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AIARA PONCE DE LEON RIBEIRO CARDOSO

EFEITO DA COMPLEXIDADE ESTRUTURAL DE NAUFRÁGIOS SOBRE A DIVERSIDADE DE ESPÉCIES DE PEIXES

João Pessoa

2019

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Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas, da Universidade Federal da Paraíba, como requisito parcial para obtenção do título de mestre em ciências biológicas.

Orientador: Prof. Dr. Bráulio Almeida Santos

João Pessoa

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Ata da 312ª Apresentação e Banca de Defesa de Mestrado de Aiara Ponce de Leon Ribeiro Cardoso

Ao(s) vinte e oito dias do mês de fevereiro de dois mil e dezenove, às 14:00 horas, no(a) Auditório DSE, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a dissertação de mestrado de **Aiara Ponce de Leon Ribeiro Cardoso**, candidato(a) ao grau de Mestre em Ciências Biológicas. A banca foi composta pelos seguintes professores/pesquisadores: **Dr.Braúlio Almeida Santos (Orientador), Dr. Ricardo de Souza Rosa (Titular) e Dr. Guilherme Ortigara Longo (Titular).** Compareceram à solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra para o(a) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **Aiara Ponce de Leon Ribeiro Cardoso**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **"O Efeito da complexidade estrutural de naufrágios sobre a diversidade de peixes"**. Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito APROVADO. Perante a aprovação, declarou-se o(a) candidato(a) legalmente habilitado(a) a receber o grau de **Mestre em Ciências Biológicas**, área de concentração **Zoologia**. Nada mais havendo a tratar eu, **Dr.Braúlio Almeida Santos**, como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

João Pessoa, 28/02/2019.

Dr.Braúlio Almeida Santos (Orientador)

Dr. Ricardo de Souza Rosa (Titular)

Dr. Guilherme Ortigara Longo (Titular)

Ciente do Resultado:

Aiara Ponce de Leon R Cardoso

Aiara Ponce de Leon Ribeiro Cardoso

Aos meus pais e avós pelos ensinamentos,

ao oceano pela inspiração

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What a wonderful things are accomplished by those rare individuals who muster the courage to leave the security of an ordered life in pursuit of a dream. (Ned DeLoach)

RESUMO

Um dos principais objetivos da ecologia é compreender como a heterogeneidade espacial determina padrões de diversidade e composição de espécies. Estudos têm demonstrado relação positiva entre heterogeneidade ambiental e diversidade, mas evidências em ecossistemas marinhos são controversas e escassas em termos de como essa relação é mediada pela heterogeneidade espacial e o período do dia. Na presente pesquisa utilizamos comunidades de peixes de quatro naufrágios do Atlântico Sudoeste para avaliar se as relações positivas entre heterogeneidade e diversidade (HDR) são válidas para esses organismos móveis e se as relações enfraquecem ao anoitecer, quando grande parte da comunidade de peixes busca refúgio, potencialmente favorecendo a diversidade em locais mais complexos. Amostramos peixes em três habitats com complexidade estrutural contrastante (alta, baixa e controle), ao longo do dia e da noite, e empregamos duas abordagens complementares de diversidade: a partição da diversidade gama em componentes alfa e beta independentes (abordagem de Jost) e a partição da diversidade beta em componentes de *turnover* e *nestedness* (abordagem de Baselga). Registramos 5005 peixes pertencentes a 76 espécies e 31 famílias. Como esperado, a diversidade alfa média de espécies raras (^{0}D) duplicou do controle para áreas de alta complexidade e diminuiu pela metade do dia para a noite. A diversidade de espécies típicas (^{1}D) foi duas vezes maior nas áreas de alta complexidade do que nas áreas controle, mas não diminuiu à noite. Complexidade e período do dia não demonstraram efeito significativo sobre a diversidade de espécies dominantes (^{2}D). As relações entre complexidade e diversidade alfa não foram enfraquecidas durante a noite. A diversidade beta das três ordens de diversidade diferiu significativamente de 1 (recife totalmente homogêneo), indicando que a complexidade regula os padrões de diversidade beta. Este efeito foi consistente em ambos os períodos do dia, contrariando expectativas de menor influência da complexidade à noite. O componente *turnover* da diversidade beta foi consistentemente maior que o *nestedness* no dia e na noite (2,8 e 1,9 vezes, respectivamente). Nossos resultados corroboram a HDR positiva para a diversidade de espécies raras e típicas. As espécies dominantes também respondem à heterogeneidade substituindo-se pelo gradiente de complexidade, mas não se tornando mais numerosas em áreas de alta complexidade. Mudanças do período do dia não afetaram a força da HDR, revelando um papel ininterrupto da heterogeneidade ambiental sobre as comunidades de peixes. A preservação de habitats heterogêneos, como naufrágios estruturalmente complexos, é fundamental para a conservação da diversidade de peixes marinhos.

Palavras-chave: biodiversidade, complexidade do habitat, diversidade beta, peixes recifais, recifes artificiais.

ABSTRACT

A major goal of ecology is to understand how spatial heterogeneity determines patterns of species diversity and composition. Studies have demonstrated positive relationship between environmental heterogeneity and diversity, but evidence from marine ecosystems is controversial and scarce in terms of how spatial heterogeneity and diel period mediate this relationship. We used fish communities from four Southwestern Atlantic vessel reefs to assess whether positive heterogeneity-diversity relationships (HDR) hold for these mobile organisms and whether the relationships weaken with nightfall. We sampled fishes in three habitats with contrasting structural complexity (high, low and control), over day and night, and employed two complementary diversity frameworks: partitioning of gamma diversity into independent alpha and beta components (Jost's approach) and partitioning of beta diversity into turnover and nestedness components (Baselga's approach). We recorded 5005 fishes belonging to 76 species and 31 families. As expected, the mean alpha diversity of rare species ($0D$) doubled from control to high complexity areas and decreased by half from day to night. The diversity of typical species ($1D$) showed a twofold increase from control to high complexity areas, but did not reduce at night. Complexity and diel period did not have significant effect on the diversity of dominant species ($2D$). No relationship between complexity and alpha diversity were weakened at night. Beta diversity of the three diversity orders significantly differed from 1 (totally homogeneous vessel reef), indicating that complexity underlies patterns of beta diversity. This effect was consistent at both diel periods, contradicting expectations of weaker influence of complexity at night. The turnover component of beta diversity was consistently greater than nestedness at day and night (2.8 and 1.9-fold, respectively). Our findings support positive HDR for the diversity of rare and typical species. Dominant species also respond to heterogeneity by replacing each other across the complexity gradient, but not by becoming more numerous in high complexity areas. Diel changes did not affect the strength of HDR, revealing an uninterrupted role of environmental heterogeneity on fish communities. Preserving heterogeneous habitats, such as structurally complex shipwrecks, is critical for conserving marine fish diversity.

Key words: beta diversity; habitat heterogeneity hypothesis; hill numbers; reef fishes; turnover.

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Figura 1. Mapa mostrando a América do Sul e o Brasil, o ponto escuro em detalhe indica a área de amostragem à esquerda. A área com zoom mostra a localização dos quatro naufrágios investigados: Alice, Alvarenga, Queimado e Vapor Bahia. À direita, desenho esquemático e fotografia de cada naufrágio na mesma ordem em que aparecem no mapa. Fotos de Diego Luna e Max Glegiston, croquis de Maurício Carvalho e Bertran Feitoza.

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Figura 4. Diversidade beta baseada nas abordagens de Jost (esquerda) e Baselga (direita). O painel da esquerda mostra o número efetivo médio de comunidades distintas dos quatro navios, considerando espécies de peixes raras (${}^{0}D$), típicas (${}^{1}D$) e dominantes (${}^{2}D$), durante o dia e a noite. Observe que todos os valores são significativamente maiores que 1, que representa a hipótese estatística nula de não haver efeito de complexidade estrutural na diversidade beta (ver Tabela S4). No painel da direita, a contribuição relativa média dos componentes de *turnover* e *nestedness* no dia e noite. Barras verticais representam erro padrão.

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FUNDAMENTAÇÃO TEÓRICA

Relação heterogeneidade-diversidade (HDR)

Os organismos vivos geralmente não estão distribuídos de forma homogênea no espaço, por isso, um dos principais objetivos da ecologia de comunidades é compreender os padrões espaciais da diversidade das espécies. Este tema intriga investigadores há mais de um século (e.g CLEMENTS, 1916) e segue estimulando a mente dos pesquisadores até os dias atuais (e.g. ANTONELLI; SANMARTÍN, 2011; GASTON; BLACKBURN, 2000; PINHEIRO et al., 2018; TITTENSOR et al., 2010). A heterogeneidade ambiental é um dos fatores conhecidos por influenciar padrões de distribuição espacial da diversidade de espécies de diferentes grupos (STEIN; GERSTNER; KREFT, 2014; TEWS et al., 2004). A primeira análise quantitativa do efeito da heterogeneidade ambiental sobre a diversidade de espécies foi apresentada por Robert H. MacArthur & MacArthur (1961). Desde então, esse se tornou um tema comum na literatura (KOVALENKO; THOMAZ; WARFE, 2012) e forneceu base para a relação heterogeneidade-diversidade (HDR, do inglês: *heterogeneity-diversity relationship*), um dos pilares da ecologia (MACARTHUR; WILSON, 1967).

HDRs positivas são amplamente demonstradas em investigações envolvendo diferentes grupos biológicos e escalas espaciais (BUHL-MORTENSEN et al., 2010; FABI; FIORENTINI, 1994; HUNTER; SAYER, 2009; MACARTHUR; MACARTHUR, 1961; ROBERTS; ORMOND, 1987). A heterogeneidade ambiental favorece a diversidade de espécies por meio de três mecanismos principais. Primeiro, o aumento de gradientes ambientais e na variedade de tipos de habitat, recursos e complexidade estrutural, deve aumentar a disponibilidade de espaço de nicho e permitir a coexistência de mais espécies (TEWS et al., 2004); Segundo: áreas com maior heterogeneidade ambiental são mais prováveis de fornecer abrigo e refúgio de condições ambientais adversas e períodos de mudanças climáticas, o que deve promover a persistência das espécies (FJELDSÅ; BOWIE; RAHBEK, 2012); Terceiro: a probabilidade de eventos de especiação como resultado do isolamento ou adaptação à condições ambientais diversas deve aumentar com a maior heterogeneidade ambiental (ANTONELLI; SANMARTÍN, 2011).

Outros autores também propõem que a alta complexidade estrutural reduz a competição e a predação (e.g. HIXON; MENGE, 1991). Ambientes complexos podem reduzir a competição ao fornecer mais refúgios ou mais recursos (ex. alimento e abrigo) e microhabitats, permitindo maior partição de nicho (MACARTHUR; LEVINS, 1964). De forma similar, habitats complexos podem reduzir a predação através da disponibilidade de refúgios para as presas e/ou pela redução nos encontros entre predadores e presas (MURDOCH; OATEN, 1975). No entanto, alguns estudos questionaram a generalidade da HDR positiva (LUNDHOLM, 2009; ROHDE, 1992) e outros encontraram efeitos unimodais ou negativos (BAR-MASSADA; WOOD, 2014; GAZOL et al., 2013). Isso sugere que a resposta da diversidade de espécies à heterogeneidade ambiental pode diferir conforme a escala espacial do estudo, o grupo de espécies e tipo de variável estrutural considerado (ATAURI; DE LUCIO, 2001).

A heterogeneidade ambiental tem sido descrita na literatura utilizando uma grande variedade de termos, mais de cem, segundo Stein et al. (2014). Alguns dos termos utilizados como sinônimos incluem, por exemplo: complexidade/diversidade ambiental, estrutural ou de habitat, heterogeneidade/variabilidade espacial, entre outros (revisão de literatura sobre os termos em Tews et al., 2004). Essas expressões são geralmente definidas de forma imprecisa ou utilizadas de maneira diferente por diferentes autores, o que dificulta a compreensão e as comparações entre estudos. No presente trabalho, utilizamos heterogeneidade ambiental como um termo genérico para todos os termos relacionados à estrutura física tridimensional do ambiente (GRAHAM; NASH, 2013), e consideramos complexidade estrutural como um componente mensurável da heterogeneidade.

Partição da diversidade de espécies

Padrões de diversidade podem variar com a escala de observação, portanto a escolha da escala de estudo pode afetar os resultados observados e a comparação de estudos com resultados semelhantes (HAMER; HILL, 2000; RAHBEK, 2005). Essa percepção levou os pesquisadores a incluir a escala como mais um fator que determina os padrões de diversidade de espécies (CHASE; LEIBOLD, 2002; GONZÁLEZ-MEGÍAS; MARÍA GÓMEZ; SÁNCHEZ-PIÑERO, 2007; RAHBEK, 2005), bem como a quantificar a parcela da diversidade total que se deve à variação entre áreas. Para descrever e comparar as diferenças entre comunidades ou habitats, uma abordagem amplamente utilizada é a partição da diversidade em três componentes: alfa (α), que representa a diversidade “local” ou “intra-habitat”; beta (β), que indica a variação entre comunidades/habitats; e gama (γ) que representa a diversidade em nível regional (WHITTAKER, 1972). A avaliação da diversidade β fornece uma estrutura conceitual para separar padrões de variação na composição de espécies de um local para outro (BASELGA, 2010a, 2012; WILSON; SHMIDA, 1984). Essa abordagem é cada vez mais usada para investigar os fatores que afetam a estrutura das comunidades (ACKERLY; CORNWELL, 2007; PINHEIRO et al., 2018; PÜTTKER et al., 2015).

As diferenças na composição de espécies entre duas (ou mais) áreas podem ser atribuídas a dois principais fenômenos: (1) a substituição de algumas espécies por outras de sítio para sítio, denominado *turnover* espacial (GASTON; BLACKBURN, 2000) e/ou

(2) aninhamento (*nestedness)*, um padrão em que o sítio mais “pobre” é um subconjunto estrito do sítio mais “rico” (BASELGA, 2012). Um glossário com definição mais detalhada dos termos diversidade alfa, beta, gama, aninhamento e *turnover* é apresentado por Socolar et al. (2016).

Os processos que controlam a diversidade de espécies também podem ser específicos para cada escala espacial (GONZÁLEZ-MEGÍAS; MARÍA GÓMEZ; SÁNCHEZ-PIÑERO, 2007). Essa ideia de processos em diferentes escalas sendo importantes e interagindo para afetar a composição e a diversidade da comunidade local é parte central da teoria da metacomunidade (LEIBOLD et al., 2004; LOGUE et al., 2011). Metacomunidade é definida como um conjunto de comunidades locais ligadas pela dispersão de múltiplas espécies em interação (WILSON, 1992). A teoria de metacomunidades é baseada em quatro paradigmas, cada um enfatiza diferentes processos de potencial importância para a estruturação das metacomunidades: *patch dynamics*, *species-sorting*, *mass-effects* e a perspectiva *neutral* (para detalhes e definições completas, ver Leibold et al., 2004).

Neste estudo, cabe destacar duas perspectivas: (i) *species sorting*, a qual enfatiza a separação de nicho espacial acima e além da dinâmica espacial. Nesse caso, a dispersão exerce um efeito importante sobre a composição das comunidades locais, mas as condições ambientais que determinam a qualidade do habitat são mais relevantes. Neste caso, habitats contrastantes podem até apresentar a mesma riqueza de espécies, mas certamente apresentarão comunidades locais muito diferentes (i.e. alta diversidade beta). (ii) *Mass-effects*, que enfoca o efeito preponderante da imigração e da emigração na dinâmica populacional local, permitindo que espécies permaneçam em habitats de baixa qualidade devido à chegada de novos indivíduos oriundos de habitats de alta qualidade (LEIBOLD et al., 2004). Este efeito de transbordamento em locais muito favoráveis, aliado à alta capacidade de dispersão, pode levar habitats contrastantes a apresentarem comunidades locais similares (i.e. baixa diversidade beta).

Medidas de diversidade

As medidas de diversidade representam outra fonte de considerável debate entre a comunidade científica por não possuírem um significado matemático único (COLWELL, 2009; KREBS, 2014). Vários índices foram propostos por diferentes autores para caracterizar quantitativamente as comunidades biológicas incorporando a riqueza e abundância de espécies, usando tanto abordagens paramétricas quanto não-paramétricas (revisões em Magurran, 2004; Magurran & McGill, 2011). Dois índices não paramétricos historicamente utilizados são o *H'* de Shannon-Wiener, que mede a heterogeneidade ou entropia entre as comunidades (SHANNON, 1948) e o *D* de Simpson (1949), que estima a probabilidade de dois indivíduos amostrados aleatoriamente pertencerem à mesma espécie. Diferentes índices medem diferentes aspectos da partição da abundância entre as espécies (HILL, 1973), e a falta de integração entre as medidas pode fornecer uma visão incompleta da estrutura da comunidade em estudo, além de dificultar a comparação entre estudos**.**

Na tentativa de unificar os índices de diversidade, MacArthur (1965) foi o primeiro a realizar transformações nas equações de Shannon e de Simpson e introduziu à ecologia o conceito de “número efetivo de espécies”. Hill (1973) incrementou essa abordagem e originou as medidas de diversidade hoje chamadas "Números de Hill" (*Hill numbers)*. Os números de Hill são uma família de índices de diversidade matematicamente unificada (diferindo entre si apenas pelo expoente *q*). Esses índices incorporam a abundância relativa e riqueza de espécies e superam muitas deficiências dos índices anteriores relacionadas à sensibilidade dos índices ao tamanho da amostra e falta de informação sobre abundância das espécies (CHAO et al., 2014). Os Números de Hill são considerados a família paramétrica que unifica vários números efetivos (CHAO; CHIU; JOST, 2014; HILL, 1973; JOST, 2006, 2007a), e representam o número equivalente de espécies igualmente abundantes que seriam necessárias para fornecer o mesmo valor de uma medida de diversidade (CHAO; CHIU; JOST, 2014; GOTELLI; CHAO, 2013).

A abordagem de Hill foi aperfeiçoada e reintroduzida aos estudos em ecologia por Jost (2006, 2007), e mantém a terminação “números de Hill” em referência a seu precursor. Os números de Hill apresentam pelo menos cinco vantagens em relação aos demais índices de diversidade (CHAO et al., 2014): (i) obedecem ao princípio de replicação ou a propriedade de duplicação; (2) são expressos em unidades de número efetivo de espécies; (iii) os principais índices de diversidade propostos na literatura (e.g. índices de Shannon e Simpson), podem ser convertidos em números de Hill por transformações algébricas simples; (iv) fornecem uma estrutura unificada para medir a biodiversidade, pois podem ser efetivamente generalizados para incorporar a diversidade taxonômica, filogenética e funcional (CHAO; CHIU; JOST, 2010; GOTELLI; CHAO, 2013); (v) na comparação entre múltiplas comunidades, há uma relação direta entre os números de Hill e a similaridade (ou diferenciação) na composição de espécies entre as comunidades (JOST, 2007a). Esta propriedade une diversidade e similaridade (ou diferenciação).

Diferentes números efetivos de espécies (${}^{q}D$) são definidos pelo parâmetro q (ou ordem q), que controla a sensibilidade da medida à abundância relativa das espécies (GOTELLI; CHAO, 2013). Os três grupos mais populares de medidas de diversidade são q = 0, 1 e 2. Quando q=0, a abundância relativa das espécies não é levada em conta porque todas as abundâncias são elevadas ao expoente q=0, fazendo com que espécies raras tenham o mesmo peso das dominantes. Assim, ^0D é igual a riqueza de espécies, e por atribuir igual peso à todas as espécies, independente da sua abundância relativa, pode-se dizer que se refere ao número de espécies "raras" na comunidade. Quando q=1, o ^1D equivale a forma exponencial da entropia de Shannon, que atribui às espécies um peso proporcional à sua frequência. ^1D pode ser interpretado como o número de "espécies típicas" (ou "comuns") na comunidade. Finalmente, quando q=2, ^2D atribui maior peso às espécies dominantes na comunidade, visto que suas abundâncias são elevadas ao quadrado, tornando-as ainda mais representativas na comunidade.

Nesse contexto, Chao & Jost (2012) propuseram uma metodologia integrada de amostragem, rarefação e extrapolação, capaz de comparar a riqueza de espécies de um conjunto de comunidades com base em amostras de igual completude (medida pela cobertura de amostra, do inglês *sample coverage*), e não necessariamente de igual tamanho. A riqueza de espécies esperada com base na cobertura de amostra satisfaz o princípio de replicação ou propriedade de duplicação, diferentemente da riqueza de espécies esperada para amostras de igual tamanho. O método baseado na cobertura da amostra, além de produzir comparações menos enviesadas da riqueza entre as comunidades, ajuda a evitar desperdício de esforço amostral. Quando a amostra atinge um valor predeterminado dessa estimativa de cobertura, que pode ser calculada em campo, a amostragem pode ser cessada (regra de parada, ou *stopping rule*). Chao & Jost (2012) recomendam 0.50 (ou seja, 50%) como valor mínimo de cobertura da amostra para assegurar a confiabilidade da extrapolação da cobertura e das estimativas da riqueza de espécies. Seguindo essa abordagem é possível comparar amostras diretamente, sem rarefação, de modo que nenhum dado extra seja coletado e nenhum seja descartado.

Ambientes recifais: Complexidade estrutural e diversidade de peixes

A distribuição das espécies de peixes, em escala global, é determinada por fatores ambientais e geográficos incluindo a temperatura da água (TITTENSOR et al., 2010), as correntes oceânicas (JONES; SRINIVASAN; ALMANY, 2007) e a profundidade (GRAY, 2001). Em escalas regional e local, há também a influência das características estruturais dos ambientes (WALKER; JORDAN; SPIELER, 2009).

Os recifes naturais (e.g. de corais e rochosos) e artificiais (e.g. blocos de concreto e navios naufragados) são ambientes estruturalmente complexos, constituídos por diversos microhabitats que variam em complexidade dependendo da arquitetura dos corais (no caso dos recifes naturais) ou das estruturas artificiais (no caso dos naufrágios). Estes habitats abrigam um conjunto diversificado de espécies de peixes de importância ecológica e econômica, que dependem da estrutura fornecida pelos recifes para utilização como áreas seguras para abrigo, alimentação, reprodução e crescimento (LUCKHURST; LUCKHURST, 1978).

A associação entre a complexidade estrutural e as comunidades de peixes é amplamente conhecida, com diversos estudos relatando impactos positivos da complexidade estrutural dos recifes sobre a abundância, riqueza e diversidade de peixes (CHARBONNEL et al., 2002; DAVIS; SMITH, 2017; DOMINICI-AROSEMENA; WOLFF, 2005; DUSTAN; DOHERTY; PARDEDE, 2013; FABI; FIORENTINI, 1994; FRIEDLANDER et al., 2003; GRATWICKE; SPEIGHT, 2005a, 2005b; RISK, 1972; TALBOT; GOLDMAN, 1972; WILSON; GRAHAM; POLUNIN, 2007), e evidências de que os recifes apresentam maior riqueza e abundância de peixes do que áreas não recifais adjacentes, com fundo inconsolidado (CONSOLI et al., 2014; SCHULTZ et al., 2012).

Os recifes artificiais são formados por estruturas que foram acidentalmente ou deliberadamente afundadas, geralmente em ecossistemas marinhos (AMARAL et al., 2010). Diferentes estruturas têm sido utilizadas como recifes artificiais (revisão em Baine, 2001), como blocos de concreto (FABI; FIORENTINI, 1994), pneus, plataformas de petróleo (LØKKEBORG et al., 2002), submarinos, aviões e navios (ZINTZEN et al., 2006). Recifes artificiais vem sendo empregados ao redor do mundo para uma variedade de finalidades (HUNTER; SAYER, 2009), inclusive como parte das estratégias de gestão de ecossistemas marinhos e da pesca (SEAMAN, 2007). Entre as aplicações mais comuns estão o uso como ferramentas para mitigar os impactos das atividades humanas sobre ecossistemas costeiros, para aumentar a produção pesqueira, para apoiar atividades recreativas (mergulho e pesca), e para promover a conservação da natureza e proteção costeira (BAINE, 2001; SEAMAN, 2007; SVANE; PETERSEN, 2001). Os benefícios econômicos e ambientais desses recifes estão ligados ao potencial de transformar substrato "improdutivo" em ambiente produtivo (STONE, 1982) e de promover o aumento das taxas de recrutamento, crescimento e sobrevivência dos peixes que habitam essas áreas (BOHNSACK, 1989; GORHAM; ALEVIZON, 1989).

Ao fornecer substrato consolidado como habitat adicional em áreas constituídas predominantemente por substratos inconsolidados (ex. areia, cascalho), a presença de recifes artificiais favorece o aumento da biomassa de peixes, incluindo espécies de interesse comercial (BURT et al., 2009; ZINTZEN et al., 2006). Essas estruturas são populares entre os pescadores por seu potencial de proporcionar acesso a espécies-alvo e ampliar as taxas de captura, e em longo prazo, por estimular a produção *in situ*, aumentando os estoques pesqueiros (BOHNSACK, 1989; BRICKHILL; LEE; CONNOLLY, 2005; SMITH et al., 2016). Além disso, recifes artificiais próximos a recifes naturais podem apresentar abundância e diversidade de espécies similares (RILOV; BENAYAHU, 2000).

Debates sobre os possíveis mecanismos responsáveis pela grande abundância de peixes nos recifes artificiais originaram as hipóteses de “*atração vs produção*”, dois modelos opostos, mas não mutuamente exclusivos (BRICKHILL; LEE; CONNOLLY, 2005; PICKERING; WHITMARSH, 1997). A hipótese de atração sugere que os recifes artificiais simplesmente atraem e agregam peixes de áreas vizinhas em consequência de suas preferências comportamentais (BOHNSACK, 1989). Já a hipótese da produção propõe que o aumento das oportunidades de alimentação e abrigo favorece o estabelecimento dos peixes nos recifes (em concordância com a hipótese anterior), mas um número maior de juvenis é capaz de se estabelecer, sobreviver e se reproduzir quando adultos, contribuindo com novos indivíduos para as populações locais (BRICKHILL; LEE; CONNOLLY, 2005). O nível de atração ou de produção após a implantação do recife dependerá das características do habitat adjacente, sobretudo no que diz respeito à heterogeneidade ambiental e disponibilidade de nutrientes. Por exemplo, é mais provável a atuação do mecanismo de atração quando um único recife é introduzido em um ambiente oligotrófico. Já a produção será mais provável no cenário de adição de mais recifes ou de recifes mais complexos (BRICKHILL; LEE; CONNOLLY, 2005).

A heterogeneidade ambiental dos recifes exerce influência sobre as taxas de recrutamento e tamanho dos organismos, e dessa forma, afeta características importantes das populações de peixes (SVANE; PETERSEN, 2001). A redução na heterogeneidade ambiental de áreas recifais pode ter profundas implicações para a biodiversidade dos recifes e serviços ecossistêmicos associados (DARLING et al., 2017). Assim, atividades que causem danos à complexidade estrutural dos recifes podem resultar em redução da abundância, extinções locais, perda de diversidade (GRAHAM et al., 2006; NEWMAN et al., 2015) e declínio da produtividade pesqueira (ROGERS; BLANCHARD; MUMBY, 2014; WESTMACOTT et al., 2000).

Os navios naufragados apresentam características particulares, pois apresentam diferentes microhabitats concentrados em uma área conhecida, que os tornam cenários adequados para investigações sobre a resposta das comunidades de peixes às mudanças nas variáveis ambientais, permitindo controlar fatores como a profundidade, turbidez da água e distância de outros recifes. Os resultados provenientes de pesquisas em naufrágios podem, portanto, auxiliar na compreensão dos mecanismos que governam os padrões de distribuição da diversidade de peixes em escala local e regional.

Uso do habitat e período do dia

O ciclo do dia é conhecido por ter forte influência no comportamento dos organismos no ambiente marinho (NAGELKERKEN et al., 2000; YEOH et al., 2017). Muitas espécies de peixes associados aos recifes realizam migrações diárias entre habitats de forrageio e de descanso. Assim, a intensidade do efeito da complexidade estrutural sobre a diversidade de espécies pode não ser constante ao longo do dia.

Espécies das famílias Acanthuridae, Chaetodontidae, Labridae e Pomacentridae, por exemplo, são geralmente ativas durante o dia, e à noite migram das áreas de forrageio para locais com maior complexidade estrutural (e.g. rochas, corais, fendas) onde podem encontrar abrigo. Já espécies de atividade noturna, como as pertencentes às famílias Apogonidae, Diodontidae, Haemulidae, Lutjanidae, Holocentridae e Sciaenidae geralmente se abrigam nas áreas recifais durante o dia e migram para áreas adjacentes para forragear à noite. A consequente mudança na composição das espécies encontradas nos recifes do dia para a noite é, portanto, um dos eventos mais dinâmicos nos ambientes recifais (SALE, 1991).

Amostragem da complexidade estrutural nos recifes

Estudos sobre a heterogeneidade ambiental em ambientes recifais utilizam uma grande variedade de variáveis e métodos para acessar a complexidade estrutural, porém em sua maioria são direcionados aos recifes naturais. A maioria das pesquisas examina apenas uma ou duas variáveis de pelo menos seis componentes reconhecidos da complexidade do habitat. São eles (1) complexidade topográfica ou rugosidade do substrato (JENNINGS; GRANDCOURT; POLUNIN, 1995; LUCKHURST; LUCKHURST, 1978; RISK, 1972); (2) diversidade do substrato (ROBERTS; ORMOND, 1987); (3) categorias de tamanho dos refúgios (ROBERTS; ORMOND, 1987); (4) relevo vertical ou altura da arquitetura do substrato (LUCKHURST; LUCKHURST, 1978); (5) percentual de substrato consolidado (KHALAF; KOCHZIUS, 2002); (6) percentual de cobertura bentônica, incluindo algas e/ou corais (KOMYAKOVA; MUNDAY; JONES, 2013; NUNES; SAMPAIO; BARROS, 2013). Outros estudos elaboraram índices incorporam todos ou quase todos desses componentes, como o Índice de Complexidade de Habitat (IHC) proposto por Medeiros, Rosa, & Francini-Filho (2011) e o Escore de Avaliação do Habitat (*Habitat Assessment Score* – HAS) proposto por Gratwicke & Speight (2005b). Tais índices possibilitam avaliar a complexidade estrutural em diferentes habitats marinhos tropicais rasos, como recifes, bancos de areia e de algas.

Diferentes métodos são aplicadas em diferentes habitats para atender as particularidades de cada um. Kovalenko et al. (2012) apresentam uma visão geral dos métodos utilizados comumente para medir a complexidade de habitats em cada um dos sistemas mais estudados (e.g. mangues, corais, bancos de algas, estruturas artificiais). Métodos para quantificar a complexidade estrutural de recifes de coral, por exemplo, variam desde medidas em nível de metros a técnicas remotas utilizando sonares (revisão em Graham & Nash, 2013). O método da corrente (*chain link method*) proposto por (LUCKHURST; LUCKHURST, 1978) é um dos mais utilizados em estudos de complexidade estrutural em ambientes recifais. Porém, nem sempre é apropriado para a medição de grandes estruturas, como as peças de um naufrágio, cujas maiores não podem ser suficientemente cobertas pelas correntes tradicionalmente empregadas. Outra limitação de vários métodos e técnicas é o fato de requererem trabalho intenso, disponibilidade de tempo e de equipamentos refinados.

Uma alternativa que vem sendo utilizada recentemente para categorizar e avaliar a complexidade dos recifes é a estimativa visual (WILSON; GRAHAM; POLUNIN, 2007). Além de viabilizar a amostragem em ambientes com diferentes características, a estimativa visual permite uma avaliação mais rápida e menos dispendiosa das características estruturais dos ambientes. Ainda que essa seja uma avaliação subjetiva e sujeita a erros do pesquisador, a estimativa visual pode fornecer resultados similares àqueles obtidos por métodos tradicionais, porém, com menor esforço (WILSON; GRAHAM; POLUNIN, 2007). Entretanto, é importante o treinamento apropriado dos observadores, e que as suas estimativas visuais sejam calibradas e padronizadas em relação a uma medida quantitativa.

Na presente pesquisa, utilizamos as comunidades de peixes associadas a quatro naufrágios na costa nordeste do Brasil para investigar se há uma relação positiva entre a heterogeneidade ambiental e diversidade de espécies e se essa relação é enfraquecida no período noturno. Para avaliar a complexidade estrutural dos naufrágios, utilizamos categorias modificadas do Escore de Avaliação de Habitat proposto por Gratwicke & Speight (2005b), as quais foram estimadas visualmente por meio de vídeo e observações *in situ*. A adaptação desse escore foi realizada para que pudéssemos estimar a variedade de atributos estruturais dos naufrágios que potencialmente fornecem recursos e refúgio para diferentes espécies de peixes. Dessa forma, selecionamos quatro tipos de variáveis de complexidade estrutural: Variedade de estruturas, altura máxima de estruturas, número de possíveis refúgios e categorias de tamanho de refúgio.

Em cada naufrágio, amostramos as comunidades de peixes através de filmagens subaquáticas durante o dia e à noite em habitats com diferentes níveis de complexidade estrutural. Na análise dos vídeos, realizamos a identificação taxonômica dos peixes e estimamos suas abundâncias relativas através da contagem do número máximo de indivíduos da mesma espécie observado simultaneamente em um frame dentro dos 7 minutos de gravação (MaxN). Para estimar a diversidade de espécies e os fenômenos responsáveis pelas diferenças na composição dos habitats, empregamos duas abordagens complementares: a partição da diversidade proposta por Jost (2007) e a partição da diversidade beta nos componentes de *turnover* e *nestedness* (BASELGA, 2010b).

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ARTIGO

Testing the environmental heterogeneity-diversity relationship in fish communities of vessel reefs

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Testing the environmental heterogeneity-diversity relationship in fish communities of vessel reefs

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Abstract

1. A major goal of ecology is to understand how spatial heterogeneity determines patterns of species diversity and composition. Studies have demonstrated positive relationship between environmental heterogeneity and diversity, but evidence from marine ecosystems is controversial and scarce in terms of how spatial heterogeneity and diel period mediate this relationship.

2. We used fish communities from four Southwestern Atlantic vessel reefs to assess whether positive heterogeneity-diversity relationships (HDR) hold for these mobile organisms and whether the relationships weaken with nightfall. We sampled fishes in three habitats with contrasting structural complexity (high, low and control), over day and night, and employed two complementary diversity frameworks: partitioning of gamma diversity into independent alpha and beta components (Jost's approach) and partitioning of beta diversity into turnover and nestedness components (Baselga's approach).

3. We recorded 5005 fishes belonging to 76 species and 31 families. As expected, the mean alpha diversity of rare species (${}^{0}D$) doubled from control to high complexity areas and decreased by half from day to night. The diversity of typical species (${}^{1}D$) showed a twofold increase from control to high complexity areas, but did not reduce at night. Complexity and diel period did not have significant effect on the diversity of dominant species (${}^{2}D$). No relationship between complexity and alpha diversity were weakened at night.

4. Beta diversity of the three diversity orders significantly differed from 1 (totally homogeneous vessel reef), indicating that complexity underlies patterns of beta diversity. This effect was consistent at both diel periods, contradicting expectations of weaker

influence of complexity at night. The turnover component of beta diversity was consistently greater than nestedness at day and nigth (2.8 and 1.9-fold, respectively).

5. Our findings support positive HDR for the diversity of rare and typical species. Dominant species also respond to heterogeneity by replacing each other across the complexity gradient, but not by becoming more numerous in high complexity areas. Diel changes did not affect the strenght of HDR, revealing a uninterrupted role of environmental heterogenity on fish communities. Conserving heterogeneous habitats, such as structurally complex shipwrecks and pristine coral reefs, is critical for conserving marine fish diversity.

Key words: biodiversity; beta diversity; habitat heterogeneity hypothesis; hill numbers; reef fishes; turnover.

Introduction

Environmental heterogeneity (EH) plays an important role on ecological patterns and processes, affecting population dynamics and community structure (see review by Tews *et al*., 2004). As a major goal in ecology is to understand spatial patterns of species diversity, the shape of the heterogeneity-diversity relationship (HDR) has been widely investigated (Stein, Gerstner, & Kreft 2014; Yang *et al*., 2015). Positive relationships are well documented (e.g. Massicotte, Proulx, Cabana, & Rodríguez, 2015; Stein *et al*., 2014), and at least two major mechanisms may underlie these patterns: First, increased EH, habitat types, resources and structural complexity should increase niche space availability, allowing more species to coexist (e.g. Tews *et al*., 2004). Second, areas of high EH provide species with shelter and refuge, promoting their persistence (e.g. Rilov & Benayahu, 2000). However, some studies have questioned the generality of positive HDR (e.g. Lundholm, 2009; Rohde, 1992) and others have found unimodal or negative effects (Bar-Massada & Wood, 2014; Gazol *et al*., 2013), suggesting that the effects of EH may vary considerably depending on the study scale and biological group. Some authors claim that in order to draw general conclusions on the HDR it is necessary to investigate the relationship not only at large but also at small scales (Ellingsen & Gray, 2002; Hewitt, Thrush, Halliday, & Duffy, 2005) and at different diel periods, as diurnal and nocturnal species explore the environment differently.

In marine ecosystems, ecologists have been showing for decades that the structural complexity of reef environments favors biodiversity, especially fish diversity (Bejarano, Mumby, & Sotheran, 2011; Caley & John, 1996; Charbonnel, Serre, Ruitton, Harmelin, & Jensen, 2002; Emslie, Cheal, Sweatman, & Delean, 2008; Fabi & Fiorentini, 1994; Friedlander, Brown, Jokiel, Smith, & Rodgers, 2003; Graham & Nash, 2013; Gratwicke

& Speight, 2005a, 2005b). These reef environments are irreplaceable and must be protected (Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011), but at least part of their structural complexity may somehow be reproduced in sunken vessels (hereafter vessel reefs), helping to shed light into community organization along marine environmental gradients (Arena, Jordan, & Spieler, 2007; Consoli *et al.*, 2014). Such artificial, structurally complex environments may harbor fish species of economic and ecological importance, as they provide refuge from predation and tidal currents and safe sites for growth, foraging and reproduction (Caley & John, 1996; Fabi & Fiorentini, 1994; Galamba, 2009; Pickering & Whitmarsh, 1997). By serving as fishery enhancement tool and recreational diving spots, vessel reefs may also reduce harvesting pressure on natural reefs (Bohnsack, 1989; Pickering & Whitmarsh, 1997). However, major knowledge gaps remain regarding their importance as biodiversity repositories, whether they are potential sources of pollutants, fish attractants from nearby natural reefs or fish producing areas (Consoli *et al.*, 2014; Renzi *et al.*, 2017).

At regional scale, vessel reefs provide hard substrata in areas dominated by soft sediments (Zintzen, Massin, Norro, & Mallefet, 2006). At local scale, they display different levels of structural complexity, representing a suitable system to empirically test how communities respond to EH at the scale of meters (Walker, Schlacher, & Schlacher-Hoenlinger, 2007). They allow examining whether within-habitat diversity (α-diversity) increases as EH increases, rising positive HDR, or whether among-habitat diversity (β-diversity) increases with habitat distinctness. Because β-diversity is related to the partitioning of environmental resources among species, it is also important to discern the mechanisms responsible for among-site variation (Anderson *et al.*, 2011). This β-component of diversity provides a conceptual framework to disentangle patterns of variation in species composition from site to site (Baselga, 2010, 2012; Wilson & Shmida, 1984), and is increasingly used to investigate the factors affecting the structure of communities (e.g. Ackerly & Cornwell, 2007; Pinheiro *et al.*, 2018; Püttker, Bueno, Prado, & Pardini, 2014). Nonetheless, their use is relatively less frequent in marine research compared to terrestrial environments (Harborne, Mumby, Zychaluk, Hedley, & Blackwell, 2006). Regardless of the environment, the differences in species composition between two (or more) sites are attributed to two main distinct phenomena: (1) the replacement of some species by others from site to site, called spatial turnover (Gaston & Blackburn, 2000) or (2) nestedness, a pattern where the poorest site is a strict subset of the richest site (Baselga, 2012). Studies based on β-diversity measures have shown that the reduction of structural complexity due to habitat degradation may promote biotic homogenization through increased community similarity and decreased species turnover (Hewitt *et al.*, 2005; Olden & Rooney, 2006).

In this study, we used fish communities from four Southwestern Atlantic vessel reefs to assess whether positive heterogeneity-diversity relationships (HDR) hold for these mobile organisms and whether the relationships weaken with nightfall. This weakening is expected because proximate shelter may become less critical at night, as predators that threaten smaller and most abundant fishes by day are largely inactive, or shift to other preys (Hobson, 1973, 1979). This way, many species that inhabit high complexity areas in daylight may be elsewhere in the vessel or explore open regions after nightfall (Fitzpatrick, McLean, & Harvey, 2013). We sampled fishes over day and night in three habitats with contrasting structural complexity and employed two complementary diversity frameworks: a community-level approach able to partition gamma diversity into independent alpha and beta components (Jost, 2007) and partitioning of beta diversity into turnover and nestedness components (Baselga, 2010). We adopted a method of assessing structural complexity in aquatic environments, the habitat assessment score

(Gratwicke & Speight, 2005b), and examined the following predictions: (1) high complexity areas would present greater alpha diversity of rare, typical and dominant species than low complexity and control areas; (2) variation in structural complexity would select particular species to occupy different areas of the vessel, preventing homogenization and increasing beta diversity along the complexity gradient; and (3) nestedness would be more important than turnover in shaping beta diversity, with local communities of less complex and control areas being a subset from those of more complex areas due to high mobility of fish species. We also expected that the effect of structural complexity on fish diversity should be diluted at night at both alpha and beta scales, resulting in smaller differences across the complexity gradient.

Materials and methods

Study sites

We conducted the study in the eastern coast of Northeast Brazil, which is part of the tropical Southwestern Atlantic province (Spalding *et al*., 2007) and composes the largest and richest reef formation of the South Atlantic ocean (Leão *et al*., 2016) (Fig. 1). The continental shelf is relatively short (35-km wide), most of it lies at depths smaller than 40 m and the break occurs at 75 m (Morais & Santos, 2018). Water temperature is relatively constant around 28-29°C up to the 50 m; after this depth a sharp thermocline of unknown seasonality reduces the temperature to about 23-24°C (Feitoza, Rosa, & Rocha, 2005). We carried out our sampling in four vessel reefs locally named Alice, Alvarenga, Queimado and Vapor Bahia, all products of accidental sinking in this region between 1873 and 1926 (Fig. 1; Table 1). They rest between 7 and 25 m depth, 6.5 to 15 km away from the coast on unconsolidated bottom (sand and/or gravel), and are quite different in terms of material, length and current status of conservation (Table 1).

Structural complexity

To estimate the level of structural complexity, we first made a detailed evaluation of each shipwreck combining information from local dive operators, sketch and visual estimates of its features. In each shipwreck we identified a representative area of high and another of low structural complexity, as well as control areas on unconsolidated bottoms about 10 m away from it, not including artificial structures (Appendix S1). To validate this classification, we adapted the habitat assessment score method (Gratwicke & Speight, 2005b) and measured five variables of structural complexity: variety of structures, maximum height of structures, number of possible refuges, refuge size categories and percentage of hard substratum (Appendix S1). The scores obtained for the three categories of complexity were clearly different, supporting our classification (Table 1).

Fish sampling

To sample the fish communities, we performed 14 SCUBA dives in 2015 and 2018. We surveyed each vessel reef twice on different days, except the Vapor Bahia, which was sampled once. In each category of complexity, we carried out 7-minutes timed transects using digital video records (GoPro Hero 4 and 5) along the high complexity, low complexity and control areas during day and night of the same day. This prevented daily variations in environmental conditions from confusing the effect of complexity on fish diversity. We proceeded a “U pattern” search technique (Oldenhuizing, 2005) which consists in swimming straight along the entire length of the area, turning 90°, swimming a short distance, then turning 90° back and swimming parallel to the initial way. We repeated the procedure each time we arrived at the other side and alternated the direction to maximize search area coverage and exclude excessive redundancy.

We focused on fishes present throughout the water column, since the cryptic species tend to hide when perceiving diver movement. We identified the observed fishes to the lowest possible taxonomic level through video observations. Their taxonomic identity was confirmed by combining information of literature (Humann & DeLoach, 2014), online databases (www.fishbase.org) and our own experience working in the region for decades (R. S. Rosa is the curator of UFPB's fish collection since the 80's). We pooled the observations of the two days of sampling in each category of complexity to represent a local community. Hence, each vessel exhibited six local communities, three at day and three at night, and two metacommunities, one at day and other at night. In each local community, we estimated species relative abundance by counting the maximum number of individuals (MaxN) of a particular species seen simultaneously in a video frame (Barley, Meekan, & Meeuwig, 2017; Fitzpatrick *et al.*, 2013; Lindfield, Harvey, Halford, & McIlwain, 2016). This procedure avoided recounting the individuals that may eventually leave and return to the angle of view of the camera.

Diversity estimation

In order to check if local communities were sufficiently sampled, we first assessed the abundance-based sample coverage through iNEXT software (Hsieh, Ma, & Chao, 2016). The sample coverage is a measure of sample completeness, giving the proportion of the total number of individuals in a community that belong to the species represented in the sample (Chao & Jost, 2012).

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 and f_2 are the number of species represented by one (singletons) and two (doubletons) individuals, respectively, and n is the total number of individuals in each local community. We assumed as standard a minimum coverage of 0.50 (i.e., 50%) per treatment following the recommendations of Chao and Jost (2012) as a reliable value for coverage extrapolation and species richness estimation. With this approach we were able to compare samples of the same completeness rather than equal size (Chao & Jost, 2012; Hsieh *et al*., 2016). Sample coverage exceeded 80% in most communities, including those of Vapor Bahia, and none was below 50%.

We estimated Jost's diversity using *entropart* (Marcon & Hérault, 2015) available on R (R Core Team, 2016), a package able to partition diversity into independent alpha and beta components. It performed multiplicative diversity decompositions based on the effective numbers of species (Hill numbers, ${}^{q}D$) in its unweighted form (Jost, 2007). ${}^{q}D$ is an ecologically intuitive measure for describing and comparing diversity (Jost, 2006). For S species, gamma (γ) diversity of order q was defined as:

$$ {}^{q}D_{\gamma} = \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)} $$

where S is the number of species in the vessel reef, p_i is the relative abundance of individuals of the ith fish species, and q is a parameter that controls the measure's sensitivity to species relative abundances (Jost, 2007; Tuomisto, 2010). Following the same rationale, the alpha (α) component of diversity was defined as:

$$ {}^{q}D_{\alpha} = \left(\frac{1}{N} \sum_{i=1}^{S} p_{i1}^q + \frac{1}{N} \sum_{i=1}^{S} p_{i2}^q + \ \dots \right)^{1/(1-q)} $$

where Pi denotes the relative abundance of the ith species in each of the N local communities (Jost, 2007). We estimated the alpha diversity of rare (${}^{0}D$), typical (${}^{1}D$), and dominant (${}^{2}D$) species. ${}^{0}D$ represents the number of species, is not sensitive to species abundance and gives a disproportionate weight to rare species (Jost, 2006). ${}^1D$ weights each species according to its proportional abundance in the sample and can be interpreted as the number of typical species in the community (Jost, 2006). Finally, ${}^2D$ raises species abundance to the power 2, giving more weight to more abundant, dominant species in the community (Jost, 2006).

To estimate the beta component of Jost's approach (Jost, 2007), we adopted the multiplicative diversity partition (Jost, 2007, 2010) defined as:

$$ {}^qD_\beta = \frac{{}^qD_\gamma}{{}^qD_\alpha} $$

This metric expresses the 'effective number of completely distinct communities' (Jost, 2007), as it ranges between 1 (when all communities are identical) and N (when all communities are completely different from each other). Because we sampled three communities per vessel, values of beta diversity could vary between 1 and 3, indicating no or strong effect of structural complexity on beta diversity, respectively.

In addition, we employed Baselga's framework to estimate the relative contribution of turnover and nestedness in determining beta diversity patterns, i.e., the total dissimilarity between two communities (Baselga, 2010a,b). Based on an additive property of both components, this approach allows the total Sorensen dissimilarity coefficient to be partitioned into components of dissimilarity due to turnover and nestedness. We carried out this analysis on R software using the *betapart* package (Baselga, Orme, Villeger, & Leprieur, 2018).

Statistical analyses

We constructed non-metric Multi-Dimensional Scaling (nMDS) ordination plots based on Bray-Curtis similarities to provide a graphical presentation of community interrelationships (Clarke, 1993). We performed Analysis of Similarity (ANOSIM) from the full set of samples to determine the extent to which fish composition differed among the complexity levels and diel periods. To determine the relative contribution of particular species to the similarity and dissimilarity among treatments, we carried out Similarity Percentage analysis (SIMPER) using the Primer 6 statistical package.

We used linear mixed models using the package *Lme4* (Bates, Mächler, Bolker, & Walker, 2015) available in R. to assess the effect of complexity and diel period on alpha diversity of rare (${}^0D$), typical (${}^1D$) and dominant species (${}^2D$). We set structural complexity level, diel period and their interaction as fixed effects and vessels as random effect, to control for potential confounding effects inherent to the vessels, such as their age, material, length, depth, and distance from the coast.

To test if beta diversity of rare, typical and dominant species were significantly different from 1 (i.e. null statistical hypothesis of no effect of complexity on Jost's beta diversity), we carried out one-sample t-tests comparing the observed means against 1. To test whether the effect of structural complexity on beta diversity was weaker at night, we performed a two-way t-test between diurnal and nocturnal beta diversity values. Two-way t-tests were also applied to compare values of turnover and nestedness between day and night.

Results

Overview of fish composition

We recorded 5005 individuals belonging to 76 fish species and 31 families (Table S1 and S2). With all vessel reefs combined, the most abundant taxa were *Clupeidae sp* (902 individuals, 18%), followed by *Haemulon squamipinna* (788 individuals, 16%), *Pempheris schomburgkii* (578 individuals, 12%), *Mulloidichthys martinicus* (456 individuals, 9%) and *Haemulon aurolineatum* (451 individuals, 9%), accounting for 63% of the fishes recorded (Fig. S1).

Overall, we found greater species richness and abundance in diurnal (71 species, 4666 individuals, 93% of richness and abundance respectively) than in nocturnal records (39 species, 339 individuals, 51% of species and 7% of individuals). Eighteen species (24%) occurred in the four vessels, and 29 species (38%) were exclusive to one vessel. Concerning to structural complexity gradient, we found 57 fish species (2836 individuals) in high complexity areas and 52 species (1385 individuals) in low complexity areas. The control areas showed the lowest abundance and richness (784 individuals, 39 species).

ANOSIM results indicated a strong effect of diel period on fish species composition ($\text{ANOSIM}_{\text{day-night}}$; R= 0.423, p= 0.001) and a weak but also significant effect of structural complexity on species composition ($\text{ANOSIM}_{\text{high-low-control}}$; R= 0.168, p= 0.013) (Fig. 2). This weak effect occurred because high and low complexity differed little to each other and made up a group that differed more from the control areas (Fig. 2). SIMPER analyses suggested a relatively high dissimilarity between diurnal and nocturnal groups of species (average dissimilarity: diurnal-nocturnal = 83.54) and among the species groups on paired complexity levels (average dissimilarity: high-low = 67.90; high-control = 82.51; low-control = 82.31; see Table S3 for the top 5 species contributing to compositional patterns).

Alpha diversity

Consistent with positive HDR, the mean effective number of rare species (${}^{0}D$) doubled from control to high complexity areas and decreased by half from day to night (Fig. 3). The increase in the diversity of rare species from control to high complexity areas occurred irrespective to diel period, as indicated by the interaction term that was not significant (Table 2).

The mean effective number of typical species (^1D) also showed a twofold increase from control to high complexity areas regardless diel period, but day and night showed similar values of diversity (Fig. 3; Table 2). On the other hand, the mean effective number of dominant species (^2D) did not vary with structural complexity, diel period and their interaction (Fig. 3; Table 2).

Beta diversity

Beta diversity of rare, typical and dominant species were significantly greater than 1, indicating a clear effect of structural complexity on spatial distribution of diversity (Fig. 4; Table S4). However, the effect was not diluted at night as expected, averaging about 1.8 distinct communities at both diel periods. Beta diversity of typical and dominant species tended to be greater at night (Fig. 4), suggesting that typical and dominant species, though less numerous at night, were more spatially segregated across the gradient of complexity. However, two-way t-tests failed to support such differences ($p>0.05$ for both beta ^1D and beta ^2D).

Baselga's beta diversity decoupled in its nestedness and turnover components showed that in both day and night periods, the community dissimilarity among the different levels of complexity was mostly driven by turnover, contradicting our expectation of greater importance of nestedness. Turnover was on average 2.8 and 1.9 greater than nestedness at day and night, respectively (Fig. 4).

Discussion

Our findings not only support the positive environmental heterogeneity-diversity relationships in fish communities, but also indicate that the positive effect of environmental heterogeneity on diversity is more constant than previously envisioned. The alpha diversity of rare and typical species clearly increased in high complexity areas. Dominant species did not become significantly more numerous in high complexity areas, but like rare and typical species, responded to heterogeneity by replacing each other across the complexity gradient. The role of structral complexity in shaping compositional patterns was also supported by the ordination, which revealed taxonomic differences between control areas and high/low complexity areas. Nighfall reduced alpha diversity of rare species and tended to rise beta diversity of typical and dominant species, but did not weaken the strenght of HDRs neither affected the contribution of nestedness and turnover in determining community dissimilarity. This suggests that the role of EH on fish community structure remains strong even in the absence of light.

Our findings are consistent with studies linking increased EH (or any equivalent terms and measures) to increased fish abundance and species diversity in both natural and artificial reefs of temperate and tropical waters (Charbonnel *et al*., 2002; Davis & Smith, 2017; Dominici-Arosemena & Wolff, 2005; Friedlander *et al*., 2003; Hunter & Sayer, 2009). Together, these studies contribute to a view of structural complexity as a driver of fish species diversity and spatial differentiation of fish communities in reef ecosystems. In the context of artificial reefs, most highlight the importance of increasing structural complexity on reef design to favor fish diversity. However, some findings challenge this notion of linear, positive HDRs. For instance, Paxton *et al*. (2017) suggests that fish community metrics (richness and abundance in this case) on natural reefs in temperate zones may be maximized in intermediate rather than high complexity levels, suggesting nonlinear HDRs depending on the biogeographic zone and reef origin (natural or artificial).

Our analyses of species composition revealed a group of control areas and another with low and high complexity areas. Apparently, the vessel reefs are acting as keystone structures on the ocean floor, which are defined as distinct spatial structures that provide species with crucial resources and shelter, as well as goods and services (Tews *et al.*, 2004). Because fishes require appropriate environmental conditions, food, refuge and areas for spawning and recruitment (Morrissey & Sumich, 2011), increased fish diversity may indicate that these structures provide high environmental quality able to support the specific requirements of many fish species. On the other hand, vessel reefs are unlikely to have a strong effect on species that recruit in non-reef habitats or whose life history stages are not dependent on reef environments. Some examples are commercially important species as snappers, groupers, grunts and barracudas, which first settle in sand, sea grasses, mangroves and estuaries (Bohnsack, 1989). Although they may be observed in reef environments (e.g. barracudas in this study), they are not strongly influenced by the structural complexity of these environments. Gregarious, roaming or facultative reef species that exhibit less substrate attachment and site dependency (as mackerels, jacks and barracudas), may be attracted by reef structures whilst production enhancement is more likely for territorial/obligatory reef species that are more habitat-limited, such as damselfishes (Medeiros, Medeiros, & Rosa, 2016).

The clear segregation in species composition between day and night was not surprising. Similar day-night shifts have also been documented in other studies (e.g. Azzurro, Pais, Consoli, & Andaloro, 2007; Harvey, Butler, McLean, & Shand, 2012;

Nagelkerken *et al*., 2000), with many more individuals and species observed in diurnal samplings. However, the higher contribution of turnover over nestedness along the complexity gradient at both diel periods contradicted our expectation that communities of control and low complexity areas would be subsets from the high complexity areas. This suggests that although fishes have enough mobility to get to any area of the vessel, they do select their environment at very fine scale. When this microhabitat selection is scaled up from population to the community level, areas with distinct structural attributes select different pools of species, resulting in high spatial turnover even at the scale of meters. Interestingly, the phenomenon of increased turnover among areas with contrasting complexity areas remains at night despite the fact that microhabitat associations may vary with diel periods (Harvey *et al*., 2012; Nagelkerken *et al*., 2000).

The high turnover along the complexity gradient in the presence of high dispersal ability indicates that the metacommunities are structured by a mix of species-sorting and mass-effects related mechanisms (Leibold *et al*., 2004). Briefly, species sorting presumes that species are separated into spatial niches, but there is insufficient dispersal to alter their distribution (Leibold *et al*., 2004). This generates high beta diversity across the local communities that compose the metacommunity. On the other hand, mass effects presume that species are not dispersal limited, sustain larger populations in high quality sites and may rescue or maintain smaller populations in low quality sites through emigration (Leibold *et al*., 2004). Because there are many movement of individuals from many species, low beta diversity is expected under this scenario (Mouquet & Loreau, 2003). In our study, the largest vessel is about 100 m length, a distance that can be virtually swamped by all species recorded. In this sense, dispersal should have resulted in low turnover and high nestedness among the complexity levels, but we found the opposite.

Besides suggesting a mixed model of metacommunity structure, the unexpected result of high turnover reinforces the importance of EH in structuring fish communities.

Our findings also highlight that protecting heterogeneous habitats, such as structurally complex shipwrecks and pristine coral reefs, is critical for conserving and managing marine fish diversity. Reef environments throughout the world are facing habitat degradation and reductions in structural complexity, which may not only affect diversity in the short term but also result in disadvantages for reef fisheries and long-term impacts on the ecosystem. Artificial reefs, often used to supplement fauna and mitigate environmental impacts to natural reefs (Abelson & Shlesinger, 2002; Ambrose, 1994; Reed, Schroeter, Huang, Anderson, & Ambrose, 2006), have the potential to provide alternative, environment-friendly fishery sources and recreation sites (Seaman & Sprague, 1991). The observed patterns of alpha and beta diversity across areas of different structural complexity imply that conservation must target multiple sites in order to capture this variation (Socolar, Gilroy, Kunin, & Edwards, 2016). We argue that (1) managers of artificial reefs should focus on maintaining structural complexity, because it may support fish diversity and enhance fishery productivity; (2) conservationists should prioritize the protection of high complexity natural reefs worldwide; and (3) politicians should focus in reducing economic activities that directly compromise reef structural complexity.

A substantial portion of both natural and artificial reefs of Brazilian northeastern coast is located over a narrow continental shelf, ranging from 15 to 50 km width (Moura, 2000). These environments are directly subjected to threats from increasing urbanization, coastal agriculture expansion, deforestation and uncontrolled reef resource exploitation (Floeter, Halpern, & Ferreira, 2006; Leão & Kikuchi, 2005), that can lead to biodiversity loss (D’agata *et al.*, 2016). The states of Paraíba and Pernambuco include other shipwrecks of economic and cultural value for sustaining fisheries and diving activities. The studied vessel reefs provide evidence of shipwrecks' potential to enhance local fish diversity. This importance has been recently recognized with the inception of the Queimado Shipwreck Marine Protected Area (*Área de Proteção Ambiental Naufrágio Queimado*; state decree no. 38,931, December 28th 2018), which also encompasses the Alice and Alvarenga along with shallow and deep natural reefs over 422 km^2. By demonstrating that the high complexity areas safeguard fish diversity, we expect to convince local practitioners involved in fishery and tourism activity about the urgent need to protect structurally complex marine habitats.

In summary, through simple measurements of structural attributes, we provide evidence of mechanisms driving spatial patterns of fish diversity in vessel reefs and emphasize the need for actively managing artificial reef habitats. By demonstrating that increased fish diversity is associated with structural complexity, our results support the view that marine habitat degradation may lead to biotic homogenization of fish communities and species loss at local scale. Further studies in other marine ecoregions will help to produce a more comprehensive picture of role of EH on fish diversity at broader spatial scales.

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Figure legends

Figure 1. On the left, map showing South America and Brazil, dark point in detail indicates the sampling area. Zoomed views show the location of the four investigated shipwrecks: Alice, Alvarenga, Queimado and Vapor Bahia. On the right, schematic drawing and photograph of the shipwrecks, in the same order as they appear on the map. Photos by Diego Luna and Max Glegiston, sketches by Maurício Carvalho and Bertran Feitoza.

Figure 2. Non-metric multidimensional scaling plots based on Bray-Curtis similarity indices showing the composition of fish communities among three different levels of complexity (high, low, control; panel A) and two diel periods (day, night; panel B).

Figure 3. Jost's alpha diversity, expressed as mean effective number of species, of rare (^{0}D), typical (^{1}D), and dominant (^{2}D) fish species in three categories of structural complexity (control, low, high) at day and night periods. Vertical bars represent standard error.

Figure 4. Beta diversity based on Jost's (left) and Baselga's (right) approaches. The left panel shows the mean effective number of distinct communities of the four vessels considering rare (^{0}D), typical (^{1}D) and dominant (^{2}D) fish species at day and night. Note that all values are significantly greater than 1, which represents the null statistical hypothesis of no effect of structural complexity on beta diversity (see Table S4). On the right panel, the mean relative contribution of nestedness and turnover components at day and night. Vertical bars represent standard error.

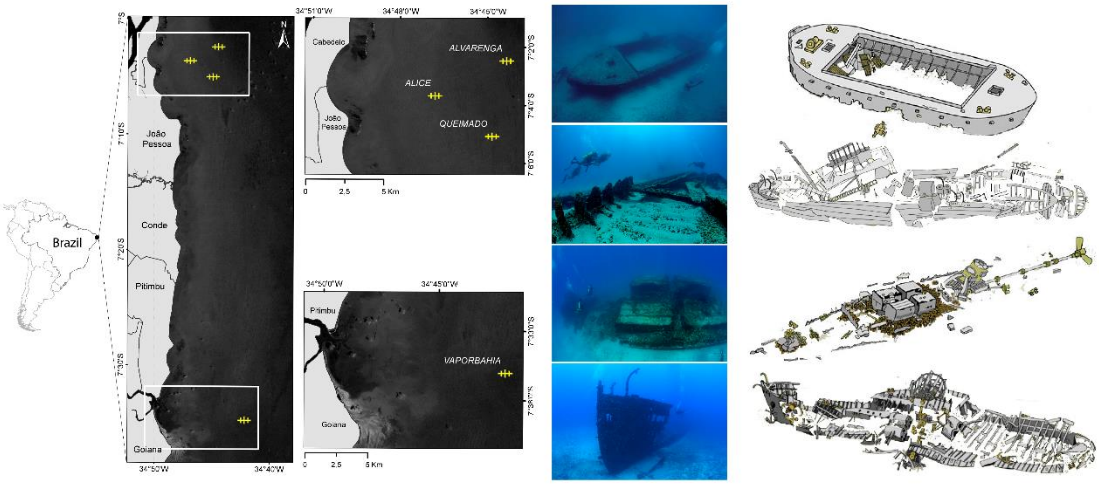
Brazil
7°S
7°10'S
7°20'S
7°30'S
João Pessoa
Conde
Pitimbu
Goiana
34°50'W
34°40'W
N
34°51'0"W
34°48'0"W
34°45'0"W
Cabedelo
João Pessoa
ALVARENGA
ALICE
QUEIMADO
7°2'0"S
7°4'0"S
7°6'0"S
0
2.5
5 Km
34°50'0"W
34°45'0"W
Pitimbu
Goiana
VAPORBAHIA
7°33'0"S
7°36'0"S
0
2.5
5 Km

Figure 1

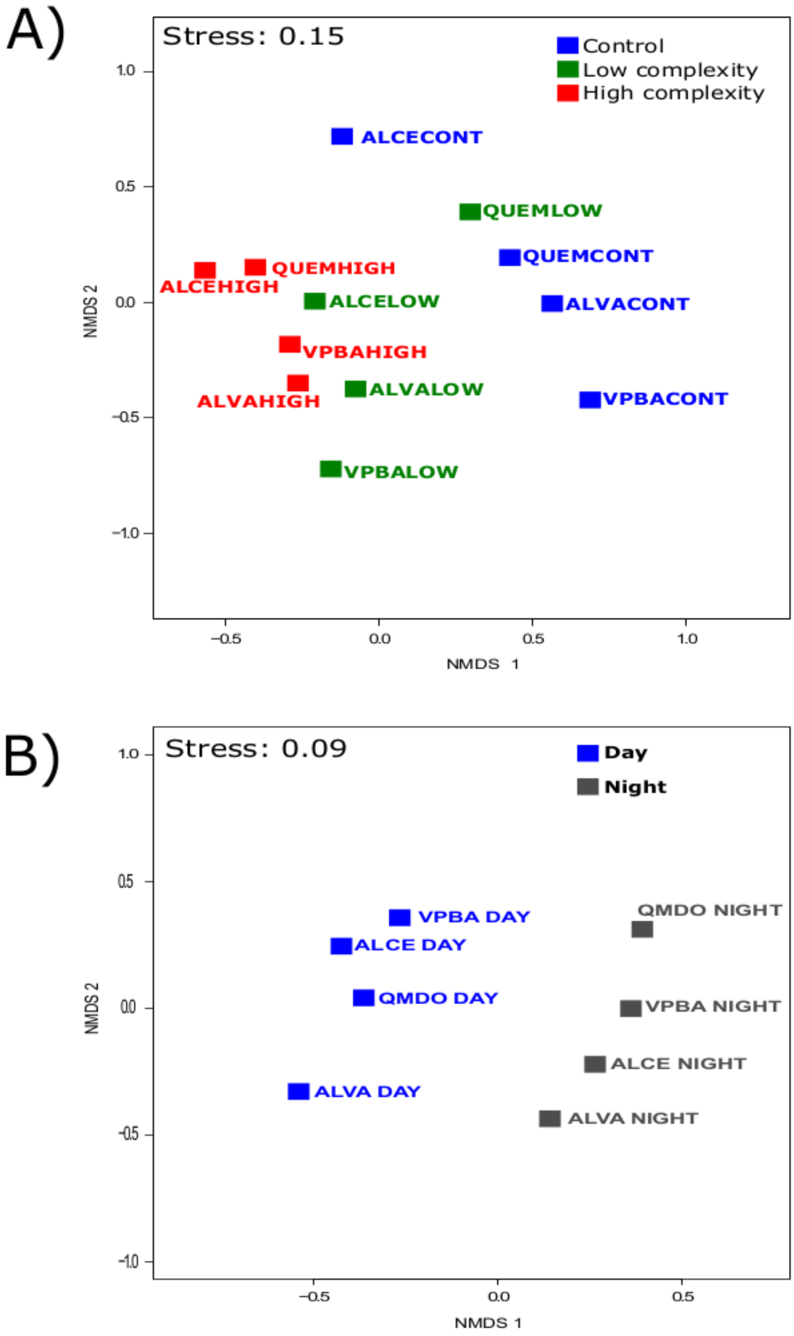
A)
Stress: 0.15
Control
Low complexity
High complexity
ALCECONT
QUEMLOW
QUEMHIGH
ALCEHIGH
QUEMCONT
ALCELOW
ALVACONT
VPBAHIGH
ALVAHIGH
ALVALOW
VPBACONT
VPBALOW
1.0
0.5
0.0
−0.5
−1.0
NMDS 2
−0.5
0.0
0.5
1.0
NMDS 1
B)
Stress: 0.09
Day
Night
VPBA DAY
QMDO NIGHT
ALCE DAY
QMDO DAY
VPBA NIGHT
ALCE NIGHT
ALVA DAY
ALVA NIGHT
1.0
0.5
0.0
−0.5
−1.0
NMDS 2
−0.5
0.0
0.5
NMDS 1

Figure 2.

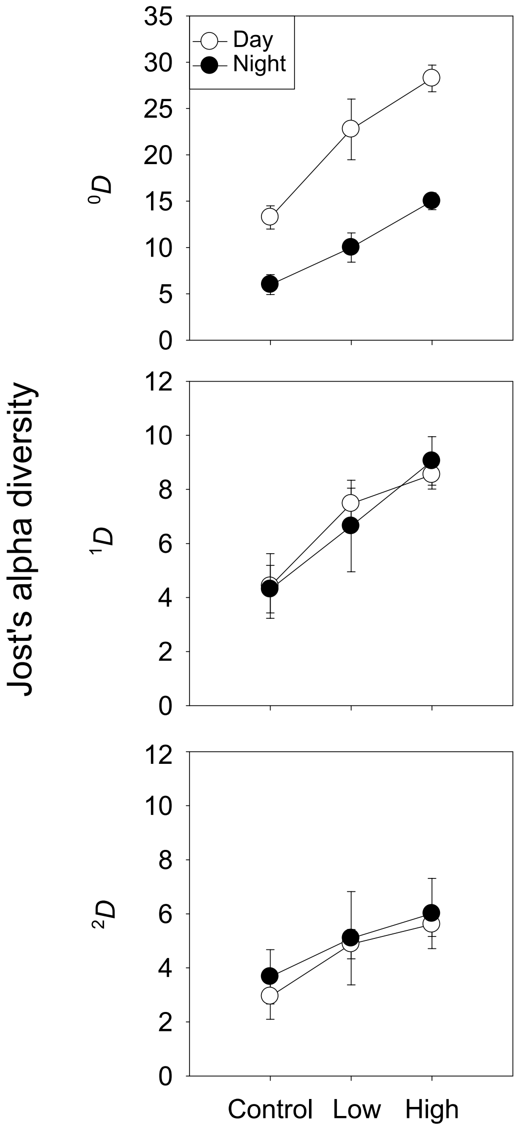
Day
Night
Jost's alpha diversity
^0D
35
30
25
20
15
10
5
0
^1D
12
10
8
6
4
2
0
^2D
12
10
8
6
4
2
0
Control
Low
High

Figure 3.

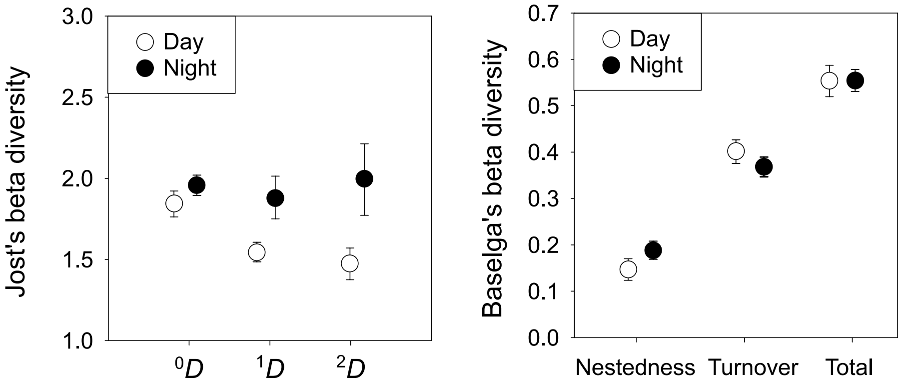
Jost's beta diversity
3.0
2.5
2.0
1.5
1.0
○ Day
● Night
^0D
^1D
^2D
Baselga's beta diversity
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
○ Day
● Night
Nestedness
Turnover
Total

Figure 4.

Table 1. General characteristics of the four shipwrecks studied in Northeast Brazil (CARVALHO; ACCIOLY, 2019; OLIVEIRA, 2010), with the total habitat assessment score (HAS; modified from Gratwicke & Speight, 2005b) used to classify high complexity, low complexity and control areas (see also Appendix S1).

General characteristics	**Alice**	**Alvarenga**	**Queimado**	**Vapor Bahia**
Type of vessel	Steamship	Barge	Steamship	Steamship
Material	Steel	Iron	Wood and metal	Iron
Condition	Dismantled	Whole	Dismantled	Dismantled
Year sunk	1911	1926	1873	1887
Distance from the coast (nmi)	3.5	6	5	8
Length overall (m)	53	20	103	80
Greatest Breadth (m)	6.7	5	13	10
Depth (m)	07 - 12	18 - 20	12 - 18	18 - 25
Total HAS				
High complexity area	24	18	23	24
Low complexity area	13	12	12	19
Control area	5	5	5	5

Table 2. Summary of results from linear mixed models testing the effect of structural complexity, diel period and their interaction on the effective number of rare (^{0}D), typical (^{1}D) and dominant (^{2}D) fish species. Coefficient in bold indicates significant p-value (p<0.05).

Response variable	**Fixed effects**	**DF**	**F-value**	**p-value**
^{0}D	Complexity	2,15	24.02	**<0.0001**
	Period	1,15	61.15	**<0.0001**
	Complexity*Period	2,15	1.84	0.193
^{1}D	Complexity	2,15	9.12	**<0.01**
	Period	1,15	0.03	0.867
	Complexity*Period	2,15	0.20	0.818
^{2}D	Complexity	2,15	2.77	0.094
	Period	1,15	0.25	0.619
	Complexity*Period	2,15	0.03	0.972

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1. Details of habitat assessment score in each shipwreck studied in Northeast Brazil.

Table S1. List of fish species recorded in the study, including their status of conservation and level of endemism in Southwestern Atlantic Ocean.

Table S2. Raw data of total fish abundance, alpha and beta diversity of rare, typical and dominant species in the 24 local communities studied in Northeast Brazil (six per shipwreck).

Table S3. Top 5 species that contributed more to compositional patterns among the three levels of structural complexity and between the diel periods.

Table S4. Results of one-way t-tests applied to assess if beta diversity of rare, typical and dominant species differed from 1 (null hypothesis of no effect of structural complexity on fish diversity).

Figure S1. Species-rank abundance curves for each shipwreck separately, by diel period and for all species together.

Appendix S1. Vessel reefs' structural complexity assessment.

To assess the structural complexity, we used modified categories of the habitat assessment score (HAS) proposed by Gratwicke and Speight (2005). The aim of this score is to estimate the variety of structural attributes of the shipwrecks that potentially provide resources and refuge for different fish species. We selected five types of structural complexity variables: variety of structures, maximum height of structures, number of possible refuges, refuge size categories and percentage of hard substratum. The HAS of these categories was estimated visually through video and author's *in situ* observations. We set five possible classes for each of these variables, every class corresponding to a score, as follows:

Table 1. Habitat assessment score (HAS) variables and categories used in this study to classify areas of high complexity, low structural complexity and control areas.

HAS variables	**Score**				
	1	**2**	**3**	**4**	**5**
Variety of structures	0 to 2	3 or 4	5 or 6	7 or 8	>8
Max height of structures (m)	<1	1-3	3-5	5-7	>7
Number of possible refuges	0 to 9	10 to 19	20 to 39	40 to 59	>60
Refuge size categories (cm)	0–5	6–15	16–30	31–50	>50
Hard substratum (%)	0-19	20-39	40-59	60-79	80-100

For variety of structures, we apprised the amount of vessel parts (e.g. winch, plate, mast, propeller, anchor, etc.) present in a particular area. If there were from none to two structures, it would score 1; three or four structures would score 2, and so on. We then estimated the average height of the observed structures and fit into the categories. We also estimated the amount and size of possible refuges, which include holes, gaps or any potential hideouts formed by these structures. Hard substratum referred to the percentage of substratum that was not mud, sand or rubble. The sum of the scores of each of the five variables for a particular area corresponded to its total habitat assessment score.

Table 2. Habitat assessment scores of high complexity, low complexity and control areas of each surveyed shipwreck (Alice, Alvarenga, Queimado and Vapor Bahia). The "+" following the shipwreck names indicates the high complexity areas, the "-" indicates the low complexity areas and the "c" indicates the control areas.

	Variety of structures	**Max height of structures**	**N^o of possible refuges**	**Refuge size categories**	**Hard substratum**	**Total**
Alice +	5	4	5	5	5	24
Alice -	2	1	3	4	3	13
Alice c	1	1	1	1	1	5
Alvar +	3	2	4	5	4	18
Alvar -	1	2	2	5	2	12
Alvar c	1	1	1	1	1	5
Queim +	4	4	5	5	5	23
Queim -	2	2	1	5	2	12
Queim c	1	1	1	1	1	5
Vapor +	5	4	5	5	5	24
Vapor -	4	3	4	5	3	19
Vapor c	1	1	1	1	1	5

The schematic representation below shows the location of the sampling areas (Fig. 1). We also present the ships parts that were identified at high and low complexity areas of the four shipwrecks (Table 3).

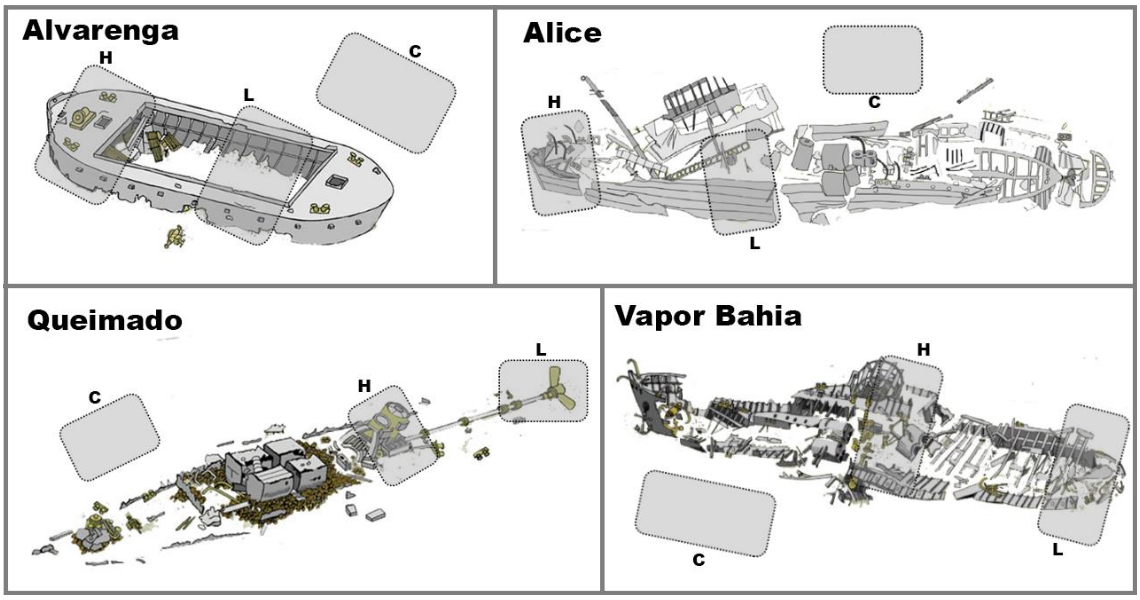

Figure 1. Schematic drawing of the shipwrecks highlighting the selected area of high (H) and low (L) structural complexity within each one, as well as the control (C) areas on adjacent unconsolidated bottom.

Table 3. Ship parts that make up the areas of high and low complexity of each surveyed shipwreck.

	Alice	**Alvarenga**	**Queimado**	**Vapor Bahia**
High complexity	Port outer plating; Starboard outer plating; Anchors; Assorted remains	Port outer plating; Starboard outer plating; Upper deck plating; Bollards; Winch; Assorted remains	Engine; Engine pistons; Assorted remains	Paddle wheel; Crankshaft; Boilers; Cockpit fragments; Starboard outer plating; Ribs; Assorted remains

	Alice	**Alvarenga**	**Queimado**	**Vapor Bahia**
Low complexity	Port outer plating; Assorted remains	Port outer plating; Starboard outer plating	Propeller shaft; Two-blade propeller	Port outer plating; Starboard outer plating; Ribs; Rudder; Assorted remains

References

Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, *66*(3), 650–667. doi:10.1111/j.1095-8649.2005.00629.x

Table S1. Checklist of the fish species recorded at four vessel reefs, locally named Alice, Alvarenga, Queimado and Vapor Bahia, in the northeastern coast of Brazil. Orders and families are listed in phylogenetic order following Nelson, Grande, and Wilson (2016). Species nomenclature follows Eschmeyer, Fricke, and Van der Laan (2019), and are listed in alphabetical order. Conservation status according to IUCN (2019): Endangered (EN), Vulnerable (VU). Southwestern Atlantic endemic (SWAE) species follow Pinheiro et al. (2018, available online at https://swatlanticreeffishes.wordpress.com).

Order	**Family**	**Species**	**IUCN**	**SWAE**
Orectolobiformes	Ginglymostomatidae	*Ginglymostoma cirratum*		
Anguilliformes	Muraenidae	*Gymnothorax funebris*		
Anguilliformes	Muraenidae	*Gymnothorax vicinus*		
Anguilliformes	Muraenidae	*Muraena pavonina*		X
Anguilliformes	Ophichthidae	*Myrichthys ocellatus*		
Clupeiformes	Clupeidae	*Clupeidae sp*		
Lophiiformes	Ogcocephalidae	*Ogcocephalus vespertilio*		
Beryciformes	Holocentridae	*Holocentrus adscensionis*		
Beryciformes	Holocentridae	*Myripristis jacobus*		
Perciformes	Serranidae	*Alphestes afer*		
Perciformes	Serranidae	*Epinephelus adscensionis*		
Perciformes	Serranidae	*Epinephelus itajara*	VU	
Perciformes	Serranidae	*Cephalopholis fulva*		
Perciformes	Serranidae	*Rypticus saponaceus*		
Perciformes	Opistognathidae	*Opistognathus aurifrons*		
Perciformes	Apogonidae	*Apogon americanus*		X
Perciformes	Malacanthidae	*Malacanthus plumieri*		
Perciformes	Echeneidae	*Echeneis naucrates*		
Perciformes	Carangidae	*Caranx bartholomaei*		
Perciformes	Carangidae	*Caranx ruber*		
Perciformes	Carangidae	*Caranx crysos*		
Perciformes	Carangidae	*Caranx latus*		
Perciformes	Carangidae	*Selene vomer*		
Perciformes	Carangidae	*Elagatis bipinnulata*		
Perciformes	Carangidae	*Trachinotus falcatus*		
Perciformes	Lutjanidae	*Lutjanus alexandrei*		X
Perciformes	Lutjanidae	*Lutjanus analis*		
Perciformes	Lutjanidae	*Lutjanus jocu*		
Perciformes	Lutjanidae	*Lutjanus synagris*		
Perciformes	Lutjanidae	*Ocyurus chrysurus*		
Perciformes	Haemulidae	*Anisotremus surinamensis*		

Order	**Family**	**Species**	**IUCN**	**SWAE**
Perciformes	Haemulidae	*Anisotremus virginicus*		
Perciformes	Haemulidae	*Haemulon aurolineatum*		
Perciformes	Haemulidae	*Haemulon parra*		
Perciformes	Haemulidae	*Haemulon plumierii*		
Perciformes	Haemulidae	*Haemulon squamipinna*		X
Perciformes	Haemulidae	*Haemulon steindachneri*		
Perciformes	Haemulidae	*Orthopristis ruber*		
Perciformes	Sciaenidae	*Odontoscion dentex*		
Perciformes	Sciaenidae	*Pareques acuminatus*		
Perciformes	Mullidae	*Mulloidichthys martinicus*		
Perciformes	Mullidae	*Pseudupeneus maculatus*		
Perciformes	Pempheridae	*Pempheris schomburgki*		
Perciformes	Kyphosidae	*Kyphosus incisor*		
Perciformes	Chaetodontidae	*Chaetodon ocellatus*		
Perciformes	Chaetodontidae	*Chaetodon striatus*		
Perciformes	Pomacanthidae	*Holacanthus ciliaris*		
Perciformes	Pomacanthidae	*Holacanthus tricolor*		
Perciformes	Pomacanthidae	*Pomacanthus paru*		
Perciformes	Cirrhitidae	*Amblycirrhitus pinos*		
Perciformes	Pomacentridae	*Abudefduf saxatilis*		
Perciformes	Pomacentridae	*Chromis multilineata*		
Perciformes	Pomacentridae	*Stegastes fuscus*		X
Perciformes	Pomacentridae	*Stegastes variabilis*		X
Perciformes	Labridae	*Bodianus rufus*		
Perciformes	Labridae	*Halichoeres brasiliensis*		X
Perciformes	Labridae	*Halichoeres dimidiatus*		X
Perciformes	Labridae	*Halichoeres penrosei*		X
Perciformes	Labridae	*Halichoeres poeyi*		
Perciformes	Labridae	*Thalassoma noronhanum*		X
Perciformes	Scaridae	*Scarus trispinosus*	EN	X
Perciformes	Scaridae	*Scarus zelindae*		X
Perciformes	Scaridae	*Sparisoma axillare*		X
Perciformes	Scaridae	*Sparisoma frondosum*		X
Perciformes	Scaridae	*Sparisoma radians*		
Perciformes	Ephippidae	*Chaetodipterus faber*		
Perciformes	Acanthuridae	*Acanthurus chirurgus*		
Perciformes	Acanthuridae	*Acanthurus coeruleus*		
Perciformes	Acanthuridae	*Acanthurus bahianus*		X
Perciformes	Sphyraenidae	*Sphyraena barracuda*		
Perciformes	Sphyraenidae	*Sphyraena guachancho*		
Perciformes	Sphyraenidae	*Sphyraena picudilla*		
Pleuronectiformes	Paralichthyidae	*Paralichthys brasiliensis*		X
Tetraodontiformes	Monacanthidae	*Cantherhines pullus*		

Order	Family	Species	IUCN	SWAE
Tetraodontiformes	Ostraciidae	*Acanthostracion polygonius*		
Tetraodontiformes	Diodontidae	*Diodon hystrix*		

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Table S2a. Fish abundances and Jost's alpha diversity values (orders ${}^{0}D$, ${}^{1}D$, ${}^{2}D$) for the four investigated shipwrecks (ALC: Alice; ALVA: Alvarenga; QMD: Queimado; VPB: Vapor Bahia) on each complexity level (high; low; control) and diel period (day; night).

Shipwreck	**Complexity**	**Period**	**Abundance**	${}^{0}D$	${}^{1}D$	${}^{2}D$
ALC	HIGH	DAY	432	26	7.43	4.57
ALC	LOW	DAY	404	25	5.91	3.57
ALC	CONTROL	DAY	93	10	2.92	1.92
ALC	HIGH	NIGHT	49	17	6.72	3.14
ALC	LOW	NIGHT	16	9	6.26	4.26
ALC	CONTROL	NIGHT	6	6	6	6
ALVA	HIGH	DAY	747	26	8.83	6.63
ALVA	LOW	DAY	554	27	8.62	5.77
ALVA	CONTROL	DAY	240	16	3.73	2.49
ALVA	HIGH	NIGHT	37	14	8.97	5.82
ALVA	LOW	NIGHT	20	12	10.9	10
ALVA	CONTROL	NIGHT	6	5	4.76	4.5
QMD	HIGH	DAY	1230	29	8.03	5.23
QMD	LOW	DAY	82	13	7.91	5.77
QMD	CONTROL	DAY	290	13	3.07	1.91
QMD	HIGH	NIGHT	29	13	11.07	9.44
QMD	LOW	NIGHT	60	6	2.63	1.89
QMD	CONTROL	NIGHT	26	9	4.64	2.79
VPB	HIGH	DAY	277	32	9.89	6
VPB	LOW	DAY	213	26	7.44	4.4
VPB	CONTROL	DAY	104	14	7.98	5.46
VPB	HIGH	NIGHT	35	16	9.45	5.64
VPB	LOW	NIGHT	36	13	6.79	4.23
VPB	CONTROL	NIGHT	19	4	1.83	1.39

Table S2b. Hill's beta diversity values (orders ^0D, ^1D, ^2D) among the three levels of complexity of each shipwreck on day- and nighttime (ALC: Alice; ALVA: Alvarenga; QMD: Queimado; VPB: Vapor Bahia).

Shipwreck	**Period**	^0D	^1D	^2D
ALC	DAY	1.81	1.41	1.3
ALC	NIGHT	1.96	2.08	2.37
ALVA	DAY	1.78	1.53	1.6
ALVA	NIGHT	1.83	1.83	1.94
QMD	DAY	2.07	1.57	1.31
QMD	NIGHT	1.92	1.52	1.39
VPB	DAY	1.7	1.65	1.68
VPB	NIGHT	2.09	2.07	2.27

Table S3. SIMPER percentages of the top 5 species contributing most to the compositional patterns among the levels of structural complexity (high, low, control) and between diel periods (day and night).

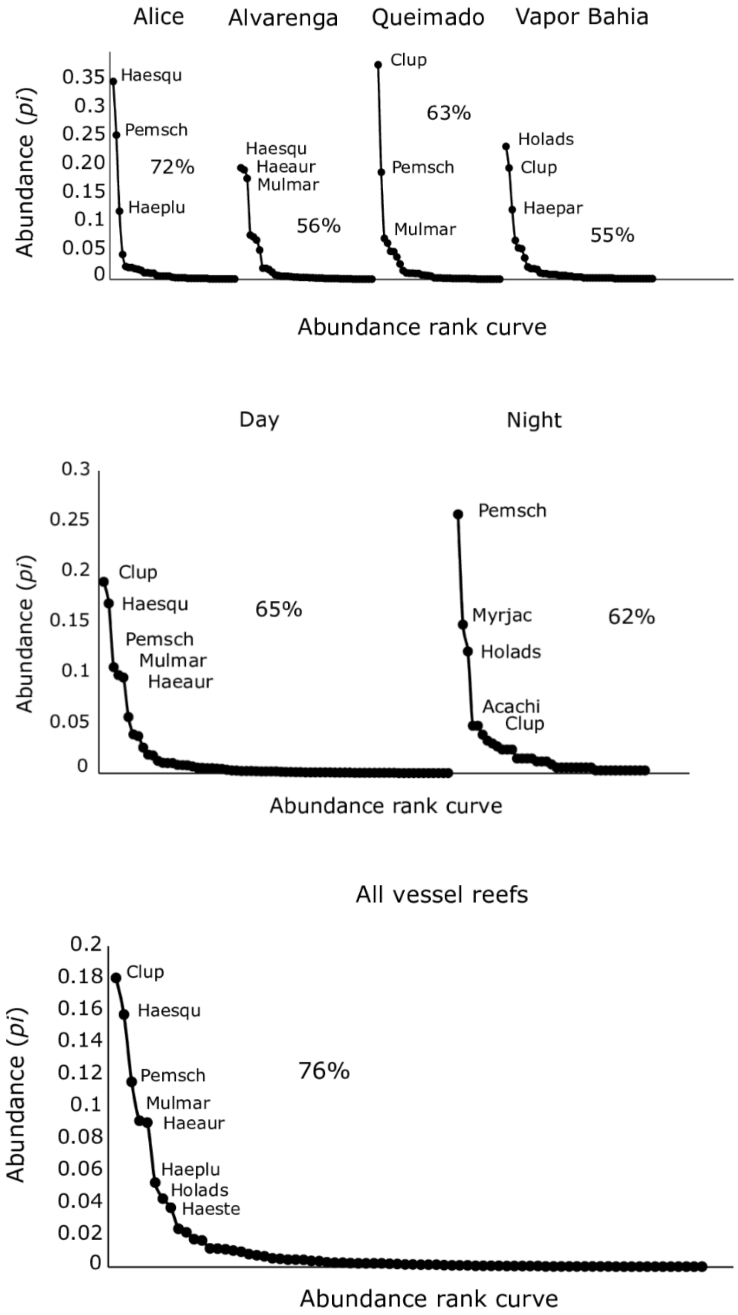
Group	**Main species**	**%Contribution**
Complexity		
High complexity		
Average similarity: 33.34	Myrjac	10.92
	Abusax	9.32
	Acacoe	8.61
	Anivir	8.15
	Holads	6.73
Low complexity		
Average similarity: 24.96	Myrjac	20.38
	Holads	15.14
	Anivir	10.2
	Acachi	8
	Acacoe	6.78
Control		
Average similarity: 15.49	Haeaur	29.07
	Anivir	11.59
	Clup	9.22
	Psemac	7.35
	Haeste	6.44
High & Low		
Average dissimilarity: 67.90	Pemsch	7.72
	Haesqu	7.62
	Clup	6.66
	Mulmar	5.16
	Holads	4.73
Low & Control		
Average dissimilarity: 82.31	Clup	7.38
	Haeaur	6.86
	Pemsch	6.76
	Haesqu	5.97
	Myrjac	5.88
High & Control		
Average dissimilarity: 82.51	Clup	7.8
	Haesqu	6.71
	Haeaur	6.16
	Pemsch	5.75

Group	**Main species**	**%Contribution**
	Myrjac	4.83
Diel period		
Day		
Average similarity: 32.18	Haeaur	13.6
	Haesqu	10.9
	Clup	9.68
	Acachi	7.78
	Mulmar	6.01
Night		
Average similarity: 28.46	Myrjac	17.33
	Holads	16.13
	Anivir	12.55
	Acacoe	6.95
	Pemsch	6.8
Day & Night		
Average dissimilarity: 83.54	Clup	8.71
	Haesqu	8.57
	Haeaur	7.52
	Mulmar	5.43
	Pemsch	5.32

Table S4. Summary of one-sample t-tests applied to assess if beta diversity of rare (^{0}D), typical (^{1}D) and dominant (^{2}D) species were significantly different from 1 (null hypothesis of no effect of structural complexity on fish diversity).

Response variable	**t**	**DF**	**p-value**
^{0}D day	10.48	3	<0.001
^{1}D day	10.8	3	<0.001
^{2}D day	4.82	3	<0.01
^{0}D night	17.59	3	<0.0001
^{1}D night	6.64	3	<0.01
^{2}D night	4.49	3	<0.05

Figure S1. Species-rank abundance curves for each shipwreck separately, by diel period and for all species together. The cumulative percentage of abundance for the species shown in each curve is presented. Acachi: *Acanthurus chirurgus*, Clup: Clupeidae sp., Haeaur: *Haemulon aurolineatum*, Haepar: *Haemulon parra*, Haeplu: *Haemulon plumierii*, Haesqu: *Haemulon squamipinna*, Haeste: *Haemulon steindachneri.* Holads: *Holocentrus adscensionis*, Myrjac: *Myripristis jacobus*, Mulmar: *Mulloidichthys martinicus*, Pemsch: *Pempheris schomburgki*.



CONSIDERAÇÕES FINAIS

Os resultados corroboram a relação positiva entre a heterogeneidade ambiental e a diversidade, especialmente para espécies raras e típicas de peixes, que se substituem e aumentam em diversidade conforme aumenta o grau de complexidade estrutural. As espécies dominantes, apesar de não aumentarem em diversidade em escala local (alfa), também respondem à heterogeneidade substituindo-se ao longo do gradiente de complexidade estrutural. Esta substituição indica que as áreas são exploradas por peixes com diferentes hábitos e requisitos, presumivelmente fornecendo-os recursos (como alimento) e refúgio.

A intensidade da relação diversidade-heterogeneidade não foi afetada pelo período do dia, o que revela uma influência contínua da heterogeneidade ambiental sobre as comunidades de peixes, seja durante o dia ou à noite. Alguns autores afirmam que os hábitos alimentares dos peixes determinam seus movimentos entre as áreas de descanso e de alimentação, sendo os peixes “diurnos” ativos de dia e inativos a noite, e os “noturnos” vice-versa. Seguindo esse ponto de vista, espera-se que enquanto os peixes estejam inativos, seu comportamento esteja relacionado primariamente à sua própria segurança, então eles utilizam o refúgio fornecido pela complexidade estrutural do ambiente. Por outro lado, quando os peixes estão ativos, suas ações são dominadas pela necessidade de alimento, então eles exploraram outras áreas independente de sua complexidade. Se as áreas de maior complexidade fornecem tanto refúgio quanto alimento, faz sentindo que apresentem maior diversidade independente do período do dia, visto que tanto os peixes de atividade diurna quanto os noturnos poderão explorar essas áreas sem a necessidade de maiores deslocamentos e mantendo-se “seguros”.

O presente trabalho contribui com evidências sobre a relação entre a heterogeneidade ambiental e os padrões de distribuição da diversidade de peixes, utilizando ambientes de recife artificial. Embora os conceitos de diversidade α, β e γ tenham sido originalmente baseados em escalas espaciais nas quais diferentes processos poderiam operar, trabalhar em pequenas escalas espaciais com organismos com alta mobilidade é um tanto desafiador. O uso dos naufrágios como modelo de estudo mostrou superar essa dificuldade, visto que a estrutura física de cada embarcação, além de ser conhecida, apresenta condições heterogêneas. Tais atributos possibilitaram a delimitação espacial segura e replicável de cada comunidade, permitindo observar como as espécies de peixes respondem às mudanças nas características ambientais. As métricas de diversidade utilizadas aqui permitem comparar efeitos da heterogeneidade ambiental em qualquer ecossistema, auxiliando a descrever padrões ecológicos gerais e contribuindo para a compreensão mais ampla do papel da complexidade estrutural sobre a biodiversidade.

A melhor compreensão das respostas das comunidades de peixes às características ambientais é de grande relevância para direcionar a tomada de decisões no âmbito da conservação e manejo da pesca, tendo em vista que os peixes constituem parte substancial da biodiversidade marinha e muitas espécies são de importância comercial. O conhecimento sobre os padrões e possíveis mecanismos permite que os gestores foquem os recursos em áreas de alta biodiversidade, além de possibilitar a previsão das respostas das comunidades a eventuais distúrbios que simplifiquem a heterogeneidade do ambiente. Assim sendo, as evidências fornecidas pela presente pesquisa sugerem fortemente que a conservação de habitats heterogêneos, tais como naufrágios estruturalmente complexos, é fundamental para conservar a diversidade de peixes marinhos.

Em termos de aplicação, a caracterização da ictiofauna dos naufrágios Alice, Alvarenga e Queimado, realizada por meio dos dados dessa pesquisa, forneceu adicional suporte para o delineamento da poligonal da Área de Proteção Ambiental Naufrágio

Queimado no litoral da Paraíba. Essa Unidade de Conservação, criada através do decreto estadual nº 38.931 de dezembro de 2018, corresponde a 10,2% da plataforma continental do estado da Paraíba e protege o patrimônio biológico e arqueológico marinho, ao incluir essas embarcações naufragadas, além dos recifes naturais rasos e profundos.

O alto custo requerido para as expedições de mergulho e amostragem subaquática justifica o número reduzido de naufrágios abrangidos pela presente pesquisa. Estudos recentes apontam o envolvimento de cidadãos cientistas como uma alternativa para reduzir os custos de monitoramento da ictiofauna em recifes artificiais. Esse tipo de iniciativa tem sido cada vez mais aplicado no monitoramento de recursos naturais, mas seu sucesso depende de uma gama de fatores, incluindo a capacitação dos participantes. Essa pode ser uma solução para pesquisas futuras, inclusive para o monitoramento da fauna marinha da APA Naufrágio Queimado.

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Ramus, F., Rosen, S., Dakin, S. C., Day, B. L., Castellote, J. M., White, S., & Frith, U. (2003). Theories of developmental dyslexia: Insights from a multiple case study of dyslexic adults. Brain, 126(4), 841–865. doi: 10.1093/brain/awg076

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- Book edition

Bradley-Johnson, S. (1994). Psychoeducational assessment of students who are visually impaired or blind: Infancy through high school (2nd ed.). Austin, TX: Pro-ed.

- Edited book

Hawkley, L. C., Preacher, K. J., & Cacioppo, J. T. (2007). Multilevel modeling of social interactions and mood in lonely and socially connected individuals: The MacArthur social neuroscience studies. In A. D. Ong & M. Van Dulmen (Eds.), *Oxford handbook of methods in positive psychology* (pp. 559–575). New York, NY: Oxford University Press.

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Authors should use the International System of Units (S.I., Système International d'Unités; see Quantities, Units and Symbols, 2nd edn (1975) The Royal Society, London). If the paper contains many symbols, they should be defined as early in the text as possible, or within the Materials and methods section. Journal style for time units are: s, min, h, days, weeks, months, years. Use 'L' for litre not 'l' to avoid confusion with 'one'. Use the negative index for units, e.g. number of insects g^{-1}dry wt (also note there is no period for wt). Probability values should be denoted as *P*.

Mathematical expressions should be carefully represented. Wherever possible, mathematical equations and symbols should be typed in-line by keyboard entry (using Symbol font for Greek characters, and superscript options where applicable). Make sure that there is no confusion between similar characters like l ('ell') and 1 ('one'). Ensure that expressions are spaced as they should appear. If there are several equations they should be identified by an equation number (i.e. 'eqn 1' after the equation, and cited in the text as 'equation 1').

Numbers from one to nine should be spelled out except when used with units, e.g. two eyes but 10 stomata; 5 °C, 3 years and 5 kg. Do not use excessive numbers of digits when writing a decimal number to represent the mean of a set of measurements. The level of significance implied by numbers based on experimental measurements should reflect, and not exceed, their precision; only rarely can more than 3 figures be justified.