., Reid, N. M., Hahn, M. E., & Nacci, D. (2017). When evolution is the solution to pollution: Key principles, and lessons from rapid repeated adaptation of killifish (Fundulus heteroclitus) populations. Evolutionary applications, 10(8), 762-783.

Whitney, F. A., Crawford, W. R., & Harrison, P. J. (2005). Physical processes that enhance nutrient transport and primary productivity in the coastal and open ocean of the subarctic NE Pacific. Deep Sea Research Part II: Topical Studies in Oceanography, 52(5-6), 681-706.

Wildish, D. J. (2012). Long distance dispersal and evolution of talitrids (Crustacea: Amphipoda: Talitridae) in the northeast Atlantic islands. Journal of Natural History, 46(37-38), 2329-2348.

Wilson, G. A., & Rannala, B. (2003). Bayesian inference of recent migration rates using multilocus genotypes. Genetics, 163(3), 1177-1191.

Wu, M. C., Dahms, H. U., Liu, C. H., Hsieh, C. Y., Wang, C. C., & Ho, Z. Y. (2021). Estuarine sediment toxicity testing with an indigenous subtropical amphipod. Marine Pollution Bulletin, 162, 111797.

Xu, W., Liu, L., He, T., Cao, M., Sha, L., Hu, Y., ... & Li, J. (2016). Soil properties drive a negative correlation between species diversity and genetic diversity in a tropical seasonal rainforest. Scientific Reports, 6(1), 1-8.

Yang, S. H., Harari, J., & Braga, E. D. S. (2019). Modelagem de plumas de efluentes entre Praia Grande e Peruíbe, litoral do estado de São Paulo, Brasil. Engenharia Sanitaria e Ambiental, 24, 697-708.

Zvuloni, A., Mokady, O., Al-Zibdah, M., Bernardi, G., Gaines, S. D., & Abelson, A. (2008). Local scale genetic structure in coral populations: a signature of selection. Marine Pollution Bulletin, 56(3), 430-438.

Supplementary 1 – Algal data, PCA and Regression analysis results

The effects of habitat size, environmental variables, and connectivity on species-genetic diversity correlations (α-SGDC) were investigated with regression analysis. This analysis was performed only for *H. niger*, since this was the only species that presented significant values of SGDC.

Habitat size was measured as the mean macroalgae wet weight in each site (Table S1.1).

Table S1.1 – Mean algal wet weight (g) in each locality

Site	Algal weight
Lamberto	27.16783333
Conchas	7.798166667
Buzios	26.081
Palmas	2.0415
Figueira	24.72366667
Baleia	12.958
Montao_de_Trigo	8.9935
Alcatrazes_ESEC	7.105166667
Alcatrazes_Refuge	6.613333333
Mar_Casado	26.74083333
Moela	3.473

For environmental variables, we first calculated a principal components analysis (PCA) considering the most important variables obtained with bioenv procedure, considering the genetic differentiation of *H. niger* populations and the beta-diversity values for invertebrate assemblages' dissimilarities. Environmental variables were normalized prior to PCA construction, which is presented in Figure SX.1. As a proxy for environmental variables, we used the first principal component (PC1) of PCA.

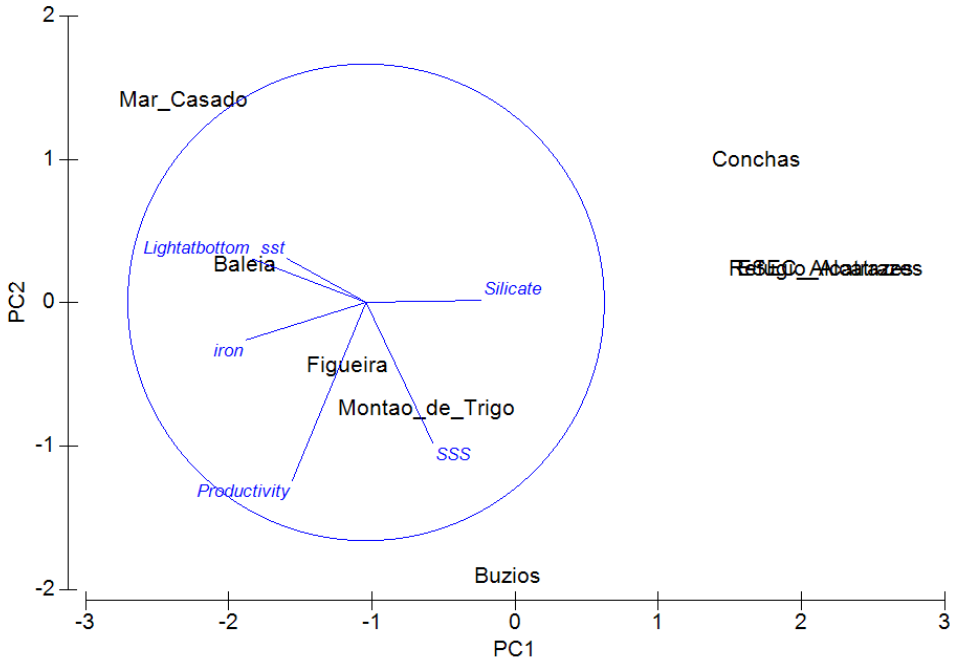


Figure S1.1 – PCA analysis for environmental variables. PC1 was considered in regression analysis.

Regression analysis results are presented in Table S1.2.

Table S1.2 – Regression analysis results

Response variable	**Predictor variable(s)**		
		P-value	R^2
Species Diversity	Environmental	0.7955	-0.1526
	Connectivity	0.7061	-0.137
	Habitat Size	0.3314	0.01636
Genetic Diversity (*H. niger*)	Environmental	0.1412	0.2107
	Connectivity	**0.04819**	**0.4225**
	Habitat Size	0.1613	0.1814

Supplementary 2 – Particle dispersal matrix.

	Lamberto	Conchas	Buzios	Palmas	Figueira	Baleia	Montao_d	ESEC_Alca	Refugio_A	Mar_Casa	Moela	Cibratel
Lamberto	49918	539	166	1485	107	0	0	0	0	0	0	0
Conchas	313	36714	412	1700	15	0	0	3	1	0	0	0
Buzios	371	2163	6602	607	504	0	0	493	537	0	0	0
Palmas	1724	865	1341	20203	545	0	0	7	1	0	0	0
Figueira	824	250	534	579	22632	110	132	141	246	10	0	0
Baleia	156	64	80	58	787	21565	2048	319	386	29	12	0
Montao_d	338	13	195	150	2735	5783	16952	146	111	0	0	0
ESEC_Alca	10	68	684	257	15	0	0	11638	8179	0	0	0
Refugio_A	3	205	1015	304	74	0	0	8722	9790	0	0	0
Mar_Casa	9	0	13	17	82	353	1261	423	415	15625	4068	28
Moela	5	0	65	9	75	200	161	192	139	5445	15306	119
Cibratel	0	0	0	0	0	0	0	0	0	15	8	19520

Supplementary 3 – PERMANOVA analysis results

Table S3.1 – PERMANOVA results

Source of variation	df	MS	Pseudo-F	P-value
Site	**9**	**6884.7**	**9.6066**	**0.0001**
Residuals	30	21500	716.66	
Transformation: log(x+1)				

Table S3.2 – Posteriori pairwise results of PERMANOVA.

	Alcatrazes ESEC	Alcatrazes Refuge	Montão de Trigo	Figueira	Baleia	Conchas	Lamberto	Palmas	Búzios
Alcatrazes Refuge	P = 0.0326 t = 3.7712 Av. dissimilarity: 57.94								
Montão de Trigo	P = 0.0261 t = 2.5069 Av. dissimilarity: 47.38	P = 0.0292 t = 3.8378 Av. dissimilarity: 65.13							
Figueira	P = 0.0293 t = 4.1131 Av. dissimilarity: 82.58	P = 0.0286 t = 4.8248 Av. dissimilarity: 91.62	P = 0.0292 t = 3.2845 Av. dissimilarity: 75.55						
Baleia	P = 0.0306 t = 2.7171 Av. dissimilarity: 49.09	P = 0.0296 t = 3.8662 Av. dissimilarity: 65.20	P = 0.0262 t = 2.2207 Av. dissimilarity: 46.94	P = 0.03 t = 3.6799 Av. dissimilarity: 80.08					
Conchas	P = 0.0295 t = 3.0239 Av. dissimilarity: 60.86	P = 0.0298 t = 3.8688 Av. dissimilarity: 73.87	P = 0.0273 t = 3.0682 Av. dissimilarity: 66.59	P = 0.0285 t = 3.4564 Av. dissimilarity: 83.53	P = 0.0265 t = 2.648 Av. dissimilarity: 59.25				
Lamberto	P = 0.0266 t = 4.8807 Av. dissimilarity: 90.47	P = 0.027 t = 4.8791 Av. dissimilarity: 88.60	P = 0.0293 t = 4.2155 Av. dissimilarity: 87.23	P = 0.0307 t = 2.9321 Av. dissimilarity: 78.75	P = 0.0271 t = 4.0465 Av. dissimilarity: 82.41	P = 0.027 t = 3.6327 Av. dissimilarity: 82.62			
Palmas	P = 0.0309 t = 3.2309 Av. dissimilarity: 82.59	P = 0.0274 t = 3.0389 Av. dissimilarity: 77.35	P = 0.0263 t = 2.9055 Av. dissimilarity: 80.40	P = 0.0281 t = 2.8325 Av. dissimilarity: 87.69	P = 0.0301 t = 2.9614 Av. dissimilarity: 80.62	P = 0.0294 t = 2.8092 Av. dissimilarity: 82.28	P = 0.0318 t = 2.5331 Av. dissimilarity: 77.54		
Búzios	P = 0.0568 t = 1.5942 Av. dissimilarity: 48.84	P = 0.0291 t = 2.3048 Av. dissimilarity: 60.31	P = 0.0255 t = 1.5572 Av. dissimilarity: 53.00	P = 0.0276 t = 2.6555 Av. dissimilarity: 81.90	P = 0.0313 t = 1.87 Av. dissimilarity: 57.09	P = 0.0292 t = 2.5366 Av. dissimilarity: 73.85	P = 0.0293 t = 3.249 Av. dissimilarity: 90.63	P = 0.0291 t = 2.433 Av. dissimilarity: 83.94	
Mar Casado	P = 0.0279 t = 2.6688 Av. dissimilarity: 55.36	P = 0.0305 t = 4.2198 Av. dissimilarity: 77.96	P = 0.0276 t = 2.601 Av. dissimilarity: 58.84	P = 0.026 t = 3.0307 Av. dissimilarity: 76.66	P = 0.0279 t = 2.0966 Av. dissimilarity: 50.47	P = 0.0259 t = 3.0126 Av. dissimilarity: 71.25	P = 0.0299 t = 3.9379 Av. dissimilarity: 89.72	P = 0.0273 t = 3.1037 Av. dissimilarity: 89.18	P = 0.0298 t = 1.6754 Av. dissimilarity: 58.63

Supplementary 4 – SIMPER Results

SIMPER
Similarity Percentages - species contributions

One-Way Analysis

Data worksheet
Name: densidades log(x+1)
Data type: Abundance
Sample selection: All
Variable selection: All

Parameters
Resemblance: S17 Bray Curtis similarity
Cut off for low contributions: 90.00%

Factor Groups

Sample	Site
ESEC_Alcatrazes	ESEC_Alcatrazes
ESEC_Alcatrazes	ESEC_Alcatrazes
ESEC_Alcatrazes	ESEC_Alcatrazes
ESEC_Alcatrazes	ESEC_Alcatrazes
Refugio_Alcatrazes	Refugio_Alcatrazes
Refugio_Alcatrazes	Refugio_Alcatrazes
Refugio_Alcatrazes	Refugio_Alcatrazes
Refugio_Alcatrazes	Refugio_Alcatrazes
Montao_de_Trigo	Montao_de_Trigo
Montao_de_Trigo	Montao_de_Trigo
Montao_de_Trigo	Montao_de_Trigo
Montao_de_Trigo	Montao_de_Trigo
Figueira	Figueira
Figueira	Figueira
Figueira	Figueira
Figueira	Figueira
Baleia	Baleia
Baleia	Baleia
Baleia	Baleia
Baleia	Baleia
Conchas	Conchas
Conchas	Conchas
Conchas	Conchas
Conchas	Conchas
Lamberto	Lamberto
Lamberto	Lamberto
Lamberto	Lamberto
Lamberto	Lamberto
Palmas	Palmas

Palmas	Palmas
Palmas	Palmas
Palmas	Palmas
Buzios	Buzios
Buzios	Buzios
Buzios	Buzios
Buzios	Buzios
Mar_Casado	Mar_Casado
Mar_Casado	Mar_Casado
Mar_Casado	Mar_Casado
Mar_Casado	Mar_Casado

Group ESEC_Alcatrazes
Average similarity: 72.87

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Hyale_niger	2.34	16.62	16.23	22.81	22.81
Stenothoe_sp	1.85	13.50	9.54	18.52	41.34
Ericthonius_brasiliensis	1.50	10.00	4.33	13.72	55.05
Podocerus_fissipes	1.38	6.98	2.06	9.58	64.63
Chondrochelia_dubia	0.83	5.82	5.98	7.99	72.62
Ampithoe_ramondi	1.13	5.68	1.30	7.80	80.42
Janaira_gracilis	0.98	5.63	2.82	7.72	88.14
Cymadusa_filosa	0.68	3.21	1.41	4.40	92.55

Group Refugio_Alcatrazes
Average similarity: 71.99

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ericthonius_brasiliensis	3.23	10.92	8.31	15.17	15.17
Stenothoe_sp	2.40	8.28	8.90	11.50	26.67
Photis_sarae	2.37	7.34	3.98	10.20	36.87
Aora_spinicornis	2.10	6.57	6.76	9.13	46.00
Alaba_incerta	1.66	6.00	6.98	8.34	54.34
Janaira_gracilis	2.01	5.98	2.18	8.30	62.64
Caprella_scaura	2.06	4.31	1.32	5.99	68.63
Rissoella_ornata	1.31	4.11	8.33	5.71	74.34
Assiminea_sp.	0.93	2.94	7.49	4.09	78.43
Ampithoe_ramondi	1.25	2.78	1.85	3.87	82.30
Paracerceis_sculpta	0.65	2.32	3.74	3.22	85.52
Chondrochelia_dubia	0.71	1.90	4.99	2.65	88.16
Pinctada_imbricata	0.70	1.80	2.79	2.50	90.66

Group Montao_de_Trigo
Average similarity: 66.13

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Hyale_niger	2.02	17.42	6.74	26.34	26.34
Stenothoe_sp	1.93	16.17	4.56	24.46	50.79
Caprella_scaura	0.97	6.35	2.62	9.60	60.40

Janaira_gracilis	0.86	5.57	1.35	8.43	68.82
Ericthonius_brasiliensis	0.35	2.85	2.48	4.31	73.14
Cymadusa_filosa	0.34	2.56	1.79	3.87	77.00
Pinctada_imbricata	0.49	2.22	0.83	3.35	80.35
Ophiactis_lymani	0.23	1.48	2.58	2.25	82.60
Gammaropsis_palmata	0.31	1.39	1.33	2.10	84.70
Alaba_incerta	0.22	1.38	3.43	2.09	86.79
Chondrochelia_dubia	0.16	1.21	2.96	1.82	88.61
Ophiothela_mirabilis	0.14	1.18	4.55	1.78	90.39

Group Figueira
Average similarity: 48.91

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Hyale_niger	0.86	17.45	3.85	35.67	35.67
Hippolyte_obliquimanus	0.26	9.22	2.05	18.84	54.52
Ophiothela_mirabilis	0.31	7.28	3.01	14.89	69.40
Janaira_gracilis	0.29	6.28	1.59	12.83	82.24
Bittiolum_varium	0.29	3.71	1.22	7.59	89.83
Cymadusa_filosa	0.12	2.92	1.00	5.98	95.80

Group Baleia
Average similarity: 67.27

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Hyale_niger	2.44	17.48	15.05	25.98	25.98
Janaira_gracilis	1.45	8.57	6.11	12.74	38.72
Stenothoe_sp	1.56	7.96	1.28	11.83	50.56
Chondrochelia_dubia	0.70	4.95	7.04	7.36	57.92
Aora_spinicornis	0.88	4.34	3.11	6.45	64.37
Pinctada_imbricata	0.70	4.03	2.93	5.99	70.37
Cymadusa_filosa	0.52	3.71	14.78	5.52	75.89
Eulithidium_affine	0.50	3.32	4.25	4.93	80.82
Ericthonius_brasiliensis	0.63	2.70	1.84	4.01	84.83
Gammaropsis_palmata	0.48	2.54	2.31	3.78	88.61
Costoanachis_sertulariarum	0.24	1.66	4.28	2.47	91.08

Group Conchas
Average similarity: 59.82

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Janaira_gracilis	1.53	6.74	1.11	11.27	11.27
Hyale_niger	1.27	6.45	4.54	10.79	22.06
Chondrochelia_dubia	1.10	5.71	1.71	9.54	31.59
Podocerus_fissipes	1.00	5.52	3.92	9.23	40.83
Stenothoe_sp	1.27	4.80	0.88	8.02	48.85
Sunampithoe_pelagica	0.71	4.54	14.56	7.59	56.44
Pinctada_imbricata	0.58	4.17	6.18	6.97	63.41
Mitrela_dichroa	0.65	3.98	5.12	6.65	70.06
Hyale_macrodactyla	1.07	3.67	1.57	6.14	76.20

Elasmopus_pectenicrus	0.73	3.40	2.84	5.68	81.87
Bittiolum_varium	0.46	2.87	2.81	4.79	86.67
Pachycheles_laevidactylus	0.39	1.22	0.88	2.05	88.71
Epialtus_bituberculatus	0.32	1.18	0.91	1.97	90.68

Group Lamberto
Average similarity: 58.04

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Bittiolum_varium	2.58	33.83	8.28	58.29	58.29
Paracerceis_sculpta	0.81	8.38	1.71	14.44	72.73
Eulithidium_affine	0.29	2.57	1.96	4.42	77.16
Hippolyte_obliquimanus	0.32	2.56	1.22	4.42	81.58
Chondrochelia_dubia	0.27	2.08	1.95	3.58	85.16
Mitrela_dichroa	0.20	1.62	3.18	2.79	87.95
Janaira_gracilis	0.27	1.06	0.61	1.83	89.78
Pinctada_imbricata	0.16	1.04	1.40	1.80	91.57

Group Palmas
Average similarity: 43.41

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ophiothela_mirabilis	0.93	6.39	1.01	14.71	14.71
Pinctada_imbricata	1.23	6.31	2.82	14.53	29.24
Bittiolum_varium	1.09	4.96	3.00	11.43	40.67
Ericthonius_brasiliensis	0.88	4.60	2.79	10.60	51.27
Ophioplocus_januarii	0.95	3.68	1.45	8.48	59.75
Alvania_auberiana	0.76	2.21	0.85	5.10	64.85
Photis_sarae	0.54	1.91	0.55	4.40	69.24
Lysianassa_teminino	0.60	1.66	0.87	3.83	73.07
Caecum_brasilicum	0.50	1.48	1.95	3.41	76.49
Chondrochelia_dubia	0.37	1.30	0.90	2.99	79.47
Cymadusa_tartarugae	0.29	1.22	4.23	2.80	82.28
Musculus_lateralis	0.25	1.02	2.21	2.36	84.63
Stenothoe_sp	0.23	0.98	2.09	2.26	86.90
Janaira_gracilis	0.12	0.60	0.82	1.37	88.27
Paracerceis_sculpta	0.20	0.59	0.77	1.36	89.63
Costoanachis_sparsa	0.16	0.57	0.77	1.32	90.95

Group Buzios
Average similarity: 47.84

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ericthonius_brasiliensis	2.04	12.77	2.50	26.69	26.69
Hyale_niger	1.72	8.61	1.78	18.01	44.70
Aora_spinicornis	0.75	4.72	3.89	9.87	54.57
Janaira_gracilis	1.11	4.45	1.13	9.31	63.88
Stenothoe_sp	1.47	3.93	0.65	8.21	72.09
Caprella_scaura	0.42	2.60	1.65	5.43	77.52
Ampithoe_ramondi	0.58	2.42	1.15	5.07	82.58

Cymadusa_filosa	0.28	1.38	1.75	2.89	85.48
Alaba_incerta	0.24	1.30	1.15	2.71	88.19
Jassa_slateryi	0.46	1.17	0.68	2.45	90.64

Group Mar_Casado
Average similarity: 61.04

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Hyale_niger	2.57	26.97	6.62	44.19	44.19
Batea_catharinensis	1.60	11.66	2.19	19.11	63.30
Janaira_gracilis	1.24	8.69	2.46	14.24	77.54
Ericthonius_brasiliensis	1.21	5.00	0.86	8.19	85.73
Stenothoe_sp	0.42	2.22	0.75	3.63	89.36
Costoanachis_sertulariarum	0.34	2.02	1.17	3.31	92.67

Groups ESEC_Alcatrazes & Refugio_Alcatrazes
Average dissimilarity = 57.94

	Group ESEC_Alcatrazes	Group Refugio_Alcatrazes
Species	Av.Abund	Av.Abund
	Av.Diss	Diss/SD
	Contrib%	Cum.%
Photis_sarae	0.06	2.37
	5.91	4.51
	10.20	10.20
Aora_spinicornis	0.08	2.10
	5.13	5.54
	8.85	19.05
Caprella_scaura	0.20	2.06
	4.45	1.85
	7.67	26.73
Ericthonius_brasiliensis	1.50	3.23
	4.36	3.42
	7.52	34.25
Hyale_niger	2.34	0.73
	4.08	2.85
	7.04	41.29
Alaba_incerta	0.12	1.66
	3.98	6.98
	6.88	48.17
Podocerus_fissipes	1.38	0.00
	3.55	1.87
	6.13	54.30
Janaira_gracilis	0.98	2.01
	2.89	1.78
	4.99	59.29

Assiminea_sp.		0.00			0.93
	2.35			8.81	
	4.06			63.34	
Ampithoe_ramondi		1.13			1.25
	2.01			1.50	
	3.47			66.81	
Rissoella_ornata		0.56			1.31
	1.85			1.77	
	3.19			70.00	
Paracerceis_sculpta		0.02			0.65
	1.65			4.13	
	2.85			72.86	
Pinctada_imbricata		0.09			0.70
	1.49			2.55	
	2.57			75.43	
Stenothoe_sp		1.85			2.40
	1.36			1.62	
	2.35			77.78	
Musculus_lateralis		0.00			0.50
	1.25			1.88	
	2.16			79.94	
Astyris_lunata		0.00			0.56
	1.25			0.96	
	2.15			82.10	
Cymadusa_filosa		0.68			0.43
	1.08			1.22	
	1.87			83.97	
Pseudaeginella_montoucheti		0.02			0.39
	0.87			1.15	
	1.50			85.47	
Chondrochelia_dubia		0.83			0.71
	0.79			1.43	
	1.36			86.84	
Anachis_fenneli		0.14			0.31
	0.71			1.21	
	1.23			88.07	
Ophioplocus_januarii		0.00			0.27
	0.67			0.65	
	1.16			89.22	
Bittiolum_varium		0.00			0.27
	0.64			1.90	
	1.11			90.34	

Groups ESEC_Alcatrazes & Montao_de_Trigo
Average dissimilarity = 47.38

	Group ESEC_Alcatrazes	Group Montao_de_Trigo

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Podocerus_fissipes	1.38	0.03	6.18	1.89	13.04	13.04
Ericthonius_brasiliensis	1.50	0.35	5.37	2.45	11.34	24.38
Ampithoe_ramondi	1.13	0.13	4.71	1.48	9.93	34.31
Caprella_scaura	0.20	0.97	3.40	1.74	7.17	41.48
Chondrochelia_dubia	0.83	0.16	3.16	2.85	6.67	48.15
Hyale_niger	2.34	2.02	2.90	1.41	6.11	54.26
Stenothoe_sp	1.85	1.93	2.50	1.97	5.27	59.53
Janaira_gracilis	0.98	0.86	2.23	1.33	4.70	64.23
Rissoella_ornata	0.56	0.09	2.14	1.40	4.52	68.75
Cymadusa_filosa	0.68	0.34	2.02	1.55	4.27	73.03
Pinctada_imbricata	0.09	0.49	1.96	1.57	4.14	77.17
Gammaropsis_palmata	0.00	0.31	1.33	1.41	2.82	79.99
Ophiactis_lymani	0.00	0.23	1.01	2.30	2.12	82.11
Anachis_fenneli	0.14	0.16	0.86	1.23	1.82	83.93
Ophiothela_mirabilis	0.00	0.14	0.64	2.74	1.35	85.29

Alaba_incerta		0.12		0.22	
0.59	1.35		1.25		
	86.54				
Perna_perna		0.01		0.13	
0.59	0.82		1.25		
	87.79				
Carpias_minutus		0.13		0.01	
0.59	1.57		1.25		
	89.03				
Paracerceis_sculpta		0.02		0.14	
0.57	0.87		1.20		
	90.23				

Groups Refugio_Alcatrazes & Montao_de_Trigo
Average dissimilarity = 65.13

	Group Refugio_Alcatrazes		Group Montao_de_Trigo	
Species	Av.Abund	Av.Diss	Av.Abund	Diss/SD
	Contrib%	Cum.%		
Ericthonius_brasiliensis	3.23	0.35		
	7.97	7.09		
	12.24	12.24		
Photis_sarae	2.37	0.02		
	6.53	4.40		
	10.03	22.26		
Aora_spinicornis	2.10	0.08		
	5.54	5.46		
	8.50	30.76		
Alaba_incerta	1.66	0.22		
	4.08	4.74		
	6.26	37.03		
Caprella_scaura	2.06	0.97		
	3.69	1.87		
	5.66	42.69		
Hyale_niger	0.73	2.02		
	3.46	1.96		
	5.31	48.00		
Janaira_gracilis	2.01	0.86		
	3.42	1.64		
	5.25	53.25		
Rissoella_ornata	1.31	0.09		
	3.31	8.25		
	5.09	58.33		
Ampithoe_ramondi	1.25	0.13		
	2.88	1.85		
	4.42	62.75		

Assiminea_sp.		0.93		0.00	
	2.54		7.73		
	3.91		66.66		
Stenothoe_sp		2.40		1.93	
	1.74		1.40		
	2.67		69.33		
Chondrochelia_dubia		0.71		0.16	
	1.52		1.84		
	2.33		71.66		
Paracerceis_sculpta		0.65		0.14	
	1.47		2.76		
	2.25		73.92		
Astyris_lunata		0.56		0.00	
	1.34		0.96		
	2.05		75.97		
Musculus_lateralis		0.50		0.01	
	1.33		1.83		
	2.04		78.01		
Pinctada_imbricata		0.70		0.49	
	1.12		1.40		
	1.71		79.72		
Pseudaeginella_montoucheti		0.39		0.04	
	0.92		1.19		
	1.41		81.14		
Carpias_minutus		0.30		0.01	
	0.85		1.07		
	1.31		82.45		
Gammaropsis_palmata		0.00		0.31	
	0.83		1.31		
	1.28		83.72		
Cymadusa_filosa		0.43		0.34	
	0.75		1.82		
	1.16		84.88		
Ophioplocus_januarii		0.27		0.00	
	0.72		0.65		
	1.11		85.99		
Anachis_fenneli		0.31		0.16	
	0.71		1.55		
	1.10		87.09		
Bittiolum_varium		0.27		0.02	
	0.65		1.75		
	1.00		88.09		
Arcidae_morfo2		0.22		0.00	
	0.55		0.92		
	0.84		88.93		
Ophiactis_lymani		0.04		0.23	
	0.54		1.62		
	0.83		89.76		

Phtisica_verae	0.24	0.00	0.53	0.56	0.82	90.58

Groups ESEC_Alcatrazes & Figueira
Average dissimilarity = 82.58

	Group ESEC_Alcatrazes	Group Figueira			
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Stenothoe_sp	1.85	0.01	12.44	7.44	15.07	15.07
Hyale_niger	2.34	0.86	10.42	1.88	12.62	27.69
Ericthonius_brasiliensis	1.50	0.01	10.31	2.87	12.49	40.18
Podocerus_fissipes	1.38	0.00	9.21	1.97	11.15	51.34
Ampithoe_ramondi	1.13	0.03	7.67	1.57	9.29	60.62
Chondrochelia_dubia	0.83	0.02	5.57	3.46	6.75	67.37
Janaira_gracilis	0.98	0.29	4.68	1.75	5.67	73.05
Rissoella_ornata	0.56	0.00	3.75	1.70	4.55	77.59
Cymadusa_filosa	0.68	0.12	3.72	1.63	4.51	82.10
Ophiothela_mirabilis	0.00	0.31	2.08	1.32	2.52	84.62
Bittiolum_varium	0.00	0.29	1.82	1.15	2.21	86.82
Hippolyte_obliquimanus	0.00	0.26	1.78	2.71	2.15	88.97
Caprella_scaura	0.20	0.01	1.33	1.12	1.61	90.58

Groups Refugio_Alcatrazes & Figueira
Average dissimilarity = 91.62

	Group Refugio_Alcatrazes	Group Figueira			
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ericthonius_brasiliensis	3.23	0.01	11.15	6.08	12.17	12.17
Stenothoe_sp	2.40	0.01	8.27	8.09	9.03	21.20

Photis_sarae		2.37	0.00	8.20
	4.14		8.95	30.15
Aora_spinicornis		2.10	0.00	7.17
	5.60		7.83	37.98
Caprella_scaura		2.06	0.01	6.43
	2.12		7.02	45.00
Janaira_gracilis		2.01	0.29	6.08
	2.28		6.63	51.63
Alaba_incerta		1.66	0.00	5.83
	5.09		6.37	58.00
Rissoella_ornata		1.31	0.00	4.43
	8.82		4.83	62.84
Ampithoe_ramondi		1.25	0.03	3.87
	2.18		4.23	67.06
Assiminea_sp.		0.93	0.00	3.16
	7.32		3.45	70.52
Chondrochelia_dubia		0.71	0.02	2.36
	2.43		2.58	73.10
Pinctada_imbricata		0.70	0.00	2.28
	3.54		2.49	75.59
Hyale_niger		0.73	0.86	2.27
	1.39		2.48	78.07
Paracerceis_sculpta		0.65	0.06	2.13
	3.28		2.33	80.39
Musculus_lateralis		0.50	0.00	1.68
	1.90		1.83	82.22
Astyris_lunata		0.56	0.01	1.61
	0.99		1.75	83.98
Pseudaeginella_montoucheti		0.39	0.06	1.14
	1.26		1.25	85.22
Carpias_minutus		0.30	0.00	1.09
	1.07		1.19	86.41
Ophiothela_mirabilis		0.00	0.31	1.08
	1.26		1.18	87.59
Cymadusa_filosa		0.43	0.12	1.07
	1.30		1.17	88.76
Anachis_fenneli		0.31	0.00	0.94
	1.22		1.03	89.79
Hippolyte_obliquimanus		0.00	0.26	0.91
	2.50		0.99	90.78

Groups Montao_de_Trigo & Figueira
Average dissimilarity = 75.55

	Group Montao_de_Trigo	Group Figueira		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Stenothoe_sp	1.93	0.01	16.02	
4.45	21.21	21.21		

Hyale_niger	2.02	0.86	10.92	
1.98	14.46	35.66		
Caprella_scaura	0.97	0.01	7.71	
2.44	10.20	45.86		
Janaira_gracilis	0.86	0.29	5.29	
1.86	7.00	52.86		
Pinctada_imbricata	0.49	0.00	3.79	
1.47	5.01	57.88		
Ericthonius_brasiliensis	0.35	0.01	3.09	
1.91	4.10	61.97		
Hippolyte_obliquimanus	0.00	0.26	2.28	
2.33	3.01	64.99		
Gammaropsis_palmata	0.31	0.01	2.25	
1.46	2.98	67.97		
Bittiolum_varium	0.02	0.29	2.14	
1.07	2.83	70.80		
Cymadusa_filosa	0.34	0.12	1.96	
1.78	2.59	73.39		
Alaba_incerta	0.22	0.00	1.71	
2.58	2.26	75.65		
Ophiactis_lymani	0.23	0.02	1.66	
1.93	2.20	77.85		
Ophiothela_mirabilis	0.14	0.31	1.51	
0.77	2.00	79.85		
Perna_perna	0.13	0.00	1.27	
0.84	1.67	81.53		
Anachis_fenneli	0.16	0.00	1.19	
1.54	1.58	83.11		
Chondrochelia_dubia	0.16	0.02	1.14	
2.15	1.51	84.62		
Batea_catharinensis	0.12	0.00	1.10	
1.40	1.46	86.07		
Paracerceis_sculpta	0.14	0.06	1.07	
0.94	1.42	87.49		
Cymodoce_brasiliensis	0.11	0.00	1.00	
0.66	1.32	88.81		
Ampithoe_ramondi	0.13	0.03	0.96	
1.42	1.26	90.08		

Groups ESEC_Alcatrazes & Baleia
Average dissimilarity = 49.09

	Group ESEC_Alcatrazes	Group Baleia		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Podocerus_fissipes	1.38	0.00	5.47	
1.92	11.15	11.15		
Ampithoe_ramondi	1.13	0.00	4.61	
1.66	9.38	20.53		

Ericthonius_brasiliensis		1.50	0.63	3.76
1.70	7.66		28.19	
Aora_spinicornis		0.08	0.88	3.05
2.05	6.21		34.40	
Stenothoe_sp		1.85	1.56	2.59
1.27	5.28		39.68	
Janaira_gracilis		0.98	1.45	2.37
1.46	4.83		44.50	
Pinctada_imbricata		0.09	0.70	2.35
2.89	4.79		49.30	
Rissoella_ornata		0.56	0.00	2.23
1.65	4.54		53.84	
Eulithidium_affine		0.00	0.50	2.04
2.90	4.16		58.00	
Gammaropsis_palmata		0.00	0.48	1.85
2.54	3.78		61.78	
Hyale_niger		2.34	2.44	1.67
1.54	3.41		65.19	
Hourstonius_wakabarae		0.00	0.39	1.47
1.19	2.99		68.18	
Cymadusa_filosa		0.68	0.52	1.40
1.59	2.85		71.03	
Batea_catharinensis		0.00	0.38	1.38
0.61	2.80		73.83	
Costoanachis_sertulariarum		0.00	0.24	0.98
4.51	2.00		75.83	
Leucothoe_spinicarpa		0.00	0.20	0.80
0.65	1.63		77.46	
Chondrochelia_dubia		0.83	0.70	0.78
1.13	1.58		79.04	
Ophiactis_lymani		0.00	0.18	0.68
2.33	1.39		80.43	
Caprella_scaura		0.20	0.04	0.67
1.06	1.36		81.79	
Mitrela_dichroa		0.00	0.13	0.57
0.95	1.16		82.95	
Anachis_fenneli		0.14	0.00	0.54
0.63	1.11		84.06	
Carpias_minutus		0.13	0.00	0.53
1.49	1.08		85.13	
Alaba_incerta		0.12	0.00	0.50
1.28	1.02		86.16	
Paracaprella_dubiaski		0.00	0.12	0.46
0.81	0.93		87.09	
Caprella_equilibra		0.00	0.12	0.42
0.56	0.86		87.95	
Elasmopus_pectenicrus		0.01	0.11	0.41
1.73	0.84		88.79	
Arcidae_morfo2		0.00	0.10	0.40
2.94	0.81		89.61	

Bittiolum_varium	0.00	0.10	0.36	
0.89	0.74	90.35		

Groups Refugio_Alcatrazes & Baleia
Average dissimilarity = 65.20

	Group Refugio_Alcatrazes	Group Baleia		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Ericthonius_brasiliensis	3.23	0.63	6.60	
	4.36	10.12	10.12	
Photis_sarae	2.37	0.00	6.00	
	4.42	9.20	19.32	
Caprella_scaura	2.06	0.04	4.76	
	1.98	7.30	26.62	
Hyale_niger	0.73	2.44	4.27	
	3.95	6.55	33.16	
Alaba_incerta	1.66	0.00	4.26	
	6.35	6.53	39.69	
Rissoella_ornata	1.31	0.00	3.26	
	7.38	5.00	44.69	
Aora_spinicornis	2.10	0.88	3.09	
	1.92	4.73	49.42	
Ampithoe_ramondi	1.25	0.00	2.99	
	2.11	4.58	54.01	
Assiminea_sp.	0.93	0.00	2.32	
	7.47	3.56	57.57	
Stenothoe_sp	2.40	1.56	2.29	
	1.31	3.51	61.08	
Janaira_gracilis	2.01	1.45	2.09	
	1.51	3.21	64.29	
Paracerceis_sculpta	0.65	0.00	1.70	
	4.01	2.60	66.89	
Eulithidium_affine	0.00	0.50	1.30	
	2.93	1.99	68.88	
Musculus_lateralis	0.50	0.00	1.24	
	1.86	1.90	70.78	
Astyris_lunata	0.56	0.00	1.23	
	0.95	1.89	72.68	
Gammaropsis_palmata	0.00	0.48	1.20	
	2.31	1.84	74.52	
Hourstonius_wakabarae	0.00	0.39	0.96	
	1.15	1.47	75.99	
Batea_catharinensis	0.00	0.38	0.91	
	0.60	1.40	77.39	
Pseudaeginella_montoucheti	0.39	0.00	0.89	
	1.14	1.36	78.75	
Carpias_minutus	0.30	0.00	0.79	
	1.07	1.21	79.95	

Pinctada_imbricata		0.70	0.70	0.78
	1.34		1.19	81.14
Anachis_fenneli		0.31	0.00	0.72
	1.19		1.10	82.24
Cymadusa_filosa		0.43	0.52	0.69
	2.01		1.05	83.30
Ophioplocus_januarii		0.27	0.00	0.66
	0.65		1.02	84.31
Costoanachis_sertulariarum		0.00	0.24	0.63
	3.89		0.96	85.28
Chondrochelia_dubia		0.71	0.70	0.62
	1.23		0.95	86.23
Arcidae_morfo2		0.22	0.10	0.54
	1.73		0.82	87.05
Leucothoe_spinicarpa		0.00	0.20	0.51
	0.64		0.79	87.84
Bittiolum_varium		0.27	0.10	0.50
	1.43		0.77	88.61
Phtisica_verae		0.24	0.00	0.50
	0.56		0.76	89.37
Caprella_equilibra		0.13	0.12	0.44
	0.77		0.68	90.04

Groups Montao_de_Trigo & Baleia
Average dissimilarity = 46.94

	Group Montao_de_Trigo	Group Baleia		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Caprella_scaura	0.97	0.04	4.04	
2.12	8.61	8.61		
Stenothoe_sp	1.93	1.56	3.54	
1.40	7.53	16.14		
Aora_spinicornis	0.08	0.88	3.41	
2.12	7.27	23.41		
Janaira_gracilis	0.86	1.45	3.07	
1.34	6.54	29.96		
Hyale_niger	2.02	2.44	3.06	
2.13	6.52	36.48		
Chondrochelia_dubia	0.16	0.70	2.47	
3.44	5.26	41.73		
Eulithidium_affine	0.02	0.50	2.26	
2.44	4.81	46.54		
Pinctada_imbricata	0.49	0.70	1.71	
1.22	3.65	50.19		
Batea_catharinensis	0.12	0.38	1.70	
0.78	3.62	53.81		
Ericthonius_brasiliensis	0.35	0.63	1.57	
1.07	3.35	57.16		

Hourstonius_wakabarae		0.02	0.39	1.56
1.13	3.32		60.48	
Gammaropsis_palmata		0.31	0.48	1.31
1.37	2.80		63.28	
Costoanachis_sertulariarum		0.01	0.24	1.09
3.64	2.32		65.60	
Alaba_incerta		0.22	0.00	0.94
2.08	2.00		67.60	
Leucothoe_spinicarpa		0.02	0.20	0.91
0.67	1.95		69.55	
Cymadusa_filosa		0.34	0.52	0.86
1.21	1.83		71.38	
Anachis_fenneli		0.16	0.00	0.67
1.39	1.43		72.81	
Mitrela_dichroa		0.00	0.13	0.66
0.93	1.40		74.21	
Paracerceis_sculpta		0.14	0.00	0.66
0.98	1.40		75.61	
Ophiothela_mirabilis		0.14	0.00	0.63
2.55	1.35		76.95	
Ampithoe_ramondi		0.13	0.00	0.62
2.02	1.32		78.27	
Perna_perna		0.13	0.02	0.60
0.86	1.28		79.55	
Caprella_equilibra		0.02	0.12	0.54
0.71	1.15		80.70	
Ophiactis_lymani		0.23	0.18	0.53
1.32	1.14		81.84	
Paracaprella_dubiaski		0.02	0.12	0.52
0.90	1.11		82.94	
Cymodoce_brasiliensis		0.11	0.00	0.51
0.68	1.10		84.04	
Elasmopus_pectenicrus		0.01	0.11	0.47
1.68	1.00		85.04	
Arcidae_morfo2		0.00	0.10	0.46
2.82	0.97		86.01	
Rissoella_ornata		0.09	0.00	0.43
1.38	0.91		86.92	
Bittiolum_varium		0.02	0.10	0.42
1.03	0.89		87.80	
Sphenia_fragilis		0.00	0.09	0.41
1.64	0.87		88.67	
Ampithoe_marcuzzi		0.00	0.09	0.38
1.58	0.80		89.48	
Turbonilla_multicostata		0.00	0.08	0.36
1.45	0.76		90.23	

Groups Figueira & Baleia
Average dissimilarity = 80.08

	Group Figueira	Group Baleia		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Hyale_niger	0.86	2.44	10.74	2.02
13.42	13.42			
Stenothoe_sp	0.01	1.56	10.50	1.97
13.12	26.53			
Janaira_gracilis	0.29	1.45	7.38	3.06
9.21	35.75			
Aora_spinicornis	0.00	0.88	5.44	2.71
6.79	42.53			
Chondrochelia_dubia	0.02	0.70	4.53	4.42
5.65	48.19			
Pinctada_imbricata	0.00	0.70	4.40	4.26
5.50	53.69			
Ericthonius_brasiliensis	0.01	0.63	4.06	1.63
5.07	58.75			
Eulithidium_affine	0.05	0.50	3.19	1.91
3.99	62.74			
Gammaropsis_palmata	0.01	0.48	2.97	2.57
3.71	66.44			
Cymadusa_filosa	0.12	0.52	2.60	4.75
3.25	69.69			
Hourstonius_wakabarae	0.01	0.39	2.26	1.18
2.82	72.51			
Batea_catharinensis	0.00	0.38	2.14	0.61
2.68	75.19			
Ophiothela_mirabilis	0.31	0.00	2.06	1.26
2.57	77.76			
Bittiolum_varium	0.29	0.10	1.66	1.14
2.08	79.84			
Costoanachis_sertulariarum	0.01	0.24	1.58	3.04
1.97	81.80			
Leucothoe_spinicarpa	0.01	0.20	1.33	0.66
1.66	83.46			
Hippolyte_obliquimanus	0.26	0.08	1.31	1.27
1.63	85.09			
Mitrela_dichroa	0.01	0.13	0.98	0.86
1.22	86.31			
Ophiactis_lymani	0.02	0.18	0.98	1.82
1.22	87.53			
Paracaprella_dubiaski	0.01	0.12	0.73	0.85
0.91	88.44			
Elasmopus_pectenicrus	0.00	0.11	0.69	1.54
0.86	89.30			
Arcidae_morfo2	0.00	0.10	0.67	2.76
0.84	90.14			

Groups ESEC_Alcatrazes & Conchas

Average dissimilarity = 60.86

	Group ESEC_Alcatrazes	Group Conchas		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Ericthonius_brasiliensis	1.50	0.08	5.70	
2.59	9.36	9.36		
Ampithoe_ramondi	1.13	0.00	4.52	
1.61	7.42	16.78		
Hyale_niger	2.34	1.27	4.46	
1.42	7.33	24.11		
Hyale_macrodactyla	0.00	1.07	3.91	
1.53	6.43	30.54		
Janaira_gracilis	0.98	1.53	3.79	
2.38	6.22	36.76		
Stenothoe_sp	1.85	1.27	3.12	
0.82	5.12	41.88		
Podocerus_fissipes	1.38	1.00	2.75	
1.21	4.52	46.40		
Sunampithoe_pelagica	0.00	0.71	2.73	
8.22	4.49	50.89		
Elasmopus_pectenicrus	0.01	0.73	2.66	
2.36	4.37	55.26		
Mitrela_dichroa	0.00	0.65	2.53	
3.20	4.16	59.42		
Cymadusa_filosa	0.68	0.10	2.33	
1.51	3.83	63.25		
Rissoella_ornata	0.56	0.00	2.19	
1.61	3.59	66.84		
Pinctada_imbricata	0.09	0.58	1.92	
5.10	3.16	70.00		
Bittiolum_varium	0.00	0.46	1.90	
2.27	3.12	73.13		
Chondrochelia_dubia	0.83	1.10	1.88	
1.93	3.09	76.21		
Pachycheles_laevidactylus	0.00	0.39	1.46	
1.42	2.40	78.61		
Epialtus_bituberculatus	0.00	0.32	1.24	
1.54	2.04	80.65		
Hourstonius_wakabarae	0.00	0.33	1.15	
0.90	1.89	82.54		
Jassa_slateryi	0.00	0.27	0.99	
0.89	1.63	84.17		
Leucothoe_spinicarpa	0.00	0.21	0.95	
0.80	1.56	85.72		
Modiolus_carvalhoi	0.00	0.22	0.81	
1.23	1.33	87.05		
Monocorophium_acherusicum	0.03	0.19	0.75	
1.27	1.23	88.28		

Caprella_scaura	0.20	0.03	0.72	
1.08	1.18	89.46		
Eulithidium_affine	0.00	0.13	0.54	
1.33	0.89	90.35		

Groups Refugio_Alcatrazes & Conchas
Average dissimilarity = 73.87

	Group Refugio_Alcatrazes	Group Conchas		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Ericthonius_brasiliensis	3.23	0.08	7.88	
	5.80	10.67	10.67	
Photis_sarae	2.37	0.10	5.67	
	3.83	7.67	18.34	
Aora_spinicornis	2.10	0.00	5.19	
	5.09	7.02	25.36	
Caprella_scaura	2.06	0.03	4.73	
	1.96	6.40	31.76	
Alaba_incerta	1.66	0.13	3.88	
	4.58	5.25	37.01	
Rissoella_ornata	1.31	0.00	3.21	
	6.39	4.35	41.36	
Stenothoe_sp	2.40	1.27	2.96	
	1.17	4.00	45.36	
Ampithoe_ramondi	1.25	0.00	2.94	
	2.08	3.99	49.35	
Hyale_macrodactyla	0.00	1.07	2.58	
	1.42	3.49	52.84	
Podocerus_fissipes	0.00	1.00	2.46	
	3.15	3.33	56.18	
Assiminea_sp.	0.93	0.00	2.29	
	6.44	3.10	59.28	
Janaira_gracilis	2.01	1.53	2.28	
	0.99	3.09	62.37	
Elasmopus_pectenicrus	0.00	0.73	1.78	
	2.11	2.41	64.78	
Paracerceis_sculpta	0.65	0.00	1.67	
	3.82	2.26	67.04	
Hyale_niger	0.73	1.27	1.65	
	1.59	2.24	69.28	
Mitrela_dichroa	0.00	0.65	1.63	
	2.94	2.21	71.48	
Sunampithoe_pelagica	0.17	0.71	1.47	
	1.83	1.99	73.47	
Chondrochelia_dubia	0.71	1.10	1.45	
	1.52	1.97	75.44	
Musculus_lateralis	0.50	0.00	1.22	
	1.84	1.65	77.09	

Astyris_lunata	0.56	0.00	1.22	
	0.95	1.65	78.74	
Pachycheles_laevidactylus	0.00	0.39	0.96	
	1.33	1.30	80.03	
Pseudaeginella_montoucheti	0.39	0.00	0.87	
	1.14	1.18	81.21	
Cymadusa_filosa	0.43	0.10	0.87	
	1.36	1.18	82.39	
Epialtus_bituberculatus	0.00	0.32	0.80	
	1.43	1.08	83.48	
Hourstonius_wakabarae	0.00	0.33	0.77	
	0.89	1.05	84.53	
Carpias_minutus	0.30	0.00	0.77	
	1.06	1.05	85.57	
Anachis_fenneli	0.31	0.00	0.71	
	1.18	0.96	86.53	
Bittiolum_varium	0.27	0.46	0.67	
	1.26	0.90	87.43	
Jassa_slateryi	0.04	0.27	0.66	
	0.99	0.90	88.33	
Pinctada_imbricata	0.70	0.58	0.65	
	1.97	0.89	89.21	
Ophioplocus_januarii	0.27	0.00	0.65	
	0.65	0.88	90.10	

Groups Montao_de_Trigo & Conchas
Average dissimilarity = 66.59

	Group Montao_de_Trigo	Group Conchas		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Janaira_gracilis	0.86	1.53	4.49	
2.04	6.74	6.74		
Stenothoe_sp	1.93	1.27	4.46	
1.03	6.69	13.43		
Hyale_macrodactyla	0.00	1.07	4.40	
1.54	6.61	20.04		
Chondrochelia_dubia	0.16	1.10	4.19	
1.95	6.29	26.33		
Podocerus_fissipes	0.03	1.00	4.14	
3.64	6.22	32.55		
Caprella_scaura	0.97	0.03	4.05	
1.98	6.08	38.63		
Hyale_niger	2.02	1.27	3.85	
1.18	5.79	44.42		
Sunampithoe_pelagica	0.00	0.71	3.10	
6.44	4.65	49.07		
Elasmopus_pectenicrus	0.01	0.73	3.01	
2.40	4.53	53.60		

Mitrela_dichroa		0.00	0.65	2.88
2.99	4.33		57.93	
Bittiolum_varium		0.02	0.46	2.11
2.01	3.17		61.09	
Pachycheles_laevidactylus		0.00	0.39	1.65
1.43	2.48		63.57	
Pinctada_imbricata		0.49	0.58	1.50
1.66	2.25		65.82	
Epialtus_bituberculatus		0.00	0.32	1.41
1.54	2.11		67.93	
Ericthonius_brasiliensis		0.35	0.08	1.31
1.46	1.96		69.90	
Hourstonius_wakabarae		0.02	0.33	1.30
0.97	1.95		71.85	
Gammaropsis_palmata		0.31	0.00	1.29
1.35	1.94		73.78	
Cymadusa_filosa		0.34	0.10	1.18
1.45	1.78		75.56	
Jassa_slateryi		0.01	0.27	1.12
0.93	1.68		77.24	
Leucothoe_spinicarpa		0.02	0.21	1.10
0.82	1.64		78.88	
Monocorophium_acherusicum		0.00	0.19	0.92
1.22	1.39		80.27	
Modiolus_carvalhoi		0.00	0.22	0.91
1.24	1.37		81.64	
Ophiactis_lymani		0.23	0.03	0.88
1.69	1.32		82.95	
Anachis_fenneli		0.16	0.00	0.66
1.36	0.99		83.94	
Perna_perna		0.13	0.06	0.64
0.97	0.97		84.91	
Paracerceis_sculpta		0.14	0.00	0.64
0.95	0.97		85.87	
Ophiothela_mirabilis		0.14	0.00	0.62
2.35	0.93		86.80	
Ampithoe_ramondi		0.13	0.00	0.61
1.91	0.91		87.72	
Epialtus_brasiliensis		0.00	0.14	0.58
0.96	0.87		88.59	
Alaba_incerta		0.22	0.13	0.58
1.08	0.86		89.45	
Eulithidium_affine		0.02	0.13	0.57
1.25	0.86		90.31	

Groups Figueira & Conchas
Average dissimilarity = 83.53

	Group Figueira	Group Conchas

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Janaira_gracilis	0.29	1.53	7.51	2.02
8.99	8.99			
Chondrochelia_dubia	0.02	1.10	7.05	2.22
8.44	17.43			
Stenothoe_sp	0.01	1.27	7.00	1.57
8.38	25.81			
Hyale_macrodactyla	0.00	1.07	6.23	1.68
7.45	33.26			
Podocerus_fissipes	0.00	1.00	6.15	4.48
7.36	40.62			
Hyale_niger	0.86	1.27	4.74	1.57
5.67	46.29			
Sunampithoe_pelagica	0.00	0.71	4.53	5.07
5.42	51.71			
Elasmopus_pectenicrus	0.00	0.73	4.36	2.79
5.22	56.93			
Mitrela_dichroa	0.01	0.65	4.18	2.62
5.00	61.93			
Pinctada_imbricata	0.00	0.58	3.81	3.30
4.57	66.50			
Pachycheles_laevidactylus	0.00	0.39	2.37	1.51
2.84	69.33			
Bittiolum_varium	0.29	0.46	2.12	1.13
2.54	71.88			
Epialtus_bituberculatus	0.00	0.32	2.06	1.60
2.47	74.34			
Ophiothela_mirabilis	0.31	0.00	2.03	1.19
2.43	76.77			
Leucothoe_spinicarpa	0.01	0.21	1.77	0.76
2.11	78.89			
Hourstonius_wakabarae	0.01	0.33	1.76	0.93
2.10	80.99			
Jassa_slateryi	0.00	0.27	1.55	0.87
1.85	82.85			
Hippolyte_obliquimanus	0.26	0.07	1.46	1.42
1.74	84.59			
Monocorophium_acherusicum	0.00	0.19	1.40	1.19
1.68	86.27			
Modiolus_carvalhoi	0.01	0.22	1.27	1.30
1.52	87.79			
Eulithidium_affine	0.05	0.13	0.84	1.30
1.00	88.79			
Cymadusa_filosa	0.12	0.10	0.82	1.15
0.98	89.77			
Epialtus_brasiliensis	0.00	0.14	0.81	0.96
0.96	90.73			

Groups Baleia & Conchas

Average dissimilarity = 59.25

Species	Group Baleia Av.Abund	Group Conchas Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Hyale_niger	2.44	1.27	4.73	1.67	7.99	7.99
Hyale_macrodactyla	0.00	1.07	3.86	1.51	6.51	14.50
Podocerus_fissipes	0.00	1.00	3.72	3.63	6.29	20.78
Stenothoe_sp	1.56	1.27	3.60	1.03	6.08	26.87
Aora_spinicornis	0.88	0.00	3.25	2.23	5.48	32.35
Janaira_gracilis	1.45	1.53	3.16	1.27	5.33	37.68
Sunampithoe_pelagica	0.00	0.71	2.69	6.09	4.55	42.22
Elasmopus_pectenicrus	0.11	0.73	2.25	1.78	3.81	46.03
Ericthonius_brasiliensis	0.63	0.08	2.13	1.32	3.59	49.62
Chondrochelia_dubia	0.70	1.10	2.04	1.70	3.45	53.06
Mitrela_dichroa	0.13	0.65	1.95	2.37	3.29	56.35
Gammaropsis_palmata	0.48	0.00	1.79	2.32	3.03	59.38
Cymadusa_filosa	0.52	0.10	1.65	2.36	2.79	62.17
Bittiolum_varium	0.10	0.46	1.52	1.54	2.57	64.73
Hourstonius_wakabarae	0.39	0.33	1.51	1.32	2.55	67.28
Eulithidium_affine	0.50	0.13	1.44	1.91	2.43	69.71
Pachycheles_laevidactylus	0.00	0.39	1.44	1.40	2.43	72.15
Batea_catharinensis	0.38	0.00	1.33	0.60	2.25	74.39
Leucothoe_spinicarpa	0.20	0.21	1.15	1.03	1.94	76.33
Epialtus_bituberculatus	0.08	0.32	1.06	1.62	1.78	78.12
Jassa_slateryi	0.00	0.27	0.98	0.88	1.65	79.77
Pinctada_imbricata	0.70	0.58	0.96	2.77	1.63	81.39

Costoanachis_sertulariarum	0.24	0.00	0.95	3.54
1.60	83.00			
Monocorophium_acherusicum	0.00	0.19	0.79	1.22
1.34	84.33			
Modiolus_carvalhoi	0.06	0.22	0.74	1.22
1.25	85.58			
Ophiactis_lymani	0.18	0.03	0.58	1.60
0.97	86.55			
Epialtus_brasiliensis	0.00	0.14	0.51	0.96
0.86	87.42			
Alaba_incerta	0.00	0.13	0.46	1.57
0.78	88.19			
Paracaprella_dubiaski	0.12	0.00	0.44	0.79
0.75	88.94			
Hippolyte_obliquimanus	0.08	0.07	0.41	1.03
0.69	89.63			
Caprella_equilibra	0.12	0.00	0.41	0.55
0.69	90.33			

Groups ESEC_Alcatrazes & Lamberto
Average dissimilarity = 90.47

	Group ESEC_Alcatrazes	Group Lamberto		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Bittiolum_varium	0.00	2.58	13.75	
5.74	15.19	15.19		
Hyale_niger	2.34	0.01	12.66	
5.69	14.00	29.19		
Stenothoe_sp	1.85	0.01	10.00	
6.24	11.06	40.25		
Ericthonius_brasiliensis	1.50	0.09	7.83	
2.67	8.66	48.90		
Podocerus_fissipes	1.38	0.00	7.42	
1.94	8.20	57.10		
Ampithoe_ramondi	1.13	0.00	6.30	
1.63	6.96	64.06		
Paracerceis_sculpta	0.02	0.81	4.25	
1.87	4.70	68.76		
Janaira_gracilis	0.98	0.27	3.98	
1.69	4.40	73.16		
Chondrochelia_dubia	0.83	0.27	3.17	
1.80	3.51	76.67		
Rissoella_ornata	0.56	0.00	3.02	
1.67	3.34	80.01		
Cymadusa_filosa	0.68	0.19	2.94	
1.43	3.25	83.26		
Hippolyte_obliquimanus	0.00	0.32	1.74	
1.25	1.93	85.19		

Eulithidium_affine		0.00	0.29	1.48
1.94	1.64		86.83	
Caprella_scaura		0.20	0.01	1.08
1.17	1.20		88.03	
Mitrela_dichroa		0.00	0.20	1.06
1.29	1.17		89.20	
Anachis_fenneli		0.14	0.00	0.74
0.63	0.82		90.01	

Groups Refugio_Alcatrazes & Lamberto
Average dissimilarity = 88.60

	Group Refugio_Alcatrazes		Group Lamberto	
Species	Av.Abund	Av.Diss	Av.Abund	Diss/SD
	Contrib%		Cum.%	
Ericthonius_brasiliensis		3.23	0.09	9.61
	6.14		10.85	10.85
Stenothoe_sp		2.40	0.01	7.32
	8.79		8.26	19.11
Photis_sarae		2.37	0.00	7.25
	4.28		8.18	27.29
Bittiolum_varium		0.27	2.58	7.15
	2.98		8.07	35.37
Aora_spinicornis		2.10	0.00	6.35
	5.61		7.17	42.54
Caprella_scaura		2.06	0.01	5.77
	2.08		6.52	49.05
Janaira_gracilis		2.01	0.27	5.40
	2.22		6.09	55.15
Alaba_incerta		1.66	0.01	5.11
	5.59		5.77	60.92
Rissoella_ornata		1.31	0.00	3.93
	8.29		4.43	65.35
Ampithoe_ramondi		1.25	0.00	3.56
	2.21		4.02	69.37
Assiminea_sp.		0.93	0.00	2.80
	7.50		3.16	72.53
Hyale_niger		0.73	0.01	2.37
	1.43		2.68	75.21
Pinctada_imbricata		0.70	0.16	1.57
	1.98		1.77	76.98
Astyris_lunata		0.56	0.01	1.45
	0.97		1.64	78.61
Chondrochelia_dubia		0.71	0.27	1.40
	1.39		1.58	80.20
Musculus_lateralis		0.50	0.07	1.28
	1.52		1.44	81.64

Paracerceis_sculpta	0.65	0.81	1.08	
	1.22	1.22	82.86	
Pseudaeginella_montoucheti	0.39	0.00	1.05	
	1.15	1.18	84.04	
Cymadusa_filosa	0.43	0.19	1.04	
	1.35	1.17	85.21	
Hippolyte_obliquimanus	0.00	0.32	0.99	
	1.19	1.12	86.33	
Carpias_minutus	0.30	0.00	0.96	
	1.07	1.08	87.41	
Eulithidium_affine	0.00	0.29	0.86	
	1.76	0.97	88.38	
Anachis_fenneli	0.31	0.00	0.85	
	1.21	0.96	89.34	
Ophioplocus_januarii	0.27	0.00	0.80	
	0.65	0.90	90.24	

Groups Montao_de_Trigo & Lamberto
Average dissimilarity = 87.23

	Group Montao_de_Trigo	Group Lamberto		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Bittiolum_varium	0.02	2.58	16.36	
4.96	18.76	18.76		
Hyale_niger	2.02	0.01	12.84	
4.74	14.72	33.47		
Stenothoe_sp	1.93	0.01	12.27	
3.95	14.07	47.54		
Caprella_scaura	0.97	0.01	5.97	
2.31	6.84	54.39		
Paracerceis_sculpta	0.14	0.81	4.39	
1.60	5.03	59.42		
Janaira_gracilis	0.86	0.27	4.27	
1.63	4.89	64.31		
Pinctada_imbricata	0.49	0.16	2.55	
1.50	2.92	67.23		
Hippolyte_obliquimanus	0.00	0.32	2.10	
1.24	2.41	69.65		
Gammaropsis_palmata	0.31	0.00	1.84	
1.45	2.10	71.75		
Ericthonius_brasiliensis	0.35	0.09	1.83	
1.42	2.09	73.84		
Cymadusa_filosa	0.34	0.19	1.80	
1.73	2.07	75.91		
Eulithidium_affine	0.02	0.29	1.66	
1.70	1.91	77.82		
Ophiactis_lymani	0.23	0.00	1.41	
2.32	1.61	79.43		

Mitrela_dichroa	0.00	0.20	1.26	
1.29	1.45	80.88		
Alaba_incerta	0.22	0.01	1.24	
2.13	1.42	82.30		
Chondrochelia_dubia	0.16	0.27	1.09	
1.08	1.25	83.55		
Perna_perna	0.13	0.00	0.94	
0.85	1.07	84.62		
Anachis_fenneli	0.16	0.00	0.93	
1.46	1.07	85.69		
Ampithoe_ramondi	0.13	0.00	0.90	
1.97	1.03	86.72		
Batea_catharinensis	0.12	0.00	0.82	
1.42	0.94	87.66		
Cymodoce_brasiliensis	0.11	0.00	0.75	
0.67	0.86	88.52		
Rissoella_ornata	0.09	0.00	0.63	
1.36	0.72	89.23		
Costoanachis_sertulariarum	0.01	0.10	0.57	
1.84	0.65	89.88		
Phyllaplysia_engeli	0.03	0.10	0.55	
1.14	0.63	90.52		

Groups Figueira & Lamberto
Average dissimilarity = 78.75

	Group Figueira	Group Lamberto		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Bittiolum_varium	0.29	2.58	26.78	3.72
	34.00	34.00		
Hyale_niger	0.86	0.01	9.28	1.46
	11.78	45.78		
Paracerceis_sculpta	0.06	0.81	9.17	1.69
	11.64	57.42		
Janaira_gracilis	0.29	0.27	3.29	1.30
	4.18	61.60		
Ophiothela_mirabilis	0.31	0.08	2.88	0.88
	3.65	65.26		
Eulithidium_affine	0.05	0.29	2.77	1.78
	3.52	68.78		
Chondrochelia_dubia	0.02	0.27	2.70	1.35
	3.43	72.21		
Hippolyte_obliquimanus	0.26	0.32	2.26	1.08
	2.87	75.07		
Mitrela_dichroa	0.01	0.20	2.16	1.28
	2.74	77.82		
Cymadusa_filosa	0.12	0.19	2.05	1.05
	2.61	80.42		

Pinctada_imbricata	0.00	0.16	1.67	1.37
	2.11	82.54		
Phyllaplysia_engeli	0.00	0.10	1.17	1.26
	1.48	84.02		
Costoanachis_sertulariarum	0.01	0.10	0.98	1.97
	1.24	85.26		
Ericthonius_brasiliensis	0.01	0.09	0.93	1.47
	1.18	86.44		
Sphenia_fragilis	0.00	0.08	0.79	0.65
	1.00	87.45		
Parvanachis_obesa	0.00	0.08	0.79	0.55
	1.00	88.45		
Musculus_lateralis	0.00	0.07	0.76	0.90
	0.97	89.41		
Amphipholis_squamata	0.00	0.06	0.65	0.87
	0.82	90.23		

Groups Baleia & Lamberto
Average dissimilarity = 82.41

	Group Baleia	Group Lamberto		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Bittiolum_varium	0.10	2.58	13.08	3.80
15.88	15.88			
Hyale_niger	2.44	0.01	12.92	8.07
15.68	31.55			
Stenothoe_sp	1.56	0.01	8.40	1.94
10.19	41.74			
Janaira_gracilis	1.45	0.27	6.05	2.40
7.34	49.08			
Aora_spinicornis	0.88	0.00	4.42	2.49
5.37	54.45			
Paracerceis_sculpta	0.00	0.81	4.33	1.82
5.25	59.70			
Ericthonius_brasiliensis	0.63	0.09	2.84	1.34
3.45	63.15			
Pinctada_imbricata	0.70	0.16	2.80	2.17
3.39	66.55			
Gammaropsis_palmata	0.48	0.00	2.46	2.51
2.98	69.53			
Chondrochelia_dubia	0.70	0.27	2.36	1.68
2.86	72.39			
Cymadusa_filosa	0.52	0.19	2.01	1.89
2.44	74.83			
Hourstonius_wakabarae	0.39	0.00	1.91	1.20
2.32	77.15			
Batea_catharinensis	0.38	0.00	1.78	0.61
2.16	79.31			

Hippolyte_obliquimanus	0.08	0.32	1.47	1.05	1.78	81.09
Eulithidium_affine	0.50	0.29	1.41	1.11	1.71	82.80
Leucothoe_spinicarpa	0.20	0.00	1.07	0.64	1.29	84.09
Ophiactis_lymani	0.18	0.00	0.90	2.41	1.09	85.19
Mitrela_dichroa	0.13	0.20	0.86	1.19	1.05	86.23
Costoanachis_sertulariarum	0.24	0.10	0.82	1.78	1.00	87.23
Paracaprella_dubiaski	0.12	0.00	0.60	0.81	0.72	87.95
Sphenia_fragilis	0.09	0.08	0.59	1.68	0.72	88.67
Caprella_equilibra	0.12	0.00	0.55	0.56	0.67	89.33
Elasmopus_pectenicrus	0.11	0.01	0.55	1.61	0.66	90.00
Arcidae_morfo2	0.10	0.00	0.54	2.76	0.65	90.65

Groups Conchas & Lamberto
Average dissimilarity = 82.62

	Group Conchas	Group Lamberto				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bittiolum_varium	0.46	2.58	10.72	3.43	12.97	12.97
Janaira_gracilis	1.53	0.27	6.37	1.96	7.71	20.68
Hyale_niger	1.27	0.01	6.15	3.87	7.44	28.12
Stenothoe_sp	1.27	0.01	5.83	1.56	7.06	35.18
Hyale_macrodactyla	1.07	0.00	5.10	1.59	6.18	41.36
Podocerus_fissipes	1.00	0.00	4.99	4.00	6.03	47.39
Chondrochelia_dubia	1.10	0.27	4.48	1.71	5.42	52.81
Paracerceis_sculpta	0.00	0.81	4.25	1.71	5.15	57.96
Sunampithoe_pelagica	0.71	0.00	3.64	5.65	4.40	62.36
Elasmopus_pectenicrus	0.73	0.01	3.50	2.47	4.24	66.60

Mitrela_dichroa	0.65	0.20	2.37	1.66	2.87	69.47
Pinctada_imbricata	0.58	0.16	2.26	2.24	2.74	72.21
Pachycheles_laevidactylus	0.39	0.00	1.92	1.46	2.33	74.54
Epialtus_bituberculatus	0.32	0.02	1.60	1.61	1.94	76.48
Hippolyte_obliquimanus	0.07	0.32	1.52	1.08	1.84	78.32
Hourstonius_wakabarae	0.33	0.00	1.46	0.89	1.77	80.09
Leucothoe_spinicarpa	0.21	0.00	1.34	0.76	1.63	81.72
Jassa_slateryi	0.27	0.00	1.28	0.88	1.55	83.27
Monocorophium_acherusicum	0.19	0.04	0.99	1.20	1.20	84.47
Cymadusa_filosa	0.10	0.19	0.99	0.94	1.19	85.66
Eulithidium_affine	0.13	0.29	0.98	1.48	1.18	86.85
Modiolus_carvalhoi	0.22	0.03	0.97	1.21	1.18	88.02
Epialtus_brasiliensis	0.14	0.00	0.67	0.96	0.81	88.83
Alaba_incerta	0.13	0.01	0.58	1.83	0.70	89.54
Fissurella_rosea	0.10	0.00	0.55	1.42	0.67	90.21

Groups ESEC_Alcatrazes & Palmas
Average dissimilarity = 82.59

	Group ESEC_Alcatrazes	Group Palmas			
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Hyale_niger	2.34	0.03	9.78	3.59	11.85	11.85
Stenothoe_sp	1.85	0.23	6.86	3.21	8.31	20.15
Podocerus_fissipes	1.38	0.03	5.68	1.73	6.88	27.03
Ampithoe_ramondi	1.13	0.00	4.87	1.55	5.90	32.93
Pinctada_imbricata	0.09	1.23	4.38	2.56	5.30	38.23
Ophiothela_mirabilis	0.00	0.93	4.25	1.74	5.14	43.37

Bittiolum_varium		0.00	1.09	4.16
2.05	5.04		48.41	
Ophioplocus_januarii		0.00	0.95	3.68
1.60	4.45		52.86	
Janaira_gracilis		0.98	0.12	3.53
2.06	4.27		57.13	
Ericthonius_brasiliensis		1.50	0.88	3.35
1.21	4.06		61.19	
Alvania_auberiana		0.00	0.76	2.67
1.33	3.23		64.42	
Cymadusa_filosa		0.68	0.10	2.56
1.51	3.10		67.52	
Photis_sarae		0.06	0.54	2.34
1.00	2.83		70.35	
Lysianassa_teminino		0.00	0.60	2.27
1.22	2.74		73.09	
Chondrochelia_dubia		0.83	0.37	2.20
1.24	2.67		75.76	
Rissoella_ornata		0.56	0.30	1.95
1.25	2.36		78.12	
Caecum_brasilicum		0.00	0.50	1.75
1.36	2.12		80.24	
Cymadusa_tartarugae		0.00	0.29	1.15
1.42	1.39		81.63	
Eulimidae_sp4		0.00	0.33	1.02
0.56	1.23		82.87	
Musculus_lateralis		0.00	0.25	0.93
1.78	1.13		84.00	
Paracerceis_sculpta		0.02	0.20	0.85
0.94	1.03		85.03	
Caprella_scaura		0.20	0.16	0.80
1.22	0.97		86.00	
Costoanachis_sparsa		0.00	0.16	0.65
1.31	0.79		86.79	
Astyris_lunata		0.00	0.17	0.60
1.40	0.73		87.52	
Anachis_fenneli		0.14	0.00	0.57
0.62	0.70		88.21	
Mithraculus_forceps		0.01	0.17	0.57
0.97	0.69		88.91	
Omalacantha_bicornuta		0.02	0.12	0.57
0.74	0.69		89.60	
Carpias_minutus		0.13	0.00	0.56
1.42	0.67		90.27	

Groups Refugio_Alcatrazes & Palmas
Average dissimilarity = 77.35

	Group Refugio_Alcatrazes	Group Palmas

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ericthonius_brasiliensis	3.23	0.88	6.24	2.85	8.07	8.07
Stenothoe_sp	2.40	0.23	5.65	5.01	7.30	15.37
Aora_spinicornis	2.10	0.00	5.42	4.58	7.00	22.37
Janaira_gracilis	2.01	0.12	4.95	2.53	6.40	28.77
Photis_sarae	2.37	0.54	4.67	2.65	6.03	34.80
Caprella_scaura	2.06	0.16	4.65	1.81	6.02	40.82
Alaba_incerta	1.66	0.09	4.17	4.44	5.39	46.21
Ampithoe_ramondi	1.25	0.00	3.06	2.06	3.96	50.17
Rissoella_ornata	1.31	0.30	2.68	2.09	3.46	53.63
Ophiothela_mirabilis	0.00	0.93	2.58	1.72	3.34	56.97
Assiminea_sp.	0.93	0.00	2.39	5.49	3.09	60.05
Ophioplocus_januarii	0.27	0.95	2.10	1.44	2.72	62.77
Bittiolum_varium	0.27	1.09	2.08	1.31	2.69	65.46
Hyale_niger	0.73	0.03	1.95	1.35	2.52	67.98
Alvania_auberiana	0.00	0.76	1.78	1.25	2.30	70.28
Pinctada_imbricata	0.70	1.23	1.63	1.21	2.11	72.38
Lysianassa_teminino	0.00	0.60	1.47	1.15	1.90	74.28
Astyris_lunata	0.56	0.17	1.31	1.28	1.69	75.98
Paracerceis_sculpta	0.65	0.20	1.20	2.05	1.56	77.53
Caecum_brasilicum	0.00	0.50	1.17	1.22	1.51	79.04
Chondrochelia_dubia	0.71	0.37	1.08	1.11	1.39	80.43
Cymadusa_filosa	0.43	0.10	0.98	1.53	1.27	81.70
Pseudaeginella_montoucheti	0.39	0.05	0.86	1.13	1.12	82.82
Musculus_lateralis	0.50	0.25	0.84	1.20	1.08	83.90

Carpias_minutus		0.30	0.00	0.81
	1.05		1.05	84.95
Cymadusa_tartarugae		0.00	0.29	0.74
	1.32		0.96	85.90
Anachis_fenneli		0.31	0.00	0.73
	1.17		0.95	86.85
Eulimidae_sp4		0.00	0.33	0.71
	0.55		0.92	87.77
Arcidae_morfo2		0.22	0.00	0.51
	0.91		0.67	88.44
Phtisica_verae		0.24	0.00	0.51
	0.55		0.65	89.09
Mithraculus_forceps		0.10	0.17	0.48
	1.09		0.63	89.72
Costoanachis_sparsa		0.00	0.16	0.42
	1.29		0.54	90.25

Groups Montao_de_Trigo & Palmas
Average dissimilarity = 80.40

	Group Montao_de_Trigo	Group Palmas		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Hyale_niger	2.02	0.03	9.56	
3.08	11.89	11.89		
Stenothoe_sp	1.93	0.23	8.15	
2.48	10.14	22.03		
Bittiolum_varium	0.02	1.09	4.65	
2.04	5.79	27.82		
Ophiothela_mirabilis	0.14	0.93	4.32	
1.58	5.37	33.18		
Ophioplocus_januarii	0.00	0.95	4.19	
1.58	5.21	38.39		
Caprella_scaura	0.97	0.16	3.91	
1.61	4.86	43.25		
Pinctada_imbricata	0.49	1.23	3.59	
1.52	4.47	47.72		
Janaira_gracilis	0.86	0.12	3.47	
1.66	4.31	52.03		
Alvania_auberiana	0.02	0.76	2.90	
1.29	3.61	55.65		
Photis_sarae	0.02	0.54	2.85	
0.98	3.54	59.19		
Lysianassa_teminino	0.00	0.60	2.57	
1.21	3.20	62.39		
Ericthonius_brasiliensis	0.35	0.88	2.20	
1.44	2.74	65.13		
Caecum_brasilicum	0.00	0.50	1.97	
1.40	2.45	67.57		

Cymadusa_filosa	0.34	0.10	1.38	
1.42	1.72	69.29		
Gammaropsis_palmata	0.31	0.12	1.37	
1.35	1.70	71.00		
Cymadusa_tartarugae	0.00	0.29	1.31	
1.43	1.63	72.62		
Chondrochelia_dubia	0.16	0.37	1.26	
2.41	1.56	74.19		
Rissoella_ornata	0.09	0.30	1.21	
1.50	1.50	75.69		
Eulimidae_sp4	0.00	0.33	1.12	
0.56	1.39	77.08		
Musculus_lateralis	0.01	0.25	1.01	
1.69	1.26	78.34		
Paracerceis_sculpta	0.14	0.20	0.94	
1.05	1.17	79.51		
Ophiactis_lymani	0.23	0.13	0.92	
1.73	1.14	80.65		
Anachis_fenneli	0.16	0.00	0.71	
1.34	0.89	81.54		
Costoanachis_sparsa	0.02	0.16	0.71	
1.36	0.88	82.42		
Omalacantha_bicornuta	0.00	0.12	0.69	
0.72	0.86	83.28		
Perna_perna	0.13	0.00	0.69	
0.83	0.85	84.13		
Astyris_lunata	0.00	0.17	0.68	
1.41	0.85	84.97		
Alaba_incerta	0.22	0.09	0.67	
1.17	0.83	85.80		
Ampithoe_ramondi	0.13	0.00	0.66	
1.81	0.83	86.63		
Mithraculus_forceps	0.00	0.17	0.66	
0.99	0.83	87.46		
Batea_catharinensis	0.12	0.00	0.60	
1.35	0.75	88.20		
Leucothoe_spinicarpa	0.02	0.15	0.56	
1.09	0.70	88.90		
Cymodoce_brasiliensis	0.11	0.00	0.55	
0.66	0.69	89.59		
Caecum_ryssotitum	0.00	0.15	0.55	
0.96	0.69	90.28		

Groups Figueira & Palmas
Average dissimilarity = 87.69

	Group Figueira	Group Palmas		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		

Pinctada_imbricata	0.00	1.23	8.16	2.92	9.30	9.30
Ophioplocus_januarii	0.00	0.95	6.24	1.58	7.12	16.42
Ophiothela_mirabilis	0.31	0.93	6.09	1.41	6.95	23.37
Hyale_niger	0.86	0.03	5.95	1.21	6.79	30.16
Ericthonius_brasiliensis	0.01	0.88	5.64	3.45	6.43	36.59
Bittiolum_varium	0.29	1.09	5.32	1.56	6.07	42.66
Photis_sarae	0.00	0.54	4.78	0.92	5.45	48.11
Alvania_auberiana	0.00	0.76	4.19	1.44	4.78	52.89
Lysianassa_teminino	0.01	0.60	3.72	1.20	4.24	57.13
Caecum_brasilicum	0.00	0.50	2.79	1.64	3.18	60.31
Chondrochelia_dubia	0.02	0.37	2.13	1.80	2.43	62.74
Hippolyte_obliquimanus	0.26	0.00	2.02	1.79	2.31	65.05
Cymadusa_tartarugae	0.00	0.29	1.95	1.57	2.22	67.27
Stenothoe_sp	0.01	0.23	1.56	1.56	1.78	69.05
Paracerceis_sculpta	0.06	0.20	1.56	0.83	1.78	70.83
Musculus_lateralis	0.00	0.25	1.54	2.07	1.75	72.58
Rissoella_ornata	0.00	0.30	1.47	0.94	1.67	74.26
Eulimidae_sp4	0.00	0.33	1.46	0.56	1.66	75.92
Janaira_gracilis	0.29	0.12	1.41	1.29	1.61	77.53
Cymadusa_filosa	0.12	0.10	1.21	1.32	1.38	78.91
Omalacantha_bicornuta	0.00	0.12	1.14	0.73	1.30	80.22
Costoanachis_sparsa	0.00	0.16	1.10	1.24	1.25	81.47
Caprella_scaura	0.01	0.16	1.00	0.99	1.14	82.60
Astyris_lunata	0.01	0.17	0.94	1.53	1.07	83.68
Mithraculus_forceps	0.00	0.17	0.92	1.06	1.05	84.73

Leucothoe_spinicarpa		0.01	0.15	0.81	1.14	
0.92	85.66					
Caecum_ryssotitum		0.00	0.15	0.74	0.96	
0.85	86.51					
Parvanachis_obesa		0.00	0.10	0.74	0.94	
0.85	87.35					
Gammaropsis_palmata		0.01	0.12	0.73	0.63	
0.83	88.18					
Ophiactis_lymani		0.02	0.13	0.71	0.95	
0.81	88.99					
Musculus_viator		0.00	0.15	0.64	0.56	
0.73	89.72					
Podochela_algicola		0.00	0.08	0.63	1.46	
0.72	90.44					

Groups Baleia & Palmas
Average dissimilarity = 80.62

	Group Baleia	Group Palmas			
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	
	Contrib%	Cum.%			
Hyale_niger	2.44	0.03	10.00	4.23	
12.40	12.40				
Stenothoe_sp	1.56	0.23	5.69	1.60	
7.06	19.46				
Janaira_gracilis	1.45	0.12	5.30	3.09	
6.57	26.03				
Ophiothela_mirabilis	0.00	0.93	4.19	1.68	
5.19	31.23				
Bittiolum_varium	0.10	1.09	3.73	1.68	
4.63	35.85				
Ophioplocus_januarii	0.00	0.95	3.63	1.56	
4.50	40.35				
Aora_spinicornis	0.88	0.00	3.48	2.16	
4.32	44.67				
Alvania_auberiana	0.00	0.76	2.63	1.31	
3.26	47.93				
Photis_sarae	0.00	0.54	2.45	0.99	
3.04	50.97				
Pinctada_imbricata	0.70	1.23	2.44	1.40	
3.03	54.00				
Lysianassa_teminino	0.00	0.60	2.24	1.20	
2.77	56.77				
Eulithidium_affine	0.50	0.03	2.04	2.05	
2.53	59.30				
Ericthonius_brasiliensis	0.63	0.88	1.90	1.30	
2.36	61.66				
Cymadusa_filosa	0.52	0.10	1.77	1.82	
2.19	63.85				

Caecum_brasilicum	0.00	0.50	1.73	1.34	2.14	65.99
Gammaropsis_palmata	0.48	0.12	1.68	1.69	2.08	68.07
Chondrochelia_dubia	0.70	0.37	1.60	1.10	1.99	70.06
Hourstonius_wakabarae	0.39	0.02	1.46	1.11	1.82	71.88
Batea_catharinensis	0.38	0.00	1.42	0.59	1.76	73.64
Cymadusa_tartarugae	0.00	0.29	1.13	1.39	1.41	75.05
Costoanachis_sertulariarum	0.24	0.00	1.02	3.13	1.27	76.32
Eulimidae_sp4	0.00	0.33	1.00	0.56	1.25	77.56
Leucothoe_spinicarpa	0.20	0.15	0.98	0.88	1.21	78.78
Rissoella_ornata	0.00	0.30	0.97	0.92	1.21	79.98
Musculus_lateralis	0.00	0.25	0.92	1.74	1.14	81.12
Paracerceis_sculpta	0.00	0.20	0.89	0.90	1.10	82.22
Ophiactis_lymani	0.18	0.13	0.66	1.83	0.82	83.04
Costoanachis_sparsa	0.01	0.16	0.62	1.31	0.77	83.82
Mitrela_dichroa	0.13	0.00	0.60	0.89	0.74	84.56
Astyris_lunata	0.00	0.17	0.60	1.38	0.74	85.30
Caprella_scaura	0.04	0.16	0.59	1.07	0.73	86.03
Mithraculus_forceps	0.00	0.17	0.59	0.97	0.73	86.75
Omalacantha_bicornuta	0.00	0.12	0.58	0.71	0.72	87.47
Caecum_ryssotitum	0.04	0.15	0.52	1.28	0.64	88.11
Musculus_viator	0.02	0.15	0.48	0.64	0.60	88.71
Paracaprella_dubiaski	0.12	0.00	0.47	0.79	0.59	89.30
Caprella_equilibra	0.12	0.00	0.44	0.55	0.54	89.84
Parvanachis_obesa	0.05	0.10	0.42	1.08	0.52	90.36

Groups Conchas & Palmas

Average dissimilarity = 82.28

	Group Conchas	Group Palmas			
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Janaira_gracilis	1.53	0.12	5.24	1.70	6.36	6.36
Hyale_niger	1.27	0.03	4.79	2.74	5.83	12.19
Stenothoe_sp	1.27	0.23	4.36	1.75	5.30	17.49
Ophiothela_mirabilis	0.00	0.93	4.11	1.61	4.99	22.48
Hyale_macrodactyla	1.07	0.00	4.05	1.46	4.92	27.40
Podocerus_fissipes	1.00	0.03	3.83	2.81	4.65	32.06
Ophioplocus_januarii	0.00	0.95	3.56	1.52	4.33	36.38
Chondrochelia_dubia	1.10	0.37	3.30	1.39	4.01	40.39
Ericthonius_brasiliensis	0.08	0.88	2.98	2.13	3.63	44.02
Sunampithoe_pelagica	0.71	0.00	2.84	4.04	3.45	47.47
Elasmopus_pectenicrus	0.73	0.03	2.72	2.00	3.30	50.77
Mitrela_dichroa	0.65	0.00	2.64	2.56	3.21	53.98
Alvania_auberiana	0.04	0.76	2.49	1.24	3.02	57.00
Pinctada_imbricata	0.58	1.23	2.46	1.48	2.99	60.00
Bittiolum_varium	0.46	1.09	2.32	1.13	2.82	62.82
Photis_sarae	0.10	0.54	2.26	0.98	2.74	65.56
Lysianassa_teminino	0.00	0.60	2.20	1.18	2.67	68.23
Caecum_brasilicum	0.00	0.50	1.70	1.32	2.06	70.29
Pachycheles_laevidactylus	0.39	0.00	1.52	1.36	1.84	72.13
Epialtus_bituberculatus	0.32	0.06	1.19	1.32	1.45	73.59
Hourstonius_wakabarae	0.33	0.02	1.19	0.91	1.45	75.03
Cymadusa_tartarugae	0.00	0.29	1.11	1.37	1.35	76.39

Jassa_slateryi	0.27	0.00	1.02	0.86	1.24	77.63
Leucothoe_spinicarpa	0.21	0.15	1.01	0.92	1.23	78.86
Eulimidae_sp4	0.00	0.33	0.99	0.55	1.20	80.06
Rissoella_ornata	0.00	0.30	0.96	0.91	1.16	81.22
Musculus_lateralis	0.00	0.25	0.90	1.70	1.10	82.32
Paracerceis_sculpta	0.00	0.20	0.87	0.88	1.06	83.37
Monocorophium_acherusicum	0.19	0.00	0.84	1.17	1.02	84.40
Modiolus_carvalhoi	0.22	0.05	0.73	1.14	0.89	85.29
Costoanachis_sparsa	0.00	0.16	0.63	1.26	0.76	86.05
Astyris_lunata	0.00	0.17	0.58	1.35	0.71	86.77
Caprella_scaura	0.03	0.16	0.58	0.93	0.70	87.47
Mithraculus_forceps	0.00	0.17	0.57	0.96	0.70	88.17
Cymadusa_filosa	0.10	0.10	0.57	0.94	0.70	88.86
Omalacantha_bicornuta	0.00	0.12	0.57	0.70	0.69	89.55
Epialtus_brasiliensis	0.14	0.03	0.55	1.12	0.67	90.22

Groups Lamberto & Palmas
Average dissimilarity = 77.54

	Group Lamberto	Group Palmas				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bittiolum_varium	2.58	1.09	9.52	1.51	12.28	12.28
Ophiothela_mirabilis	0.08	0.93	5.61	1.49	7.23	19.51
Pinctada_imbricata	0.16	1.23	5.55	2.22	7.16	26.68
Ophioplocus_januarii	0.00	0.95	4.95	1.58	6.38	33.06
Ericthonius_brasiliensis	0.09	0.88	4.02	2.39	5.19	38.25
Paracerceis_sculpta	0.81	0.20	3.62	1.41	4.66	42.91

Photis_sarae	0.00	0.54	3.56	0.95	4.59	47.51
Alvania_auberiana	0.00	0.76	3.45	1.37	4.46	51.96
Lysianassa_teminino	0.01	0.60	3.00	1.20	3.87	55.83
Caecum_brasilicum	0.00	0.50	2.28	1.48	2.94	58.77
Hippolyte_obliquimanus	0.32	0.00	1.89	1.14	2.44	61.21
Cymadusa_tartarugae	0.00	0.29	1.55	1.47	1.99	63.20
Chondrochelia_dubia	0.27	0.37	1.53	1.48	1.97	65.17
Eulithidium_affine	0.29	0.03	1.50	1.51	1.93	67.10
Janaira_gracilis	0.27	0.12	1.44	1.06	1.85	68.95
Eulimidae_sp4	0.00	0.33	1.26	0.56	1.62	70.58
Rissoella_ornata	0.00	0.30	1.24	0.93	1.60	72.18
Stenothoe_sp	0.01	0.23	1.24	1.48	1.60	73.78
Cymadusa_filosa	0.19	0.10	1.20	0.94	1.54	75.32
Mitrela_dichroa	0.20	0.00	1.14	1.19	1.47	76.79
Musculus_lateralis	0.07	0.25	1.00	1.46	1.29	78.08
Omalacantha_bicornuta	0.00	0.12	0.85	0.72	1.10	79.18
Costoanachis_sparsa	0.06	0.16	0.81	1.18	1.04	80.22
Caprella_scaura	0.01	0.16	0.79	0.94	1.02	81.24
Astyris_lunata	0.01	0.17	0.78	1.47	1.00	82.24
Mithraculus_forceps	0.00	0.17	0.76	1.02	0.99	83.23
Parvanachis_obesa	0.08	0.10	0.73	1.08	0.95	84.18
Caecum_ryssotitum	0.04	0.15	0.69	1.40	0.89	85.06
Leucothoe_spinicarpa	0.00	0.15	0.69	1.10	0.88	85.95
Musculus_viator	0.02	0.15	0.62	0.67	0.80	86.75
Phyllaplysia_engeli	0.10	0.00	0.59	1.15	0.76	87.51

Ophiactis_lymani		0.00	0.13	0.56	0.83	
0.73	88.24					
Gammaropsis_palmata		0.00	0.12	0.56	0.56	
0.72	88.96					
Costoanachis_sertulariarum		0.10	0.00	0.54	1.81	
0.70	89.66					
Podochela_algicola		0.00	0.08	0.48	1.49	
0.62	90.28					

Groups ESEC_Alcatrazes & Buzios
Average dissimilarity = 48.84

	Group ESEC_Alcatrazes	Group Buzios		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Stenothoe_sp	1.85	1.47	5.83	
1.79	11.94	11.94		
Podocerus_fissipes	1.38	0.68	5.55	
1.60	11.37	23.31		
Hyale_niger	2.34	1.72	4.55	
1.05	9.31	32.61		
Ericthonius_brasiliensis	1.50	2.04	3.84	
1.99	7.86	40.47		
Ampithoe_ramondi	1.13	0.58	3.56	
1.18	7.29	47.77		
Chondrochelia_dubia	0.83	0.09	3.36	
2.35	6.87	54.64		
Janaira_gracilis	0.98	1.11	2.99	
1.39	6.11	60.75		
Aora_spinicornis	0.08	0.75	2.81	
2.21	5.75	66.50		
Batea_catharinensis	0.00	0.42	2.31	
0.70	4.72	71.22		
Rissoella_ornata	0.56	0.06	2.20	
1.36	4.51	75.74		
Cymadusa_filosa	0.68	0.28	2.11	
1.35	4.31	80.05		
Jassa_slateryi	0.00	0.46	1.70	
1.16	3.48	83.53		
Caprella_scaura	0.20	0.42	1.24	
1.24	2.53	86.06		
Alaba_incerta	0.12	0.24	0.76	
1.21	1.55	87.62		
Anachis_fenneli	0.14	0.02	0.61	
0.69	1.25	88.86		
Caprella_equilibra	0.00	0.18	0.60	
0.62	1.23	90.09		

Groups Refugio_Alcatrazes & Buzios

Average dissimilarity = 60.31

	Group Refugio_Alcatrazes		Group Buzios		
Species	Av.Abund		Av.Abund	Av.Diss	
	Diss/SD		Contrib%	Cum.%	
Photis_sarae	2.37		0.01	6.28	
	3.99		10.41	10.41	
Caprella_scaura	2.06		0.42	4.16	
	1.75		6.89	17.30	
Alaba_incerta	1.66		0.24	3.82	
	5.18		6.33	23.63	
Stenothoe_sp	2.40		1.47	3.78	
	1.28		6.26	29.89	
Aora_spinicornis	2.10		0.75	3.57	
	2.35		5.92	35.81	
Ericthonius_brasiliensis	3.23		2.04	3.39	
	1.19		5.62	41.43	
Rissoella_ornata	1.31		0.06	3.28	
	4.74		5.43	46.87	
Janaira_gracilis	2.01		1.11	3.09	
	1.23		5.12	51.99	
Hyale_niger	0.73		1.72	3.03	
	1.69		5.03	57.02	
Assiminea_sp.	0.93		0.01	2.43	
	5.70		4.03	61.05	
Ampithoe_ramondi	1.25		0.58	2.09	
	1.33		3.47	64.52	
Chondrochelia_dubia	0.71		0.09	1.67	
	1.87		2.77	67.29	
Podocerus_fissipes	0.00		0.68	1.57	
	0.63		2.60	69.89	
Pinctada_imbricata	0.70		0.07	1.56	
	2.65		2.59	72.47	
Paracerceis_sculpta	0.65		0.10	1.50	
	3.39		2.49	74.97	
Batea_catharinensis	0.00		0.42	1.31	
	0.70		2.18	77.14	
Astyris_lunata	0.56		0.00	1.29	
	0.95		2.14	79.28	
Musculus_lateralis	0.50		0.04	1.18	
	1.68		1.96	81.24	
Jassa_slateryi	0.04		0.46	1.08	
	1.14		1.79	83.03	
Pseudaeginella_montoucheti	0.39		0.01	0.92	
	1.13		1.52	84.56	
Cymadusa_filosa	0.43		0.28	0.76	
	1.42		1.26	85.81	
Anachis_fenneli	0.31		0.02	0.72	
	1.20		1.19	87.00	

Carpias_minutus		0.30	0.09	0.70
	1.05		1.17	88.17
Ophioplocus_januarii		0.27	0.01	0.69
	0.66		1.15	89.32
Caprella_equilibra		0.13	0.18	0.55
	0.81		0.92	90.24

Groups Montao_de_Trigo & Buzios
Average dissimilarity = 53.00

	Group Montao_de_Trigo		Group Buzios	
Species	Av.Abund		Av.Abund	Av.Diss
	Diss/SD		Contrib%	Cum.%
Ericthonius_brasiliensis		0.35	2.04	7.66
2.52	14.46		14.46	
Stenothoe_sp		1.93	1.47	6.86
1.45	12.95		27.41	
Hyale_niger		2.02	1.72	4.89
1.16	9.24		36.64	
Janaira_gracilis		0.86	1.11	3.47
1.30	6.55		43.19	
Aora_spinicornis		0.08	0.75	3.19
2.27	6.03		49.22	
Caprella_scaura		0.97	0.42	2.82
1.34	5.32		54.54	
Podocerus_fissipes		0.03	0.68	2.53
0.64	4.77		59.31	
Batea_catharinensis		0.12	0.42	2.49
0.68	4.70		64.01	
Ampithoe_ramondi		0.13	0.58	2.18
1.83	4.11		68.12	
Pinctada_imbricata		0.49	0.07	2.14
1.56	4.04		72.16	
Jassa_slateryi		0.01	0.46	1.86
1.14	3.51		75.68	
Gammaropsis_palmata		0.31	0.07	1.22
1.33	2.30		77.98	
Ophiactis_lymani		0.23	0.01	1.05
1.87	1.98		79.96	
Cymadusa_filosa		0.34	0.28	0.96
1.17	1.81		81.78	
Alaba_incerta		0.22	0.24	0.81
1.24	1.53		83.30	
Caprella_equilibra		0.02	0.18	0.70
0.70	1.32		84.62	
Chondrochelia_dubia		0.16	0.09	0.67
1.67	1.26		85.88	
Anachis_fenneli		0.16	0.02	0.63
1.26	1.19		87.08	

Paracerceis_sculpta	0.14	0.10	0.61	
1.11	1.15	88.23		
Ophiothela_mirabilis	0.14	0.02	0.60	
2.11	1.13	89.36		
Cymodoce_brasiliensis	0.11	0.00	0.58	
0.66	1.09	90.44		

Groups Figueira & Buzios
Average dissimilarity = 81.90

	Group Figueira	Group Buzios		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Ericthonius_brasiliensis	0.01	2.04	14.35	4.32
17.52	17.52			
Stenothoe_sp	0.01	1.47	8.64	1.19
10.54	28.06			
Hyale_niger	0.86	1.72	8.23	1.42
10.04	38.11			
Janaira_gracilis	0.29	1.11	6.02	1.97
7.35	45.46			
Aora_spinicornis	0.00	0.75	5.60	2.67
6.84	52.29			
Batea_catharinensis	0.00	0.42	5.17	0.65
6.31	58.60			
Ampithoe_ramondi	0.03	0.58	3.55	1.70
4.34	62.94			
Caprella_scaura	0.01	0.42	3.55	1.51
4.34	67.28			
Podocerus_fissipes	0.00	0.68	3.49	0.66
4.26	71.54			
Jassa_slateryi	0.00	0.46	2.71	1.21
3.30	74.85			
Ophiothela_mirabilis	0.31	0.02	2.33	1.07
2.84	77.69			
Hippolyte_obliquimanus	0.26	0.00	2.17	1.69
2.65	80.34			
Alaba_incerta	0.00	0.24	2.16	1.30
2.64	82.98			
Bittiolum_varium	0.29	0.08	1.91	1.04
2.33	85.31			
Cymadusa_filosa	0.12	0.28	1.40	1.41
1.71	87.02			
Phtisica_marina	0.00	0.08	0.93	0.66
1.14	88.16			
Caprella_equilibra	0.00	0.18	0.90	0.63
1.10	89.27			
Pinctada_imbricata	0.00	0.07	0.82	0.78
1.01	90.27			

Groups Baleia & Buzios
Average dissimilarity = 57.09

	Group Baleia	Group Buzios		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Ericthonius_brasiliensis	0.63	2.04	5.85	2.12
10.25	10.25			
Stenothoe_sp	1.56	1.47	5.60	1.46
9.80	20.05			
Hyale_niger	2.44	1.72	4.47	1.02
7.83	27.88			
Janaira_gracilis	1.45	1.11	3.39	1.21
5.93	33.81			
Chondrochelia_dubia	0.70	0.09	2.70	2.52
4.72	38.54			
Batea_catharinensis	0.38	0.42	2.60	0.82
4.55	43.09			
Pinctada_imbricata	0.70	0.07	2.53	2.93
4.42	47.51			
Podocerus_fissipes	0.00	0.68	2.28	0.64
4.00	51.51			
Ampithoe_ramondi	0.00	0.58	2.23	1.69
3.91	55.42			
Eulithidium_affine	0.50	0.00	2.21	2.32
3.88	59.30			
Aora_spinicornis	0.88	0.75	1.77	1.16
3.11	62.41			
Caprella_scaura	0.04	0.42	1.70	1.50
2.98	65.38			
Jassa_slateryi	0.00	0.46	1.68	1.15
2.94	68.32			
Gammaropsis_palmata	0.48	0.07	1.64	1.93
2.87	71.19			
Hourstonius_wakabarae	0.39	0.03	1.49	1.09
2.61	73.81			
Cymadusa_filosa	0.52	0.28	1.15	1.29
2.01	75.82			
Alaba_incerta	0.00	0.24	1.09	1.35
1.92	77.74			
Costoanachis_sertulariarum	0.24	0.00	1.06	3.18
1.86	79.60			
Leucothoe_spinicarpa	0.20	0.00	0.86	0.64
1.51	81.11			
Caprella_equilibra	0.12	0.18	0.85	0.84
1.48	82.60			
Ophiactis_lymani	0.18	0.01	0.69	1.90
1.21	83.80			

Mitrela_dichroa	0.13	0.00	0.62	0.89	1.09	84.89
Paracaprella_dubiaski	0.12	0.00	0.49	0.79	0.86	85.75
Bittiolum_varium	0.10	0.08	0.48	1.09	0.84	86.59
Paracerceis_sculpta	0.00	0.10	0.47	1.20	0.82	87.42
Elasmopus_pectenicrus	0.11	0.01	0.45	1.55	0.79	88.21
Arcidae_morfo2	0.10	0.00	0.43	2.47	0.76	88.97
Phtisica_marina	0.00	0.08	0.41	0.69	0.72	89.69
Sphenia_fragilis	0.09	0.00	0.39	1.54	0.68	90.37

Groups Conchas & Buzios
Average dissimilarity = 73.85

	Group Conchas	Group Buzios				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ericthonius_brasiliensis	0.08	2.04	7.74	2.72	10.49	10.49
Stenothoe_sp	1.27	1.47	5.36	1.52	7.25	17.74
Chondrochelia_dubia	1.10	0.09	4.33	1.83	5.86	23.60
Podocerus_fissipes	1.00	0.68	4.28	2.77	5.80	29.40
Janaira_gracilis	1.53	1.11	4.22	1.32	5.71	35.11
Hyale_macrodactyla	1.07	0.00	4.19	1.48	5.67	40.78
Hyale_niger	1.27	1.72	3.95	1.43	5.35	46.12
Aora_spinicornis	0.00	0.75	3.04	2.40	4.12	50.25
Sunampithoe_pelagica	0.71	0.00	2.94	4.16	3.99	54.23
Elasmopus_pectenicrus	0.73	0.01	2.88	2.21	3.90	58.14
Mitrela_dichroa	0.65	0.00	2.74	2.59	3.71	61.84
Batea_catharinensis	0.00	0.42	2.23	0.67	3.02	64.87
Ampithoe_ramondi	0.00	0.58	2.19	1.64	2.97	67.83

Pinctada_imbricata	0.58	0.07	2.08	5.26	2.81	70.65
Caprella_scaura	0.03	0.42	1.75	1.43	2.36	73.01
Bittiolum_varium	0.46	0.08	1.72	1.59	2.33	75.34
Jassa_slateryi	0.27	0.46	1.67	1.27	2.26	77.60
Pachycheles_laevidactylus	0.39	0.00	1.57	1.37	2.12	79.72
Epialtus_bituberculatus	0.32	0.00	1.34	1.46	1.81	81.53
Hourstonius_wakabarae	0.33	0.03	1.23	0.93	1.67	83.20
Leucothoe_spinicarpa	0.21	0.00	1.04	0.77	1.41	84.61
Cymadusa_filosa	0.10	0.28	0.90	1.32	1.22	85.83
Monocorophium_acherusicum	0.19	0.00	0.87	1.17	1.18	87.01
Modiolus_carvalhoi	0.22	0.00	0.87	1.20	1.17	88.19
Alaba_incerta	0.13	0.24	0.76	1.00	1.03	89.21
Eulithidium_affine	0.13	0.00	0.59	1.26	0.79	90.01

Groups Lamberto & Buzios
Average dissimilarity = 90.63

	Group Lamberto	Group Buzios				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bittiolum_varium	2.58	0.08	15.05	3.03	16.60	16.60
Ericthonius_brasiliensis	0.09	2.04	10.78	3.21	11.90	28.50
Hyale_niger	0.01	1.72	9.24	2.13	10.20	38.70
Stenothoe_sp	0.01	1.47	7.08	1.16	7.81	46.51
Janaira_gracilis	0.27	1.11	4.94	1.67	5.45	51.96
Aora_spinicornis	0.00	0.75	4.34	2.58	4.79	56.75
Paracerceis_sculpta	0.81	0.10	4.31	1.48	4.75	61.50
Batea_catharinensis	0.00	0.42	3.57	0.66	3.93	65.44

Ampithoe_ramondi	0.00	0.58	3.01	1.75	3.33	68.76
Podocerus_fissipes	0.00	0.68	2.94	0.65	3.24	72.01
Caprella_scaura	0.01	0.42	2.69	1.56	2.97	74.98
Jassa_slateryi	0.00	0.46	2.22	1.18	2.45	77.43
Hippolyte_obliquimanus	0.32	0.00	1.99	1.14	2.19	79.62
Eulithidium_affine	0.29	0.00	1.67	1.71	1.84	81.46
Alaba_incerta	0.01	0.24	1.52	1.28	1.68	83.14
Cymadusa_filosa	0.19	0.28	1.45	1.37	1.60	84.74
Chondrochelia_dubia	0.27	0.09	1.37	1.12	1.51	86.25
Mitrela_dichroa	0.20	0.00	1.19	1.20	1.32	87.57
Caprella_equilibra	0.00	0.18	0.76	0.62	0.84	88.41
Pinctada_imbricata	0.16	0.07	0.73	1.21	0.81	89.22
Phtisica_marina	0.00	0.08	0.65	0.67	0.71	89.93
Phyllaplysia_engeli	0.10	0.00	0.58	1.11	0.64	90.57

Groups Palmas & Buzios
Average dissimilarity = 83.94

	Group Palmas	Group Buzios			
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Hyale_niger	0.03	1.72	7.09	1.84	8.44	8.44
Ericthonius_brasiliensis	0.88	2.04	5.66	1.71	6.74	15.18
Stenothoe_sp	0.23	1.47	5.17	1.10	6.16	21.34
Pinctada_imbricata	1.23	0.07	4.73	2.47	5.63	26.98
Ophiothela_mirabilis	0.93	0.02	4.59	1.52	5.47	32.44
Bittiolum_varium	1.09	0.08	4.12	1.73	4.90	37.35
Janaira_gracilis	0.12	1.11	4.01	1.54	4.77	42.12

Ophioplocus_januarii	0.95	0.01	3.90	1.47	4.65
46.76					
Aora_spinicornis	0.00	0.75	3.30	2.26	3.93
50.70					
Alvania_auberiana	0.76	0.00	2.82	1.28	3.36
54.06					
Photis_sarae	0.54	0.01	2.69	0.94	3.21
57.27					
Batea_catharinensis	0.00	0.42	2.50	0.65	2.97
60.24					
Lysianassa_teminino	0.60	0.00	2.45	1.17	2.91
63.16					
Podocerus_fissipes	0.03	0.68	2.36	0.63	2.81
65.97					
Ampithoe_ramondi	0.00	0.58	2.35	1.61	2.80
68.77					
Caecum_brasilicum	0.50	0.01	1.85	1.32	2.20
70.98					
Jassa_slateryi	0.00	0.46	1.76	1.12	2.10
73.07					
Caprella_scaura	0.16	0.42	1.62	1.26	1.93
75.01					
Chondrochelia_dubia	0.37	0.09	1.32	1.51	1.57
76.58					
Cymadusa_tartarugae	0.29	0.00	1.24	1.37	1.48
78.06					
Cymadusa_filosa	0.10	0.28	1.12	1.51	1.34
79.40					
Rissoella_ornata	0.30	0.06	1.09	1.11	1.30
80.69					
Eulimidae_sp4	0.33	0.00	1.07	0.55	1.28
81.97					
Alaba_incerta	0.09	0.24	0.87	0.98	1.04
83.00					
Paracerceis_sculpta	0.20	0.10	0.83	0.95	0.99
83.99					
Musculus_lateralis	0.25	0.04	0.80	1.36	0.95
84.95					
Costoanachis_sparsa	0.16	0.00	0.70	1.23	0.84
85.78					
Gammaropsis_palmata	0.12	0.07	0.69	0.97	0.82
86.60					
Omalacantha_bicornuta	0.12	0.00	0.65	0.69	0.78
87.38					
Astyris_lunata	0.17	0.00	0.65	1.36	0.77
88.15					
Mithraculus_forceps	0.17	0.00	0.63	0.97	0.75
88.90					
Caprella_equilibra	0.00	0.18	0.62	0.61	0.74
89.64					

Leucothoe_spinicarpa	0.15	0.00	0.56	1.06	0.66
	90.30				

Groups ESEC_Alcatrazes & Mar_Casado
Average dissimilarity = 55.36

	Group ESEC_Alcatrazes	Group Mar_Casado		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Batea_catharinensis	0.00	1.60	7.23	
	2.59	13.06	13.06	
Stenothoe_sp	1.85	0.42	6.72	
	3.44	12.15	25.21	
Podocerus_fissipes	1.38	0.00	6.56	
	1.86	11.85	37.06	
Ampithoe_ramondi	1.13	0.05	5.33	
	1.52	9.63	46.70	
Ericthonius_brasiliensis	1.50	1.21	4.50	
	1.23	8.14	54.83	
Chondrochelia_dubia	0.83	0.24	3.06	
	1.64	5.52	60.36	
Janaira_gracilis	0.98	1.24	2.87	
	1.38	5.18	65.53	
Cymadusa_filosa	0.68	0.11	2.75	
	1.46	4.97	70.50	
Rissoella_ornata	0.56	0.00	2.67	
	1.61	4.83	75.33	
Hyale_niger	2.34	2.57	2.17	
	1.54	3.92	79.26	
Costoanachis_sertulariarum	0.00	0.34	1.50	
	1.78	2.71	81.97	
Elasmopus_pectenicrus	0.01	0.34	1.43	
	1.37	2.59	84.55	
Eulithidium_affine	0.00	0.25	1.13	
	1.06	2.05	86.60	
Caprella_scaura	0.20	0.00	0.98	
	1.19	1.77	88.37	
Anachis_fenneli	0.14	0.00	0.65	
	0.62	1.18	89.55	
Carpias_minutus	0.13	0.00	0.63	
	1.46	1.14	90.69	

Groups Refugio_Alcatrazes & Mar_Casado
Average dissimilarity = 77.96

	Group Refugio_Alcatrazes	Group Mar_Casado

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Photis_sarae	2.37	0.02	6.65	4.02	8.53	8.53
Ericthonius_brasiliensis	3.23	1.21	5.91	1.70	7.59	16.11
Aora_spinicornis	2.10	0.00	5.89	5.17	7.55	23.67
Stenothoe_sp	2.40	0.42	5.54	5.37	7.11	30.77
Caprella_scaura	2.06	0.00	5.39	2.04	6.92	37.69
Hyale_niger	0.73	2.57	5.12	4.12	6.56	44.25
Alaba_incerta	1.66	0.01	4.73	5.24	6.07	50.33
Batea_catharinensis	0.00	1.60	4.43	2.26	5.68	56.01
Rissoella_ornata	1.31	0.00	3.64	6.85	4.67	60.68
Ampithoe_ramondi	1.25	0.05	3.18	2.01	4.08	64.76
Janaira_gracilis	2.01	1.24	2.87	1.37	3.68	68.44
Assiminea_sp.	0.93	0.00	2.60	6.56	3.33	71.77
Paracerceis_sculpta	0.65	0.00	1.90	3.64	2.44	74.21
Pinctada_imbricata	0.70	0.00	1.89	3.17	2.42	76.63
Chondrochelia_dubia	0.71	0.24	1.53	1.61	1.96	78.59
Musculus_lateralis	0.50	0.00	1.38	1.85	1.77	80.36

Astyris_lunata		0.56		0.04	
1.37	1.04		1.76		
	82.12				
Pseudaeginella_montoucheti		0.39		0.00	
0.98	1.14		1.25		
	83.38				
Costoanachis_sertulariarum		0.00		0.34	
0.93	1.68		1.19		
	84.57				
Elasmopus_pectenicrus		0.00		0.34	
0.91	1.29		1.16		
	85.73				
Cymadusa_filosa		0.43		0.11	
0.90	1.18		1.15		
	86.88				
Carpias_minutus		0.30		0.00	
0.88	1.06		1.13		
	88.02				
Anachis_fenneli		0.31		0.00	
0.79	1.19		1.02		
	89.03				
Ophioplocus_januarii		0.27		0.00	
0.74	0.65		0.95		
	89.98				
Eulithidium_affine		0.00		0.25	
0.70	1.03		0.90		
	90.88				

Groups Montao_de_Trigo & Mar_Casado
Average dissimilarity = 58.84

	Group Montao_de_Trigo		Group Mar_Casado		
Species	Av.Abund		Av.Abund	Av.Diss	
	Diss/SD		Contrib%	Cum.%	
Stenothoe_sp	1.93		0.42	8.12	
	2.52		13.81	13.81	
Batea_catharinensis	0.12		1.60	7.70	
	2.34		13.09	26.90	
Ericthonius_brasiliensis	0.35		1.21	5.30	
	1.66		9.01	35.90	
Caprella_scaura	0.97		0.00	5.22	
	2.14		8.88	44.78	
Hyale_niger	2.02		2.57	4.18	
	2.00		7.10	51.88	
Janaira_gracilis	0.86		1.24	3.74	
	1.44		6.36	58.25	
Pinctada_imbricata	0.49		0.00	2.58	
	1.38		4.39	62.64	

Costoanachis_sertulariarum	0.01	0.34	1.70	
	1.69	2.89	65.53	
Elasmopus_pectenicrus	0.01	0.34	1.65	
	1.35	2.81	68.34	
Gammaropsis_palmata	0.31	0.00	1.61	
	1.38	2.73	71.07	
Cymadusa_filosa	0.34	0.11	1.40	
	1.41	2.38	73.45	
Eulithidium_affine	0.02	0.25	1.29	
	1.07	2.19	75.65	
Ophiactis_lymani	0.23	0.00	1.22	
	2.14	2.08	77.72	
Chondrochelia_dubia	0.16	0.24	1.13	
	1.12	1.92	79.65	
Alaba_incerta	0.22	0.01	1.09	
	1.88	1.86	81.51	
Paracerceis_sculpta	0.14	0.00	0.82	
	0.94	1.40	82.91	
Anachis_fenneli	0.16	0.00	0.82	
	1.39	1.39	84.30	
Perna_perna	0.13	0.00	0.80	
	0.84	1.36	85.66	
Ophiothela_mirabilis	0.14	0.00	0.79	
	2.21	1.34	87.00	
Cymodoce_brasiliensis	0.11	0.01	0.65	
	0.68	1.10	88.10	
Caprella_danilevskii	0.00	0.12	0.58	
	0.91	0.98	89.08	
Ampithoe_ramondi	0.13	0.05	0.57	
	1.23	0.97	90.05	

Groups Figueira & Mar_Casado
Average dissimilarity = 76.66

	Group Figueira	Group Mar_Casado		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Hyale_niger	0.86	2.57	16.79	1.74
	21.90	21.90		
Batea_catharinensis	0.00	1.60	13.44	3.08
	17.54	39.44		
Ericthonius_brasiliensis	0.01	1.21	8.98	1.37
	11.71	51.15		
Janaira_gracilis	0.29	1.24	7.89	1.87
	10.30	61.45		
Stenothoe_sp	0.01	0.42	4.50	1.09
	5.87	67.32		
Ophiothela_mirabilis	0.31	0.00	2.98	1.13
	3.89	71.21		

Costoanachis_sertulariarum	0.01	0.34	2.62	1.75
	3.42	74.63		
Hippolyte_obliquimanus	0.26	0.00	2.59	1.65
	3.38	78.00		
Elasmopus_pectenicrus	0.00	0.34	2.54	1.32
	3.31	81.32		
Bittiolum_varium	0.29	0.01	2.43	1.02
	3.17	84.49		
Eulithidium_affine	0.05	0.25	2.03	1.16
	2.64	87.13		
Chondrochelia_dubia	0.02	0.24	1.67	0.84
	2.18	89.30		
Cymadusa_filosa	0.12	0.11	1.01	0.88
	1.32	90.62		

Groups Baleia & Mar_Casado
Average dissimilarity = 50.47

	Group Baleia	Group Mar_Casado		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Batea_catharinensis	0.38	1.60	6.13	1.80
	12.14	12.14		
Stenothoe_sp	1.56	0.42	5.80	1.84
	11.50	23.64		
Ericthonius_brasiliensis	0.63	1.21	4.29	1.57
	8.49	32.13		
Aora_spinicornis	0.88	0.00	3.93	2.32
	7.80	39.92		
Pinctada_imbricata	0.70	0.00	3.17	3.27
	6.29	46.21		
Janaira_gracilis	1.45	1.24	2.98	1.23
	5.91	52.12		
Chondrochelia_dubia	0.70	0.24	2.42	1.69
	4.80	56.92		
Gammaropsis_palmata	0.48	0.00	2.18	2.36
	4.32	61.24		
Cymadusa_filosa	0.52	0.11	1.98	2.70
	3.92	65.16		
Hyale_niger	2.44	2.57	1.59	1.33
	3.16	68.31		
Hourstonius_wakabarae	0.39	0.10	1.50	1.04
	2.97	71.28		
Eulithidium_affine	0.50	0.25	1.47	1.03
	2.91	74.19		
Elasmopus_pectenicrus	0.11	0.34	1.25	1.40
	2.47	76.65		
Costoanachis_sertulariarum	0.24	0.34	0.95	2.07
	1.89	78.54		

Leucothoe_spinicarpa	0.20	0.01	0.95	0.65
	1.88	80.42		
Ophiactis_lymani	0.18	0.00	0.80	2.25
	1.59	82.01		
Mitrela_dichroa	0.13	0.04	0.60	0.85
	1.19	83.20		
Paracaprella_dubiaski	0.12	0.00	0.53	0.80
	1.05	84.25		
Caprella_danilevskii	0.00	0.12	0.50	0.91
	0.98	85.23		
Caprella_equilibra	0.12	0.00	0.49	0.55
	0.97	86.21		
Arcidae_morfo2	0.10	0.00	0.47	2.58
	0.94	87.15		
Monocorophium_acherusicum	0.00	0.11	0.46	0.86
	0.91	88.06		
Bittiolum_varium	0.10	0.01	0.43	0.95
	0.85	88.90		
Sphenia_fragilis	0.09	0.00	0.42	1.58
	0.84	89.74		
Ampithoe_marcuzzi	0.09	0.00	0.39	1.53
	0.77	90.52		

Groups Conchas & Mar_Casado
Average dissimilarity = 71.25

	Group Conchas	Group Mar_Casado		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Batea_catharinensis	0.00	1.60	6.99	2.30
	9.82	9.82		
Hyale_niger	1.27	2.57	6.30	1.65
	8.85	18.66		
Ericthonius_brasiliensis	0.08	1.21	4.89	1.32
	6.87	25.53		
Stenothoe_sp	1.27	0.42	4.60	2.05
	6.45	31.98		
Hyale_macrodactyla	1.07	0.00	4.56	1.52
	6.40	38.38		
Podocerus_fissipes	1.00	0.00	4.43	3.46
	6.22	44.60		
Chondrochelia_dubia	1.10	0.24	4.23	1.65
	5.93	50.53		
Janaira_gracilis	1.53	1.24	4.11	1.26
	5.78	56.31		
Sunampithoe_pelagica	0.71	0.00	3.22	4.62
	4.52	60.83		
Mitrela_dichroa	0.65	0.04	2.81	2.41
	3.95	64.78		

Pinctada_imbricata	0.58	0.00	2.69	3.69
	3.77	68.54		
Bittiolum_varium	0.46	0.01	2.23	1.81
	3.12	71.67		
Elasmopus_pectenicrus	0.73	0.34	2.18	1.38
	3.06	74.73		
Pachycheles_laevidactylus	0.39	0.00	1.71	1.40
	2.40	77.13		
Epialtus_bituberculatus	0.32	0.00	1.46	1.50
	2.05	79.18		
Costoanachis_sertulariarum	0.00	0.34	1.45	1.66
	2.04	81.22		
Hourstonius_wakabarae	0.33	0.10	1.37	1.07
	1.92	83.14		
Leucothoe_spinicarpa	0.21	0.01	1.16	0.77
	1.62	84.77		
Jassa_slateryi	0.27	0.00	1.15	0.87
	1.61	86.38		
Eulithidium_affine	0.13	0.25	1.07	1.60
	1.50	87.88		
Modiolus_carvalhoi	0.22	0.00	0.95	1.22
	1.33	89.21		
Monocorophium_acherusicum	0.19	0.11	0.83	1.13
	1.16	90.37		

Groups Lamberto & Mar_Casado
Average dissimilarity = 89.72

	Group Lamberto	Group Mar_Casado		
Species	Av.Abund	Av.Abund	Av.Diss	
	Diss/SD	Contrib%	Cum.%	
Hyale_niger	0.01	2.57	17.72	4.13
	19.75	19.75		
Bittiolum_varium	2.58	0.01	17.56	3.34
	19.57	39.32		
Batea_catharinensis	0.00	1.60	10.20	2.66
	11.37	50.69		
Ericthonius_brasiliensis	0.09	1.21	6.91	1.40
	7.70	58.40		
Janaira_gracilis	0.27	1.24	6.42	1.86
	7.15	65.55		
Paracerceis_sculpta	0.81	0.00	5.69	1.66
	6.34	71.89		
Stenothoe_sp	0.01	0.42	3.18	1.11
	3.55	75.44		
Hippolyte_obliquimanus	0.32	0.00	2.26	1.17
	2.52	77.96		
Elasmopus_pectenicrus	0.01	0.34	1.98	1.33
	2.20	80.16		

Chondrochelia_dubia	0.27	0.24	1.78	1.25
	1.99	82.15		
Costoanachis_sertulariarum	0.10	0.34	1.73	1.75
	1.93	84.08		
Eulithidium_affine	0.29	0.25	1.67	1.35
	1.86	85.94		
Cymadusa_filosa	0.19	0.11	1.20	0.91
	1.34	87.28		
Mitrela_dichroa	0.20	0.04	1.10	0.95
	1.23	88.51		
Pinctada_imbricata	0.16	0.00	1.02	1.25
	1.13	89.64		
Phyllaplysia_engeli	0.10	0.00	0.70	1.18
	0.78	90.42		

Groups Palmas & Mar_Casado
Average dissimilarity = 89.18

	Group Palmas	Group Mar_Casado		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Hyale_niger	0.03	2.57	12.88	3.25
	14.45	14.45		
Batea_catharinensis	0.00	1.60	7.63	2.20
	8.56	23.01		
Pinctada_imbricata	1.23	0.00	5.65	2.63
	6.33	29.34		
Ophiothela_mirabilis	0.93	0.00	5.22	1.54
	5.86	35.20		
Janaira_gracilis	0.12	1.24	5.21	1.88
	5.84	41.04		
Bittiolum_varium	1.09	0.01	4.87	1.99
	5.46	46.49		
Ericthonius_brasiliensis	0.88	1.21	4.43	1.46
	4.97	51.46		
Ophioplocus_januarii	0.95	0.00	4.37	1.52
	4.89	56.36		
Alvania_auberiana	0.76	0.00	3.09	1.33
	3.47	59.83		
Photis_sarae	0.54	0.02	3.00	0.92
	3.37	63.19		
Lysianassa_teminino	0.60	0.01	2.63	1.15
	2.95	66.14		
Caecum_brasilicum	0.50	0.00	2.04	1.40
	2.28	68.42		
Stenothoe_sp	0.23	0.42	1.77	1.03
	1.98	70.40		
Costoanachis_sertulariarum	0.00	0.34	1.58	1.61
	1.77	72.17		

Chondrochelia_dubia	0.37		0.24	1.56	1.54
	1.75	73.93			
Elasmopus_pectenicrus	0.03		0.34	1.48	1.23
	1.66	75.59			
Cymadusa_tartarugae	0.29		0.00	1.36	1.41
	1.53	77.12			
Eulithidium_affine	0.03		0.25	1.18	1.02
	1.32	78.43			
Eulimidae_sp4	0.33		0.00	1.15	0.55
	1.29	79.72			
Rissoella_ornata	0.30		0.00	1.13	0.92
	1.26	80.98			
Paracerceis_sculpta	0.20		0.00	1.11	0.84
	1.25	82.23			
Musculus_lateralis	0.25		0.00	1.10	1.77
	1.23	83.46			
Costoanachis_sparsa	0.16		0.01	0.75	1.35
	0.84	84.31			
Cymadusa_filosa	0.10		0.11	0.73	1.25
	0.82	85.13			
Omalacantha_bicornuta	0.12		0.00	0.73	0.70
	0.82	85.94			
Caprella_scaura	0.16		0.00	0.70	0.89
	0.79	86.73			
Mithraculus_forceps	0.17		0.00	0.69	0.99
	0.77	87.50			
Astyris_lunata	0.17		0.04	0.66	1.48
	0.74	88.24			
Leucothoe_spinicarpa	0.15		0.01	0.60	1.06
	0.67	88.91			
Caecum_ryssotitum	0.15		0.01	0.58	1.03
	0.65	89.56			
Caprella_danilevskii	0.00		0.12	0.53	0.88
	0.59	90.15			

Groups Buzios & Mar_Casado
Average dissimilarity = 58.63

	Group Buzios	Group Mar_Casado		
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD
	Contrib%	Cum.%		
Ericthonius_brasiliensis	2.04	1.21	6.42	1.30
	10.96	10.96		
Batea_catharinensis	0.42	1.60	6.14	2.06
	10.47	21.43		
Hyale_niger	1.72	2.57	6.11	0.96
	10.42	31.85		
Stenothoe_sp	1.47	0.42	6.00	1.41
	10.24	42.09		

Janaira_gracilis	1.11		1.24	4.16	1.26
	7.10	49.19			
Aora_spinicornis	0.75		0.00	3.79	2.39
	6.47	55.66			
Podocerus_fissipes	0.68		0.00	2.65	0.64
	4.53	60.18			
Ampithoe_ramondi	0.58		0.05	2.51	1.61
	4.28	64.46			
Caprella_scaura	0.42		0.00	2.35	1.52
	4.02	68.48			
Jassa_slateryi	0.46		0.00	1.98	1.15
	3.38	71.86			
Costoanachis_sertulariarum	0.00		0.34	1.64	1.62
	2.80	74.66			
Elasmopus_pectenicrus	0.01		0.34	1.57	1.27
	2.68	77.34			
Alaba_incerta	0.24		0.01	1.32	1.22
	2.25	79.59			
Eulithidium_affine	0.00		0.25	1.24	1.00
	2.11	81.70			
Chondrochelia_dubia	0.09		0.24	1.09	0.88
	1.86	83.56			
Cymadusa_filosa	0.28		0.11	1.03	1.34
	1.76	85.32			
Caprella_equilibra	0.18		0.00	0.69	0.62
	1.17	86.50			
Paracerceis_sculpta	0.10		0.00	0.59	1.16
	1.01	87.51			
Caprella_danilevskii	0.00		0.12	0.55	0.88
	0.93	88.44			
Phtisica_marina	0.08		0.00	0.54	0.66
	0.92	89.36			
Monocorophium_acherusicum	0.00		0.11	0.51	0.84
	0.86	90.22			

Supplementary 5. Results of the Spearman correlations between genetic diversity and species diversity for the four species studied. Rho: Spearman's rank correlation coefficient. Bold indicates statistically significant results.

Species	**Variables**	*Rho*	*P*
Hyale niger	Allelic Richness X Species Richness (Chao-1)	-0.8809	**0.007242**
Cymadusa filosa		-0.0333	0.9484
Pinctada imbricata		0.0424	0.9186
Costoanachis sertulariarum		-0.6797	0.2068

Supplementary 6. Regression coefficient (ß), coefficient of determination (R^2) and significance (P-value) of the multiple matrix regression with randomization analysis in the association between beta diversity of invertebrate assemblages and genetic distance among populations of each species in this study. Bold indicates statistically significant results.

	Combination of variables	β community	P-value	R^2	P-value
Hyale niger	*Dcom*	0.6266	0.0002	0.3926	**< 0.0001**
Cymadusa filosa	*Dcom*	0.2662	0.1293	0.0709	0.1293
Pinctada imbricata	*Dcom*	-0.1724	0.324	0.0297	0.324
Costoanachis sertulariarum	*Dcom*	0.4369	0.2118	0.1909	0.2118

CONSIDERAÇÕES FINAIS

Neste estudo, nós mostramos que diferentes espécies-chave de invertebrados associados aos bancos de macroalgas marinhas apresentam diferentes padrões de estruturação genética dentro de uma mesma escala espacial de dezenas de quilômetros. Os moluscos, com uma fase larval planctônica, apresentaram uma ausência de estrutura genética entre suas populações, ao passo que os anfípodes, de desenvolvimento direto, apresentaram diferenciação genética. Mesmo entre anfípodes, também pudemos observar diferenças nos padrões estruturação de suas populações, sendo esta mais forte em *Hyale niger* do que em *Cymadusa filosa*. Portanto, o potencial de dispersão em espécies que apresentam parte de seu desenvolvimento no plâncton, conforme esperado, é maior do que espécies que apresentam todo seu ciclo de vida bentônico. No entanto, espécies de desenvolvimento direto como os anfípodes também apresentam um elevado potencial de dispersão, e que difere entre espécies, e que possivelmente está relacionado a aspectos da história de vida de cada uma delas, tais como crescimento, mobilidade, sobrevivência e potencial reprodutivo.

Além disso, vimos que a variabilidade ambiental entre os locais, principalmente relacionado à concentração de nutrientes, foi o principal fator modulador da diferenciação genética dos anfípodes, de modo geral, porém para *H. niger*, a distância geográfica e os padrões de circulação de correntes também tiveram alto poder explicativo.

Nós também observamos variações morfológicas entre as populações de *H. niger*, mas que não apresentaram relação com as variações genéticas, tratando-se possivelmente de plasticidade fenotípica. Da mesma forma, também pudemos observar variação nos parâmetros de comunidade das assembleias de invertebrados associados às macroalgas marinhas, porém somente encontramos relações não-positivas entre a diferenciação genética e a diferenciação das comunidades, indicando que processos não-paralelos seriam responsáveis por modular esses dois níveis de diversidade para estes organismos.

Portanto, a partir dos resultados obtidos, podemos concluir que para se melhor compreender os padrões de dispersão e conectividade entre diferentes manchas de hábitats formados por bancos de macrófitas, com o intuito, por exemplo, de se estabelecer medidas efetivas de conservação a estes hábitats, devemos preferencialmente considerar o desenvolvimento de estudos com múltiplas espécies, comparando a resposta não só entre espécies com hábitos de vida distintos, mas também entre espécies com hábitos semelhantes, e que a diversidade genética e a diversidade de espécies aparentemente são modulados por fatores independentes, portanto informações acerca de um nível não podem ser utilizadas para de inferir informações acerca do outro. Além disso, mostramos também que o uso de marcadores

moleculares de polimorfismos de nucleotídeo único (SNPs) e de técnicas de sequenciamento de nova geração podem apresentar um grau de estruturação genética mais refinado, quando comparados com o uso de marcadores moleculares de sequência de genes específicos (no caso deste estudo, o gene mitocondrial COI) e com técnicas de sequenciamento tradicionais, o que não invalida a importância destes últimos, que podem sim ser muito informativos, porém destacamos a importância de se usar diferentes tipos de marcadores quando possível.

Por fim, nossos resultados demonstram também a grande importância das áreas de proteção integral marinhas (MPAs) do nosso litoral paulista, uma vez que Alcatrazes, por exemplo, foi o principal ponto de diferenciação genética para as duas espécies de anfípodes em estudo, mostrando que esta região porta agrupamentos genéticos quase exclusivos, algo que pode ocorrer também para outras espécies que ali habitam; e, além disso, vimos que áreas de proteção integral como a Ilha das Palmas, pertencente à ESEC Tupinambás, apresentou valores mais altos de riqueza e diversidade de espécies, mesmo sendo uma ilha tão próxima do continente, inclusive próxima de áreas impactadas como o Saco do Ribeira em Ubatuba, demonstrando a grande importância que manter e conservar estas áreas possui para a manutenção da biodiversidade nos hábitats de macroalgas.

REFERÊNCIAS

Airoldi, L., Balata, D., & Beck, M. W. (2008). The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. Journal of experimental marine biology and ecology, 366(1-2), 8-15.

Bierne, N., Bonhomme, F., & Arnaud-Haond, S. (2016). Editorial dedicated population genomics for the silent world: the specific questions of marine population genetics. Current zoology, 62(6), 545-550.

Bravo, M., Astudillo, J. C., Lancellotti, D., Luna-Jorquera, G., Valdivia, N., & Thiel, M. (2011). Rafting on abiotic substrata: properties of floating items and their influence on community succession. Marine Ecology Progress Series, 439, 1-17.

Chatzigeorgiou, G., Sarropoulou, E., Vasileiadou, K., Brown, C., Faulwetter, S., Kotoulas, G., & Arvanitidis, C. D. (2014). Community structure and population genetics of Eastern Mediterranean polychaetes. Frontiers in Marine Science, 1, 47.

Christie, H., Norderhaug, K. M., & Fredriksen, S. (2009). Macrophytes as habitat for fauna. Marine ecology progress series, 396, 221-233.

Christie, M. R., Tissot, B. N., Albins, M. A., Beets, J. P., Jia, Y., Ortiz, D. M., ... & Hixon, M. A. (2010). Larval connectivity in an effective network of marine protected areas. PloS one, 5(12), e15715.

Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. Annual review of marine science, 1(1), 443-466.

Foggo, A., Bilton, D. T., & Rundle, S. D. (2007). Do developmental mode and dispersal shape abundance–occupancy relationships in marine macroinvertebrates?. Journal of Animal Ecology, 76(4), 695-702.

Gill, D. A., Mascia, M. B., Ahmadia, G. N., Glew, L., Lester, S. E., Barnes, M., ... & Fox, H. E. (2017). Capacity shortfalls hinder the performance of marine protected areas globally. Nature, 543(7647), 665-669.

Havermans, C., De Broyer, C., Mallefet, J., & Zintzen, V. (2007). Dispersal mechanisms in amphipods: a case study of Jassa herdmani (Crustacea, Amphipoda) in the North Sea. Marine Biology, 153(1), 83-89.

von der Heyden, S., Beger, M., Toonen, R. J., van Herwerden, L., Juinio-Meñez, M. A., Ravago-Gotanco, R., ... & Bernardi, G. (2014). The application of genetics to marine management and conservation: examples from the Indo-Pacific. Bulletin of Marine Science, 90(1), 123-158.

Hohenlohe, P. A., Hand, B. K., Andrews, K. R., & Luikart, G. (2018). Population genomics provides key insights in ecology and evolution. In Population genomics (pp. 483-510). Springer, Cham.

Kliman, R., Sheehy, B., & Schultz, J. (2008). Genetic drift and effective population size. Nature Education, 1(3), 3.

Lubchenco, J., Palumbi, S. R., Gaines, S. D., & Andelman, S. (2003). Plugging a hole in the ocean: the emerging science of marine reserves. Ecological applications, 13(1), S3-S7.

Mardis, E. R. (2008). The impact of next-generation sequencing technology on genetics. Trends in genetics, 24(3), 133-141.

Miller, K. J., & Ayre, D. J. (2008). Protection of genetic diversity and maintenance of connectivity among reef corals within marine protected areas. Conservation Biology, 22(5), 1245-1254.

Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G., & Worm, B. (2011). How many species are there on Earth and in the ocean?. PLoS biology, 9(8), e1001127.

Norton, T. A. (1992). Dispersal by macroalgae. British Phycological Journal, 27(3), 293-301.

Oleksiak, M. F. (2018). Adaptation without boundaries: population genomics in marine systems. In Population Genomics (pp. 587-612). Springer, Cham.

Oleksiak, M. F., & Rajora, O. P. (2019). Marine population genomics: challenges and opportunities. Population genomics: Marine organisms, 3-35.

Palumbi, S. R. (2003). Population genetics, demographic connectivity, and the design of marine reserves. Ecological applications, 13(sp1), 146-158.

Parsons, E. C. M., Favaro, B., Aguirre, A. A., Bauer, A. L., Blight, L. K., Cigliano, J. A., ... & Sutherland, W. J. (2014). Seventy-one important questions for the conservation of marine biodiversity. Conservation Biology, 28(5), 1206-1214.

Pereira, R. C., & Soares-Gomes, A. (2009). Biologia Marinha. 2ª Edição. Editora Interciência, Rio de Janeiro. 631p.

Pérez-Portela, R., & Riesgo, A. (2018). Population genomics of early-splitting lineages of metazoans. In Population genomics: marine organisms (pp. 103-137). Springer, Cham.

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., & Treml, E. A. (2016). Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. Current zoology, 62(6), 581-601.

Roberts, D. A., Johnston, E. L., & Poore, A. G. (2008). Contamination of marine biogenic habitats and effects upon associated epifauna. Marine Pollution Bulletin, 56(6), 1057-1065.

Selkoe, K. A., Aloia, C. C., Crandall, E. D., Iacchei, M., Liggins, L., Puritz, J. B., ... & Toonen, R. J. (2016a). A decade of seascape genetics: contributions to basic and applied marine connectivity. Marine Ecology Progress Series, 554, 1-19.

Thiel, M., & Gutow, L. (2004). The ecology of rafting in the marine environment. I. The floating substrata. Oceanography and Marine Biology: an annual review, 42, 181-264.

Waples, R. S. (1998). Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. Journal of Heredity, 89(5), 438-450.

Waycott, M., Duarte, C. M., Carruthers, T. J., Orth, R. J., Dennison, W. C., Olyarnik, S., ... & Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the national academy of sciences, 106(30), 12377-12381.

ANEXOS

COORDENADORIA DE PÓS-GRADUAÇÃO
INSTITUTO DE BIOLOGIA
Universidade Estadual de Campinas
Caixa Postal 6109. 13083-970, Campinas, SP, Brasil
Fone (19) 3521-6378. email: cpgib@unicamp.br

DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada "***GENÔMICA POPULACIONAL E SEUS FATORES MODULADORES EM INVERTEBRADOS ASSOCIADOS A MACROALGAS MARINHAS***", desenvolvida no Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

Assinatura: _____
Nome do(a) aluno(a): Pedro Augusto dos Santos Longo

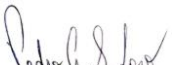
Assinatura: _____
Nome do(a) orientador(a): Fosca Pedini Pereira Leite

Data: 03/04/2023

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **GENÔMICA POPULACIONAL E SEUS FATORES MODULADORES EM INVERTEBRADOS ASSOCIADOS A MACROALGAS MARINHAS**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 03 de abril de 2023

Assinatura : 
Nome do(a) autor(a): **Pedro Augusto dos Santos Longo**
RG n.° 48.402.970-8

Assinatura : 
Nome do(a) orientador(a): **Fosca Pedini Pereira Leite**
RG n.° 4.125.410-7