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DÉBORAH MAGALHÃES DE MELO

A importância ecológica das baleias jubarte (*Megaptera novaeangliae* (Borowski, 1781)) no funcionamento e na estrutura dos recifes de corais do Banco de Abrolhos – BA, Brasil.

ILHÉUS – BAHIA
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Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutora em Ecologia e Conservação da Biodiversidade

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Nesses quatro anos, aprendi sobre resiliência e a me reinventar quando preciso. Trabalhar com experimentos exige criatividade, humildade e a capacidade de abrir mão do controle. Houve muito olho tremendo, mas também muitas cervejinhas, pagodes, forrós e histórias do mar. A vida acontece no ordinário e são os pequenos momentos que criam o extraordinário. Fui rodeada por mulheres incríveis, cheias de atitude, que partilharam conhecimento na pesquisa, no mar, no mergulho e na amizade, e que mostraram como são fortes e boas no que fazem. Se há uma certeza que levo dessa etapa, é que a ciência só se constrói em conjunto, pela união de pessoas dispostas a contribuir para melhorar, de alguma forma, o mundo ao seu redor. A ciência não pode se limitar ao papel, ela precisa romper os muros das universidades, sair das bancadas do laboratório, e dialogar com o mundo ao redor, plantando sementes diárias de mudança. Ela se constrói em diferentes camadas e depende do afeto e atenção das pessoas que nos cercam. O mar me ensinou que uma superfície calma pode esconder forças intensas e que só mergulhando se aprende a lidar com elas. Descobri que o vai e vem diário das marés é como a respiração: inevitável e natural, basta confiar e deixar fluir.

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A importância ecológica das baleias jubarte (*Megaptera novaeangliae* (Borowski, 1781)) no funcionamento e na estrutura dos recifes de corais do Banco de Abrolhos – BA, Brasil.

RESUMO GERAL

Ecossistemas recifais tropicais são altamente produtivos e biodiversos, especialmente quando conectados a paisagens costeiras, desempenhando papéis essenciais como berçários, áreas de alimentação e refúgio para diversas espécies. No inverno austral, o litoral brasileiro abriga a reprodução de uma crescente população de baleias jubarte (*Megaptera novaeangliae*), migrantes de latitudes mais altas do hemisfério sul. Para além de sua relevância cultural, esses cetáceos introduzem nos ambientes costeiros uma variedade de materiais orgânicos – como placenta, leite, tecidos epidérmicos e carcaças de adultos e neonatos – que representam um importante fluxo alóctone de energia e nutrientes, com potencial de influenciar a estrutura e o funcionamento dos recifes de corais. Esta tese avaliou, em três abordagens complementares, os serviços ecossistêmicos associados às baleias jubarte e seus efeitos ecológicos nos recifes de corais. Primeiramente, uma revisão sistemática identificou os principais serviços ecossistêmicos prestados por espécies migratórias da família Balaenopteridae, evidenciando a concentração de benefícios em áreas marinhas não protegidas, incluindo corredores migratórios, o que aponta para a urgência de políticas de conservação integradas. Em seguida, um experimento *in situ* a partir da adição de carcaça de baleia nos recifes do banco dos Abrolhos (Bahia, Brasil), investigou – em diferentes espécies recifais – a assimilação desse nutriente alóctone através da análise de isótopos estáveis de carbono e nitrogênio. Revelando a assimilação principalmente por produtores primários, mas também a presença da assinatura isotópica da baleia em múltiplos níveis tróficos. Espécies-alvo da pesca artesanal, inclusive, apresentaram sinais de assimilação dos nutrientes alóctones, reforçando o valor ecológico e socioeconômico desse fluxo detrítico. Por fim, testou-se os efeitos ecológicos da entrada alóctone na estrutura da assembleia de peixes recifais. Os resultados demonstraram aumento na abundância e diversidade de peixes recifais refletindo uma agregação temporária, além de estimular a produtividade secundária, indicando que esse aporte orgânico atua como subsídio trófico. Os resultados desta tese destacam o papel das baleias jubarte como vetores ecológicos de nutrientes entre diferentes ambientes marinhos, atuando de forma pontual, porém significativa sobre o funcionamento dos recifes de corais de baixa profundidade. Além disso, revelam o potencial desses processos naturais para contribuir com o armazenamento de carbono e a resiliência dos ecossistemas frente à crise climática. O estudo reforça a necessidade de ampliar a proteção de áreas que assegurem a conectividade ecológica entre zonas de alimentação e reprodução, integrando esforços de conservação à gestão pesqueira e às políticas públicas. Dessa forma, promove-se a valorização dos serviços ecossistêmicos prestados por grandes cetáceos, beneficiando tanto a biodiversidade marinha quanto as comunidades humanas que dela dependem.

Palavras-chave: Engenheiro ecossistêmico. Isótopos estáveis. Nutrientes alóctones. Produtividade secundária. Serviços ecossistêmicos.

The ecological importance of humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) for the functioning and structure of coral reefs in the Abrolhos Bank – BA, Brazil.

GENERAL ABSTRACT

Tropical coral reef ecosystems are highly productive and biodiverse, particularly when connected to coastal landscapes, serving as essential nurseries, feeding grounds, and refuges for a wide range of species. During the austral winter, the Brazilian coast hosts the reproduction of a growing population of humpback whales (*Megaptera novaeangliae*), migrants from higher latitudes of the Southern Hemisphere. Beyond their cultural significance, these cetaceans introduce a variety of organic materials into coastal environments – including placenta, milk, epidermal tissues, and carcasses of adults and calves – which represent an important allochthonous flux of energy and nutrients, with the potential to influence the structure and functioning of coral reefs. This thesis evaluated, through three complementary approaches, the ecosystem services associated with humpback whales and their ecological effects on coral reefs. First, a systematic review identified the main ecosystem services provided by migratory species of the family Balaenopteridae, revealing a concentration of benefits in non-protected marine areas, including migratory corridors, thus highlighting the urgent need for integrated conservation policies. Next, an in situ experiment involving the addition of a humpback whale carcass to the reefs of the Abrolhos Bank (Bahia, Brazil) investigated the assimilation of this allochthonous nutrient by different reef species using stable carbon and nitrogen isotope analyses. The results revealed assimilation primarily by primary producers, but also the whale's isotopic signature across multiple trophic levels. Notably, species targeted by artisanal fisheries also exhibited signs of assimilating allochthonous nutrients, underscoring the ecological and socioeconomic value of this detrital input. Finally, the ecological effects of this allochthonous input on the structure of reef fish assemblages were tested. The results showed an increase in reef fish abundance and diversity, reflecting a temporary aggregation, in addition to stimulating secondary productivity, indicating that this organic input acts as a trophic subsidy. The findings of this thesis highlight the role of humpback whales as ecological vectors of nutrients across different marine environments, acting in a punctual yet significant manner on the functioning of shallow coral reefs. Moreover, they reveal the potential of these natural processes to contribute to carbon storage and to the resilience of ecosystems in the face of the climate crisis. This study reinforces the need to expand the protection of areas that ensure ecological connectivity between feeding and breeding grounds, integrating conservation efforts with fisheries management and public policy. In doing so, it promotes the recognition of the ecosystem services provided by large cetaceans, benefiting both marine biodiversity and the human communities that depend on it.

Keywords: Allochthonous nutrients. Ecosystem engineer. Ecosystem services. Secondary productivity. Stable isotopes.

INTRODUÇÃO GERAL

Ecossistemas são definidos como um sistema ecológico formado por comunidades de organismos vivos que interagem entre si e com os componentes físicos e químicos do ambiente e cujos limites frequentemente não tem uma definição clara (Ricklefs, 2016). Esses sistemas são moldados por processos internos que envolvem o fluxo de energia e de matéria, sendo considerados abertos ao fluxo desta última, já que sempre há algum nível de influxo ou efluxo, mesmo que em forma de sedimentação (DeAngelis et al., 1989). Neste contexto, a teoria de metaecossistemas tem sido aplicada para descrever a interação entre distintos ecossistemas e compreender o fluxo espacial da matéria, de energia e de organismos (Loreau et al., 2003). Sendo necessário considerar também a complexidade dos diversos tipos de movimentação entre os ecossistemas e os efeitos que essas trocas podem gerar em diferentes escalas (Gounand et al., 2018).

O movimento de organismos compreende qualquer comportamento que resulte no deslocamento de um organismo de um local para o outro, como a dispersão, o movimento ontogenético, deslocamentos para forrageamento e as migrações sazonais (Gounand et al., 2018). Além dos deslocamentos de organismos, há também os fluxos de recursos que interligam a dinâmica de distintas comunidades por meio da geração e transferência de nutrientes inorgânicos ou detritos, contribuindo para o aumento da disponibilidade de recursos no ecossistema que os recebe (Gounand et al., 2017; Gounand et al., 2018). Tais deslocamentos podem desencadear efeitos de consumidor (*top-down*) ou de recurso (*bottom-up*). No primeiro caso, a movimentação atua gerando uma pressão de consumo no ecossistema receptor; enquanto o segundo faz com que as entradas enriqueçam o ecossistema (Gounand et al., 2018). Nesse último caso, a conexão se dá por meio da movimentação de materiais e organismos que introduzem recursos extrínsecos (alóctones) provindos de sistemas externos (Polis e Strong, 1996; Robinson et al., 2023). Além do deslocamento de animais, tal transferência pode acontecer por processos como o vento, deposição atmosférica, fluxo fluvial ou correntes (Subalusky e Post, 2019).

Os materiais que são produzidos em um sistema doador e são transferidos para um sistema receptor, alterando a dinâmica dos consumidores nesses locais, são conhecidos como subsídios de recursos (Subalusky e Post, 2019). Tais subsídios conectam a produtividade dos sistemas e podem exercer consequências importantes e diversas na dinâmica das teias alimentares e dos ecossistemas, como o aumento da produtividade secundária (Polis e Strong, 1996; Marcarelli et al., 2011; Subalusky et al., 2018). A produtividade é entendida como a geração de biomassa ou energia, sendo a produção secundária a geração de biomassa através do consumo de outros organismos, seja em nível populacional ou comunitário, e normalmente é perdida devido à mortalidade ou emigração (Benke, 2010; Eddy et al., 2021). Enquanto a biomassa é a quantidade de tecido vivo dos indivíduos por área, funcionando como estoque permanente, sendo que a produtividade secundária é a taxa dessa geração (Allen, 1971; Dolbeth et al., 2012; Eddy et al., 2021).

Os subsídios incorporados ao ecossistema, conhecidos também como *inputs*, são controlados pelo sistema doador e variam em quantidade, qualidade, sazonalidade e duração (Polis et al., 1997; Subalusky e Post, 2019). Os *inputs* de origem animal influenciam o sistema receptor por meio da interação entre as características abióticas do sistema doador e os atributos dos vetores animais. A influência é modulada por fatores como a composição química do ambiente (Elser et al., 2000), a massa corporal do animal (Pershing et al., 2010), o tamanho populacional (Post et al., 1998), e os aspectos relacionados à história de vida e ao comportamento da espécie (Naiman et al., 2009; Twining et al., 2017). Características abióticas do ecossistema receptor como as barreiras de isolamento (Post et al., 2007) e a sazonalidade, também podem moldar o impacto final do *input*, atenuando ou intensificando os efeitos (Anderson et al., 2008; Tiegs et al., 2011). Além disso, as características dos consumidores, como identidade taxonômica, guildas tróficas, história de vida e mobilidade, desempenham um papel importante na resposta do sistema (Levi et al., 2015; Subalusky e Post, 2019). A duração da disponibilidade do *input* no sistema receptor também influencia sua qualidade, uma vez que as taxas de decomposição e/ou lixiviação afetam diretamente as propriedades químicas do recurso (Sitters et al., 2015).

As migrações sazonais representam um exemplo clássico de movimentação de organismos, ocorrendo repetidamente entre áreas de reprodução, alimentação e descanso. Esses deslocamentos – diários, mensais, anuais ou em escalas temporais maiores – geram *inputs* animais por meio da excreção, egestão, liberação de gametas ou deposição de carcaças (Gounand et al., 2018; Subalusky e Post, 2019). Os salmões anádromos e semélparos (*Oncorhynchus* spp.) migram de ecossistemas marinhos para sistemas fluviais para se reproduzirem, liberando gametas e introduzindo grandes quantidades de carcaças no ambiente (Moore e Schindler, 2004). No sul do Brasil, os juvenis de tainhas (*Mugil liza*) migram para o interior dos estuários transportando nutrientes, incorporando-os a ecossistemas de água doce; e ao atingirem a maturidade, iniciam a migração reprodutiva para o ambiente marinho, onde ocorre a desova (Oliveira et al., 2014). Tartarugas marinhas migram entre áreas de alimentação e nidificação, liberando nutrientes através da deposição de ovos na praia (Bouchard e Bjorndal, 2000). Em áreas de alimentação de grandes mamíferos marinhos no Golfo do Maine, o movimento vertical durante o forrageamento em maiores profundidades libera plumas fecais ricas em nutrientes na superfície, aumentando a produtividade primária por meio do “whale pump” (Roman e McCarthy, 2010).

Movimentação das baleias jubarte e sua importância ecológica

A *Megaptera novaeangliae* (Borowski, 1781), conhecida popularmente como baleia jubarte, é caracterizada por suas extensas migrações anuais pelos oceanos. Esses deslocamentos visam evitar as águas frias polares e buscar refúgio em águas tropicais para fins reprodutivos (Lodi e Borobia, 2013). Ao longo dessa migração a espécie enriquece temporariamente as comunidades marinhas por onde passa com nutrientes fundamentais para a produtividade primária. Contribuem para a manutenção da biodiversidade ao fertilizar os oceanos vertical e horizontalmente por meio de excretas, carcaças, placentas e leite (Roman et al., 2014; James et al., 2017; Cook et al., 2020; Roman et al., 2025). Esses aportes orgânicos podem impulsionar a produtividade dos ecossistemas receptores, estimulando indiretamente a fixação e o armazenamento do carbono detrítico na teia alimentar, desempenhando um papel regulador (Nicol et al., 2010; Lavery et al., 2010; Roman et al., 2014). De forma direta, o carbono acumulado ao longo de suas vidas – estimado entre 2.5 e 6 toneladas, a depender da massa corporal (Pearson et al., 2022) – pode ser sequestrado para o leito oceânico profundo após a morte, ficando indisponível para a atmosfera. Esse evento é entendido como uma forma de auxiliar na mitigação das mudanças climáticas (Pershing et al., 2010; Chami et al., 2019; Dufort et al., 2020). Além disso, são consideradas engenheiras de ecossistemas, pois aumentam a heterogeneidade do habitat, influenciam a estrutura e a distribuição dos recursos e deixam impactos ambientais que perduram além de seu tempo de vida e escala individual (Hastings et al., 2007).

Além de desempenhar esses serviços ecossistêmicos fundamentais, as baleias jubarte se destacam pelo serviço cultural, como o turismo de observação, a educação e o entretenimento (Cook et al., 2020). Destacando-se anteriormente também pelo serviço de provisão oriundo da caça (Cook et al., 2022), prática que levou a espécie à beira da extinção. Mas desde a proibição da caça comercial no Brasil em 1987, aliada a esforços de conservação, sua população vem se recuperando. Atualmente, é classificada como quase ameaçada (NT) no Livro Vermelho da Fauna Brasileira (ICMBio, 2018). Tal recuperação impulsionou significativamente o estoque reprodutor do Atlântico Sudoeste. Em 2019, estimativas indicaram que a população atingiu aproximadamente 93% dos níveis pré-exploração, totalizando cerca de 21.878 indivíduos (Bortolotto et al., 2021). A recuperação das populações de baleias impulsiona a economia do turismo sustentável (Cunningham et al., 2012; Dufort et al., 2020), configurando-se como um pilar econômico em comunidades costeiras (Antošová et al., 2019). No entanto, a espécie ainda enfrenta diversas ameaças, como colisões com embarcações, emaranhamento em artefatos pesqueiros, poluição – incluindo a sonora –, além dos impactos das mudanças climáticas e do aquecimento dos oceanos (Lodi e Borobia, 2013; Bezamat et al., 2014; Rossi-Santos, 2015; Chami et al., 2019).

Recifes de corais: fluxos de energia, de nutrientes e conectividade ecológica

O funcionamento dos ecossistemas recifais é determinado pelas taxas de fluxos de energia e de matéria, mediados por fatores intrínsecos e extrínsecos, que dependem de processos ecológicos complementares de ganhos e perdas (Brandl et al., 2019). Um dos pilares desse funcionamento é a dinâmica do carbonato de cálcio, essencial para a estruturação dos habitats (Brandl et al., 2019). Sua produção está principalmente relacionada à atuação dos corais hermatípicos e das algas coralinas incrustantes (Hart e Kench, 2007; McLaughlin et al., 2023). Em contrapartida, atividades de pastoreio e perfuração – realizados por organismos como os peixes papagaio (Lellys et al., 2019) e ouriços-do-mar (Perry et al., 2016) – bioerodem as estruturas e influenciam nos balanços de carbonato. Outro processo fundamental é a produção de biomassa pela fotossíntese e a assimilação na teia a partir da herbivoria (Brandl et al., 2019). Os produtores primários exercem o papel central na reciclagem de nutrientes particulados e dissolvidos, tornando-os disponíveis para outros níveis tróficos (Lønborg et al., 2021). Corais zooxantelados, por exemplo, além de estruturar fisicamente o recife, apresentam uma complexa rede de trocas de nutrientes com suas algas simbióticas, favorecendo a absorção e retenção de nutrientes (Martinez et al., 2022). Já as cianobactérias, por exemplo, destacam-se pela fixação de nitrogênio atmosférico e pela produção a partir dos nutrientes disponíveis na zona eufótica (Sigman e Hain, 2012).

De forma complementar, a transferência de nutrientes e energia heterotróficos sustenta níveis tróficos mais elevados por meio da produção secundária e da predação (Brandl et al., 2019). Peixes e invertebrados desempenham papéis cruciais nessa dinâmica ao ingerirem nutrientes particulados – vivos ou detríticos – e ao liberarem grandes quantidades de nitrogênio e fósforo na coluna d’água por excreção e egestão (Allgeier et al., 2014; Allgeier, 2021; Schiettekatte et al., 2023). Além de reservatórios de nutrientes, os peixes herbívoros tendem a dominar a biomassa recifal e contribuírem de forma significativa para a ciclagem de nutrientes nos recifes (Polunin et al., 1995; Robinson et al., 2023). Por fim, tais interações resultam na introdução, retenção e reintegração de nutrientes no ecossistema a partir da ciclagem destes (Brandl et al., 2019). As esponjas também contribuem de forma expressiva para a ciclagem de nitrogênio ao disponibilizar amônio para a produção primária (Gantt et al., 2019). Já o loop microbiano é fundamental no processo de ciclagem, com a atuação das bactérias heterotróficas, por exemplo, decompondo a matéria orgânica e mantém reservatórios biológicos relevantes de nutrientes orgânicos dissolvidos (Pomeroy et al., 2007; Lønborg et al., 2009).

Grande parte da produtividade biológica em ecossistemas recifais depende diretamente da disponibilidade de nutrientes na zona eufótica e da eficiência com que estes circulam entre os diferentes reservatórios de biomassa (Hatcher, 1990; Fallowski et al, 1998, Sigman e Hain, 2012). Dessa forma, dependem de mecanismos e estruturas que proporcionem um alto grau de reciclagem para a regulação biológica (DeAngelis et al, 1989). Esse processo foi investigado biogeoquimicamente, com foco no nitrogênio e fósforo, revelando que a retenção biológica é essencial para sustentar a produtividade (Karl et al., 2003), sendo os animais o principal *pool* de armazenamento e reciclagem desses nutrientes (Allgeier et al, 2017). Na Grande Barreira de Corais, por exemplo, observou-se que os processos internos dominam o orçamento de nutrientes, enquanto as entradas externas representam apenas uma pequena proporção do suporte à produtividade (Tait et al., 2023). Assim, a taxa de produção nesses ecossistemas abertos é determinada pela combinação entre as entradas alóctones e as taxas de reciclagem (DeAngelis et al, 1989).

A estrutura da comunidade e a eficiência de suas interações não apenas sustentam a ciclagem interna, mas também determinam como os ecossistemas recifais respondem à chegada de novos insumos de energia e matéria. Essas características tornam os recifes de corais tropicais ecossistemas altamente produtivos, biodiversos e sustentadores de teias alimentares complexas (Atkinson, 2011; Allgeier et al., 2014). Quando em regiões costeiras, conectam-se com uma paisagem marinha altamente produtiva como os manguezais, bancos de rodolitos e bancos de ervas marinhas, contribuindo com o recrutamento, diversidade e produtividade dos peixes recifais (Davis et al., 2014; Moura et al., 2021; Lima et al., 2025). Tal conectividade é bem conhecida para espécies de *Haemulon* que se movimentam diariamente entre os recifes de corais e as pradarias vegetadas no entorno, transportando nutrientes por meio das fezes e da egestão (Meyer e Schultz, 1985). Nesse contexto, compreender a dinâmica espacial e o funcionamento do ecossistema torna a estrutura do metaecossistemas uma ferramenta robusta para investigar a dinâmica de ecossistemas conectados (Gounand et al., 2018).

Baleias jubarte como subsídio alóctone para recifes de corais rasos

Todos os anos, diferentes subpopulações de baleias jubarte do hemisfério norte e sul migram para áreas tropicais recifais, como os arquipélagos da Oceania (Gaguirre et al., 2020), a costa da Nicaragua (De Weerdt et al., 2023), o Hawai (Henderson et al., 2022), as ilhas de Cabo Verde (Stevick et al., 2016) e a Austrália (Andrews-Goff et al., 2023), representando um aporte alóctone relevante. Durante essas migrações ocorrem eventos de mortalidade (Meynecke e Meager, 2016; da Cunha Ramos et al., 2024; Toro et al., 2025), e as carcaças dessas baleias podem atuar como importantes pulsos de nutrientes e energia para os ecossistemas recifais (Subalusky e Post, 2019). Atuando como reservatórios detríticos, essas carcaças fornecem matéria orgânica e nutrientes para as cadeias alimentares, com potencial para alterar a estrutura e a dinâmica das comunidades locais (Moore et al., 2004; Wilson e Wolkovich, 2011). Os detritos, considerados materiais não vivos, podem servir como habitat, modificar a estrutura física e as condições do local, e assim, afetar a estrutura e dinâmica das espécies vivas (Moore et al., 2004). A energia derivada desse detrito pode aumentar o comprimento da cadeia alimentar, sendo transferida por múltiplos níveis tróficos antes de ser mineralizada, necessitando considerar sua fonte, quantidade e qualidade, para entender como afeta a estrutura das comunidades (Moore et al, 2004).

Esses pulsos alimentares atraem uma diversidade de forrageadores, como tubarões, que exploram as carcaças em diferentes estágios de decomposição, reduzindo o esforço de forrageamento dos consumidores (Bornatowski et al., 2012; Fallows et al., 2013). As agregações de consumidores em torno das carcaças podem gerar efeitos ecológicos que ultrapassam o local do *input*, desencadeando respostas indiretas que se propagam por toda a paisagem marinha (Holt et al., 2008; Fallows et al., 201; Allgeier et al., 2017). O consumo de carcaças acelera o processo de ciclagem de nutrientes e é fundamental para os ecossistemas já que aumenta o número de conexões tróficas, aprimorando o multicanal alimentar (Wilson e Wolkovich, 2011). Os organismos podem atuar como necrófagos e desempenhar um papel fundamental na redistribuição de nutrientes dentro do ecossistema (Payne e Moore, 2006). Embora pouco estudadas, a via de incremento detrítica por meio da necrofagia geram conexões que são importantes devido aos efeitos que podem ter nas vias tróficas e no efeito cascata sobre a estabilidade de um sistema (Wilson e Wolkovich, 2011).

Investigações sobre o impacto das carcaças de baleias vêm sendo amplamente realizadas em ambientes de leito oceânico profundo, revelando sua importância para o enriquecimento e sustento de comunidades receptoras e o sequestro de carbono (e.g., Roman et al., 2014; Smith e Baco, 2003; Fallows et al., 2013; Lea et al., 2018). Em ambientes marinhos rasos, porém, ainda é escasso. Alguns exemplos incluem investigações com carcaça de foca cinzenta (*Halichoerus grypus*) na costa da Escócia (Quaggiotto et al., 2017), ossos de baleia minke, vaca e porco no Mediterrâneo (Taboada et al., 2016) e uma carcaça de golfinho no Noroeste do Mediterrâneo (Francescangeli et al., 2023), nos quais observou o consumo por invertebrados e peixes. Entretanto, não há evidências específicas sobre o impacto da chegada anual de carcaças de baleias no funcionamento de recifes de corais rasos. Sendo assim, investigar se a baleia jubarte atua como um pulso de recurso que funcione como subsídio animal para a teia trófica de recifes de corais é especialmente relevante em ambientes de baixa profundidade, onde a produtividade primária é elevada e a ciclagem de nutrientes ocorre de forma relativamente rápida (Heenan et al. 2019). Nessas regiões, mesmo sem se alimentarem – ou se alimentando muito pouco – as baleias se reproduzem e morrem, potencialmente influenciando a redistribuição espaço-temporal de energia e nutrientes (Roman et al., 2014).

No Brasil, a população de baleia jubarte pertence a um dos sete estoques reprodutores primários do Hemisfério Sul (Morete et al., 2008). O Banco dos Abrolhos - Bahia destaca-se como principal destino dessa população durante o inverno austral, amplamente reconhecido pelo ecoturismo devido à alta densidade de baleias. Além de rota migratória para menores latitudes, a região é um importante berçário da espécie (Engel e Martin, 2009; Andriolo et al., 2010; Lodi e Borobia, 2013). A região abriga três megahabitats resultantes da interação entre entrada costeira de sedimentos, profundidade e geologia: bancos de rodolitos, fundos não consolidados e recifes de coral (Moura et al., 2013). Os recifes, complexos e estruturalmente diversos, destacam-se por suas estruturas singulares e elevada taxa de endemismo (Leão, 1999; Leão e Kikuchi, 2005). O coral endêmico *Mussismilia braziliensis* é o principal construtor desses recifes, associada a outros corais, algas coralíneas crustosas e, principalmente, briozoários incrustantes (Leão et al., 2003; Bastos et al., 2018). Nas áreas protegidas, observa-se uma comunidade bentônica saudável, com maior cobertura de corais vivos que de macroalgas e elevadas biomassas de peixes (Bruce et al., 2012). Apesar da alta turbidez causada por aportes fluviais, sedimentação terrígena e ressuspensão sazonal de sedimentos (Leão et al., 2003; Segal et al., 2008; Dominguez, 2009), os recifes de Abrolhos apresentam concentrações elevadas de nitrogênio inorgânico dissolvidos e fósforo, favorecendo suspensívoros heterotróficos como os briozoários e sustentando elevada produtividade fitoplanctônica (Bruce et al., 2012; Silveira et al., 2015; Bastos et al., 2018).

Diante desse contexto, torna-se fundamental sintetizar os papéis ecossistêmicos das jubarte em áreas recifais de baixa profundidade. Como a espécie pode enriquecer temporariamente as cadeias tróficas em sua área reprodutiva? E quais possíveis efeitos sua presença pode ter na estrutura e no funcionamento da comunidade recifal? Dessa maneira, esta tese buscou avaliar o impacto das baleias jubarte na estrutura e funcionamento dos recifes de corais durante sua temporada reprodutiva. A hipótese central é que a carcaça de baleia atua como um pulso de recurso e subsídio animal, sendo assimilada por diferentes vias tróficas, influenciando temporariamente a comunidade recifal, e impulsionando a produtividade secundária. Para testa-la buscamos no primeiro capítulo revisar os serviços ecossistêmicos fornecidos por espécies da família Balaenopteridae em escala global, mapeando sua distribuição a partir dos estudos publicados e identificando hotspots de serviço em Áreas Marinhas Protegidas. Buscou-se compreender, por meio da análise espacial, como esses importantes serviços estão distribuídos e encontram-se protegidos frente aos impactos antrópicos, além de identificar regiões que carecem de ações conservacionistas. O segundo capítulo, a partir de um experimento *in situ*, analisa por meio de isótopos estáveis de carbono e nitrogênio a assimilação e transferência de nutrientes e energia provenientes da carcaça da baleia ao longo da teia trófica recifal, desde a base até os níveis tróficos superiores. Objetivou-se compreender se há um fluxo trófico promovido pela presença da carcaça, e como esses nutrientes podem estar sendo assimilados. Por fim, o terceiro capítulo investiga, também pelo experimento *in situ*, como a entrada alóctone de matéria orgânica proveniente das carcaças pode afetar a estrutura e o funcionamento da comunidade recifal, analisando os efeitos sobre as assembleias de peixes, em relação à descritores como abundância, biomassa, diversidade, estrutura trófica e produtividade secundária.

Considerando toda influencia descrita anteriormente sobre a presença das baleias jubarte, essa trajetória representa um recorte da importância da chegada da espécie em ambientes rasos nas áreas reprodutivas (Figura 1). A tese percorre desde a compreensão da importância das baleias nos ecossistemas, passando pela análise da incorporação de seu aporte nutricional pelo ecossistema receptor e possíveis entradas diretas e indiretas, até os efeitos de sua presença na comunidade recifal. Assim, ao integrar abordagens ecológicas, experimentais e espaciais, esta tese contribui de forma empírica para uma visão mais abrangente dos papéis ecológicos das baleias em ambientes recifais tropicais, destacando sua relevância na manutenção da biodiversidade e na conectividade ecológica marinha. Demonstrando que a compreensão do impacto dos consumidores de carcaças é fundamental para avanços na ecologia de populações, comunidades e conservação da biodiversidade (Moleon e Sanchez-Zapata, 2015). Assim oferece embasamento para ações conservacionistas a partir de uma ecologia espacial mais integrativa, destacando a importância de proteger ecossistemas interconectados. Subsidiando discussões que contribuam para o fortalecimento da conservação marinha e para a sustentabilidade pesqueira.

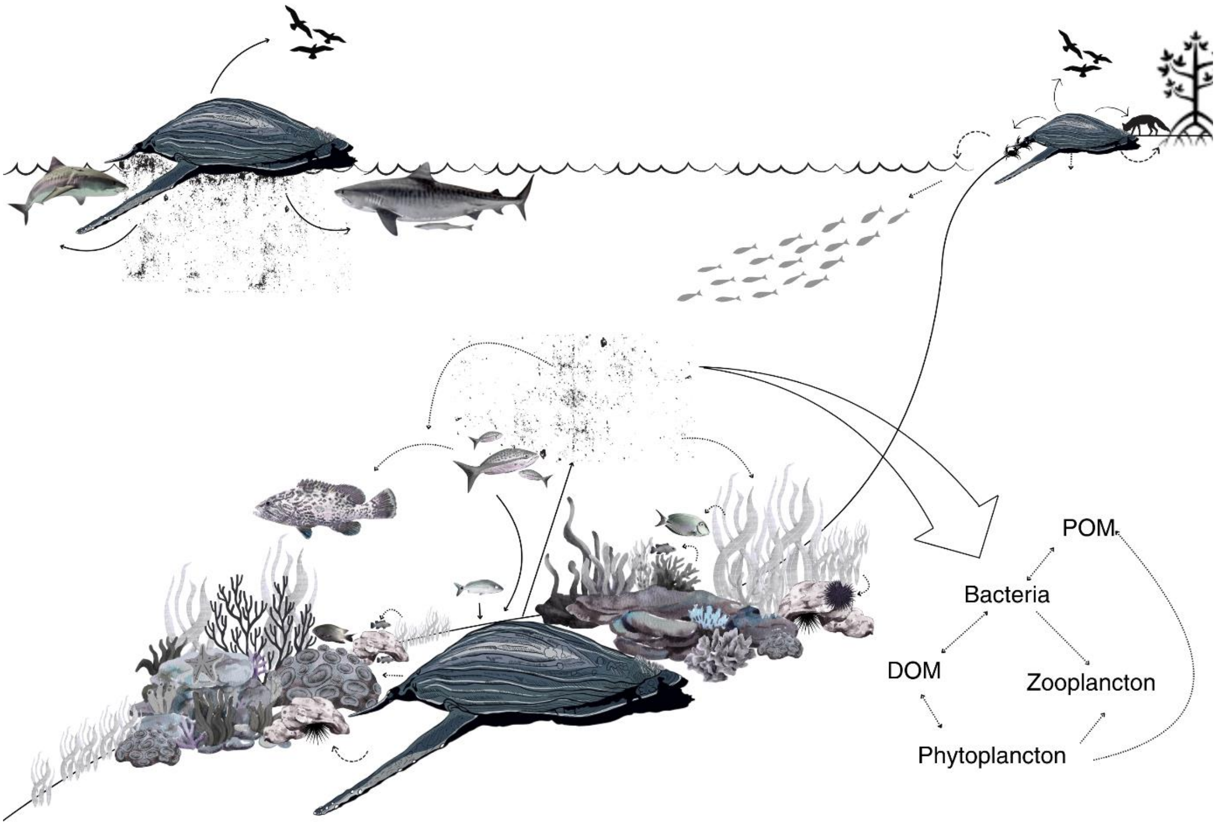

Figura 1: Esquema geral que demonstra os possíveis destinos de uma carcaça de baleia jubarte (*Megaptera novaeangliae*) em áreas de reprodução. Três cenários são representados: a carcaça pode ficar à deriva no oceano pelágico, podendo encalhar na praia ou entre raízes de manguezais, assim como afundar sobre os recifes de corais. Setas cheias indicam as possíveis rotas de consumo direto por predadores e necrófagos (e.g. aves, tubarões, vertebrados e invertebrados terrestres ou marinhos). As setas pontilhadas representam rotas de assimilação indireta dos nutrientes da carcaça na teia alimentar. Esta pode ocorrer por meio da matéria orgânica dissolvida ou particulada disponibilizada na água para: os decompositores, o *loop* microbiano e os produtores primários. A direção da seta indica o sentido do fluxo de nutriente proveniente da carcaça. Os Capítulos II e III estão focados na chegada das carcaças em fundos recifais, investigando as possíveis rotas de entrada de matéria orgânica alóctone ao longo da teia alimentar recifal, e os efeitos da presença de carcaças sobre a estrutura da assembleia de peixes recifais.

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CHAPTER I

GREAT BALEEN WHALES, GREAT SERVICES

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GREAT BALEEN WHALES, GREAT SERVICES

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ABSTRACT

Over centuries, the human-whale interactions has evolved from perceiving them as monsters to recognition of whales as vital contributors, particularly for coastal communities. Great baleen whales play a crucial role in connecting the oceans through their migrations, facilitating a flow of nature's benefits to humans. Ecosystem services, encompassing tourism, education, and religious practices, offer returns. In addition, whales stimulate primary productivity, maintain biodiversity, and fertilize oceans with nutrient-rich excretions. Moreover, through their direct/indirect carbon fixation and sequestration, whales can be viewed as mitigators of climate change. Species of the family Balaenopteridae are distributed across different latitudes and oceans. Mapping tool serves as an effective method for characterizing the actual benefits that ecosystems provide to society, allowing the identification of priority areas for conservation. This study synthesized, mapped and verified the presence of "hotspots" of services provided by *Balaenoptera musculus*, *Balaenoptera physalus*, *Balaenoptera borealis*, *Balaenoptera acutorostrata*, and *Megaptera novaeangliae*, revealing provisioning, cultural, regulatory, and maintenance services through a systematic literature review. Recognizing the complex spatial dynamics of these roles as crucial socioeconomically and culturally, it is imperative to integrate them into spatial and management planning. This inclusive approach brings a pluralistic perspective and clarifies the provision of ecosystem services by area, ultimately ensuring more efficient marine management and the sustainability of marine ecosystems.

KEYWORDS: ecosystem engineer, ecosystem services, geoprocessing, human wellbeing, marine protected areas, spatial analysis

1. Introduction

The perception of whales by human beings has changed over the centuries, from great marine monsters to charismatic megafauna. The great baleen whales were heavily hunted as a source of nutrition and their carcasses were used for many different purposes, offering provisioning services to specific communities across the world (Herrera and Hoagland, 2006; Higgs et al., 2011). Due to overexploitation, stock reductions and the need to manage whaling, the International Whaling Commission (IWC) was created. The Commission subdivided hunting for commercial, research and subsistence purposes for traditional communities (Freeman, 1993; Herrera and Hoagland, 2006). Following a series of conservation measures, a worldwide moratorium on commercial hunting was voted in 1982 and came into effect during the 1985/86 Antarctic whaling season (Herrera and Hoagland, 2006). However, following failed attempts by Japan to persuade the IWC to lift the moratorium, the Japanese government opted to leave the Commission in 2019, and resume commercial hunting in Japanese coastal waters (Kolmas, 2020). Additionally, some indigenous communities in the Northern Hemisphere justify the reinforcement of their cultural identity through the hunting, preparation and sharing of traditional foods, passing knowledge and culture down through generations (Malinauskaite et al., 2021).

Due to the need for some countries to reinvent themselves economically following the moratorium, whale watching tourism grew, and whales became valued by the tourism industry (Roman et al., 2014). Tourism is considered a non-extractive practice, incurring low costs to the environment, generating jobs, revenue in local economies and direct and indirect economic well-being (Pacheco et al., 2011; Buultjens et al., 2016; Cook et al., 2022). The IWC (1994) defined whale watching as any commercial initiative which permits the observation of cetaceans in their natural habitat. This activity, together with other entertainment, education and religious practices, for example, promote the cultural continuity and community identity of several coastal regions (Cook et al., 2022), as well as representing a multimillion-dollar industry which generates a global revenue of 2.1 billion dollars per year (O'Connor et al., 2009).

In addition to their direct interaction with human beings, the great baleen whales are fundamental to ecosystem functioning. One basic activity that they perform is water fertilisation by vertically making nutrients available, the absence of which are limiting to primary productivity (Lavery et al., 2010; Nicol et al., 2010; Roman and McCarthy, 2010; Roman et al., 2014). Many species are known for their long migrations, which facilitate the horizontal transport of nutritional faeces, thus, promoting an increase in productivity in oligotrophic regions and contributing to the creation of biodiversity hotspots (Allgeier et al., 2017; Roman et al., 2014). Additionally, baleen whales indirectly stimulate atmospheric carbon sequestration due to the increase in productivity therefore, contribute to climate change mitigation (Roman et al., 2014; Roman and McCarthy, 2010). Furthermore, when they die, whales fall to the depths of the ocean, known as whale-fall, directly sequestering all the carbon accumulated in their bodies throughout their lives (Chami et al., 2019; Dufort et al., 2020; Pershing et al., 2010). Whale-fall events are feeding pulses that reach the ocean floor, changing the spatial-temporal dynamics of the benthic communities of the sea floor and creating islands of resources which can sustain diverse and specialised communities (Holt, 2008; Smith and Baco, 2003). These carcasses create nutrient-rich environments that sustain specialized communities in exploiting the resources available under these unique conditions. They can form biodiversity hotspots, where these distinct ecological niches facilitate the adaptive radiation of organisms. Therefore, they can be considered evolutionary springboards for many species, promoting, for example, speciation in taxa associated with hydrothermal vents and cold seeps (Danise et al., 2014; Estes et al., 2016; Higgs et al., 2011; Smith et al., 2015).

Baleen whales are fundamental elements in marine systems, however, changes in the density and composition of their populations can have local and global impacts, affecting the general productivity of ecosystems and the roles they play in the human society (Chami et al., 2019; Nicol et al., 2010; Roman and McCarthy, 2010). Even after a decrease in hunting pressure and an increase in conservation strategies, it is estimated that industrialized hunting reduced whale populations by ¼ compared to their initial numbers. This drastic decline makes it difficult to accurately quantify the impact that baleen whales have on the functioning of the ecosystem, hindering a comprehensive assessment of their ecosystem services (Chami et al., 2019; Roman et al., 2014). Currently, the remaining populations also suffer from direct and indirect anthropic impacts, such as collisions with boats, entanglement in fishing gear, chemical and sound pollution, seismic activity, habitat degradation and climate change (Chami et al., 2019; Davidson et al., 2012; Lodi and Borobia, 2013; Roman et al., 2014).

The blue whale, *Balaenoptera musculus*; the fin whale, *Balaenoptera physalus*; the sei whale *Balaenoptera borealis*; the common minke whale, *Balaenoptera acutorostrata* and the humpback whale, *Megaptera novaeangliae* all belong to the Balaenopteridae family, and are examples of great baleen whales, also known as rorquals. They are distributed throughout all the world's oceans and hemispheres and perform extensive migrations across different latitudes.

As they are cosmopolitan species with extensive migratory processes, whales perform roles in the ecosystems of all of the world's oceans, providing a series of ecosystem services. Ecosystem services (ES) are streams of benefits to ecosystems and their components that sustain human well-being (Cook et al., 2022; MEA, 2005). These services are complex, diverse and synergistic and can be evaluated using a biophysical, sociocultural and economical scale. Additionally, they can generate life-sustaining values in scientific, educational, cultural, aesthetic and monetary terms, as well as benefitting ecosystems through the maintenance of biodiversity (Malinauskaite et al., 2021). To maintain and recover the ecosystem services provided by whales, a healthy and biodiverse ecosystem is required, where numerous populations of these species can be established.

Mapping is an effective method for characterising and spatially understanding the benefits provided by these species. This process aids those responsible for making decisions in marine spatial planning, as well as in the formation of conservation policies, in the evaluation of environmental compensation and in the promotion of efficient socioeconomic and financial co-benefits in mitigating climate change (Cook et al., 2020a; Deininger et al., 2016; Dufort et al., 2020; Malinauskaite et al., 2021). Thus, this paper aims to review and synthesise the ecosystem services provided by selected members of the family Balaenopteridae and to understand how individuals of this family are distributed throughout the latitudinal gradient of the world's oceans, allowing for the identification of service hotspots and whether these important areas are inserted in Marine Protected Areas (MPAs).

2. Materials and Methods

This study employed the PSALSA approach (Planning, Search, Appraisal, Synthesis, Analysis, Reporting) to conduct a precise systematic review on this topic. The objectives and scope of the review were defined during the planning phase. The keywords "whale", "ecosystem service", "ecosystem functionality", "carbon sequestration", "ocean fertilisation", "primary production", "cultural service" and "whale watching" were used. This research included all published articles up to august 2022 on the platforms Scopus and Web of Science. To test the efficiency of the search, sentinel articles — Cook et al. (2020), Lavery et al. (2010), Ratnarajah et al. (2014), and Roman et al. (2014) — were used due to their significant contributions to the scope of our research. The efficiency test involved ensuring that the selected keywords could successfully retrieve these sentinel articles, thereby validating the robustness of our search strategy. We selected the articles that included great baleen whales of the family Balaenopteridae, that are distributed across a latitudinal gradient and all the world's oceans: *Balaenoptera musculus* (Linnaeus 1758), *Balaenoptera physalus* (Linnaeus 1758), *Balaenoptera borealis* (Lesson 1828), *Balaenoptera acutorostrata* (Lacépède 1804) and *Megaptera novaeangliae* (Borowski 1781).

Service classification followed the Common International Classification for Ecosystem Services (CICES) (Haines-Young and Potschin, 2018), adapted by Cook et al. (2020), which separates services into the categories of provisioning, cultural, regulation and maintenance. In the first search, only articles that described or named some of the ecosystem services in English, Portuguese and Spanish were included. Full-text articles were selected, and duplicate articles were discarded. Only the articles that talked about at least one of the five species, whose data collection was independent and that provided the geographic study location, were selected. In addition to information about each article, the following information was collected: study species, geographic position, service category and description and when possible, the direct and indirect return of the service to the community and whether the study area was inserted in a Marine Protected Area (MPA).

For the spatial analyses, the collected data were inserted into the program QGIS 3.22.8. To identify the ecosystem services provided across a latitudinal gradient, services were mapped and separated based on category and species. A density map was constructed to visualise potential ecosystem service hotspots. To identify the level of protection that important ecosystem service areas experience, we calculated the overlap between global Marine Protected Areas (UNEP-WCMC and ICUN, 2022) and the service points described in the literature.

3. Great Whale Ecosystem Services

By using the search criteria, it was possible to identify 51 valid articles, of which some articles cited more than one ecosystem service therefore, the same article was counted more than once. Of these, 31 articles talked about cultural services, 19 about regulation and maintenance services and six about provisioning services. Publications that included at least one of the five species and that talked about at least one ecosystem service, are relatively recent, starting in 1997 and increasing over the past ten years (Fig. 1A). Provisioning services were the least documented, whereas cultural services have received greater attention from scientists over the years. Essentially, this type of ecosystem service is evaluated in articles as an alternative to hunting practices in whaling nations and the need to regulate tourism practices. Articles that dealt with regulation and maintenance services appeared more subtly over the years, however they presented a marked increase in 2022. In terms of publications per species, minke whales were the most documented species in the articles, with the registration of three more visible services compared to other species. Humpback whales contribution more in terms of cultural and regulation and maintenance services, similar to blue and fin whales. Sei whales were the least registered in our review and had a similar contribute of each service type (Fig. 1B).

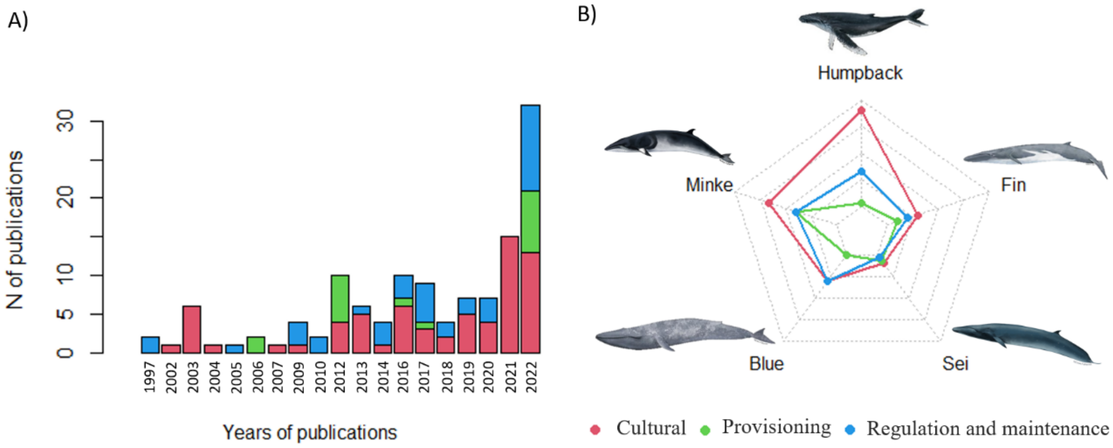

Fig. 1: Review of the ecosystem services provided by the whales *Balaenoptera musculus, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera acutorostrata* and *Megaptera novaeangliae* according to the publication years (A) and according to the species (B).

Some review articles were excluded due to the lack of basic information, such as not citing at least one of the target species or the geographic location of the study, as these papers were review articles focusing on services, ecological modelling or discussions on public policies. The focus on ecosystem services stood out for great baleen whales, as it is a topic that has only started to be discussed recently and very few articles have been published on this topic over the years. The definition of an appropriate methodology, aligning research design, adequate analyses and creating evaluation protocols, can contribute to difficulties in researching the topic of ecosystem services (Deininger et al., 2016). Such difficulties can be intensified by the temporal and spatial variability of ecosystems (Deininger et al., 2016), since establishing global patterns and making inferences at different locations can be biased or even problematic.

The five great baleen whales discussed here promote all three ecosystem services identified in the CICES categories: provisioning, cultural and regulation and maintenance services. Blue whales were the only species that was not mentioned regarding provisioning services, and sei whales were cited only for tourism within cultural services (Table 1).

Table 1: Ecosystem services provided by *Balaenoptera musculus, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera acutorostrata* and *Megaptera novaeangliae*, and the bibliographic references of the reviewed articles.

CICES classification	Service	Species	Bibliographic reference[a]
Cultural	Tourism	Blue Fin Humpback Minke Sei	Cardenas et al. (2021);
	Educational; Aesthetics; Community cohesiveness and cultural identity; Music and arts; Existence; Bequest	Blue Fin Humpback Minke	Choi (2017); Cook et al. (2022); Malinauskaite et al. (2019); Ressurreição et al. (2022)
Regulation and maintenance	Enhanced biodiversity and evolutionary potencial	Blue Fin Humpback Minke Sei	Amon et al. (2017); Cook et al. (2022) Ratnarajah et al. (2014); Roman and McCarthy (2010)
	Climate regulation	Blue Fin Humpback Minke Sei	Cook et al. (2022)
Provisioning	Food products (meat, blubber, skin and intestines)	Fin Humpback Minke Sei	Cook et al. (2022); Cunningham et al. (2012)

[a]For the complete list of the bibliographic references of the reviewed articles, please refer to the supplementary material (SM.1)

3.1 – Provisioning Services

The reviewed provisioning ESs include the use of meat, fat, skin, intestines, bones, teeth, baleen and oil for food and other functions (Cook et al., 2022). The bibliographic records of provisioning services occurred in specific areas restricted to the Northern Hemisphere, near whaling nations such as the Japanese Sea, Iceland and Norway (Fig. 2). In these pro-hunting locations, resident opinions are divided regarding the continuation of this practice or the end of exploitation (Choi, 2017). In Disko Bay on the west coast of Greenland, for example, there are annual quotas for aboriginal subsistence minke whale hunting, where the meat is used to feed the population and as a tourist attraction in restaurants. However, many inhabitants believe these quotas to be low, restricting subproduct potential and undermining food security, as food supply is expensive, and harvests are limited in Greenland (Cook et al., 2022). Hunting is also part of the culture of some areas, where indigenous subsistence hunting is permitted for Inuit communities in the Arctic and others communities in Faroe Islands (Cunningham et al., 2012).

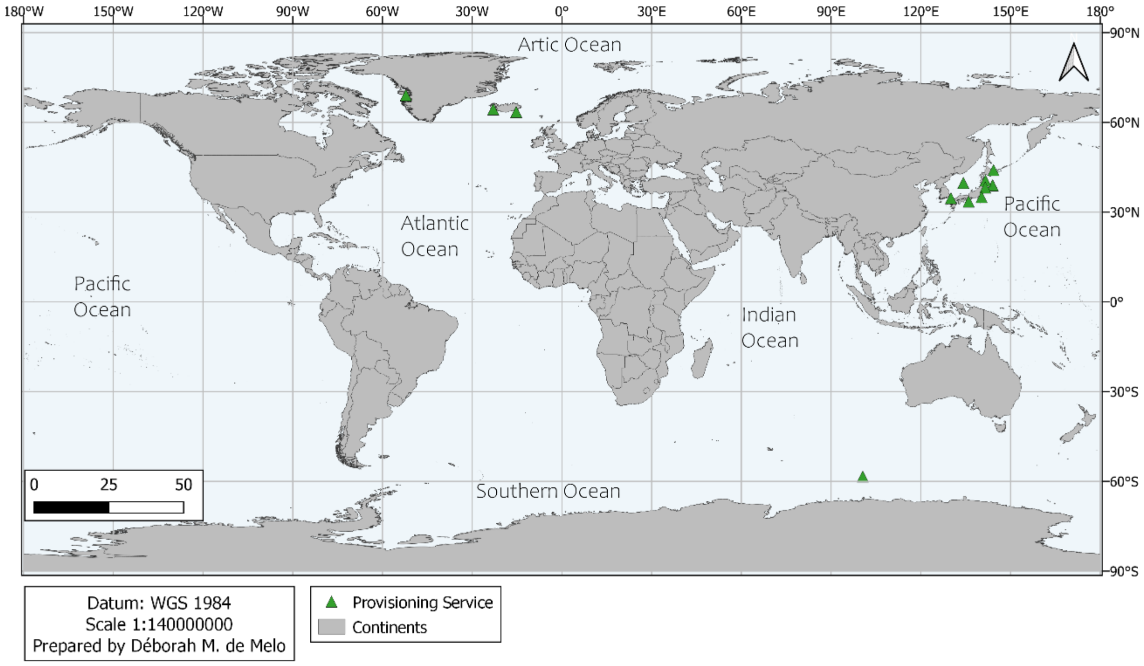

Fig. 2: Recording the distributions of articles that cited the provisioning service of *Balaenoptera musculus, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera acutorostrata* and *Megaptera novaeangliae*.

For years, the Japanese government justified the continuation of hunting as scientific, capturing minke, sei and fin whale quotas annually (Cunningham et al., 2012). However, in 2019, despite international pressure from different anti-whaling nations and environmental NGOs, the country announced their resumption of commercial whaling in territorial waters and in the Exclusive Economic Zone (EEZ), only ending this practice in Antarctic waters (Kolmas, 2020). Japan justifies hunting as part of its culture and the constant anti-hunting actions were seen as radical attacks on whalers, society and culture to the Japanese state, stirring nationalist sentiments and cultural relativism (Hirata, 2005). Kolmas (2020) suggests that this decision was a fight against Euro-American cultural imperialism.

Japan's decision was exclusively political, since the practice has not significantly contributed to its economy since its peak in 1960, requiring government incentives, thus decreasing profitability (Cunningham et al., 2012; Endo and Yamao, 2006; Kolmas, 2020). As long as pro-whaling government agencies continue to exert hegemonic control over political decisions, the complex interaction of cultural, governmental, and political factors, including pressure from interest groups and the fishing lobby, will sustain Japan's unwavering support for whaling (Danaher, 2002; Hirata, 2005). In South Korea, the practice generates discussions between different groups and the local government, since Japan mediates trade with other countries, generating trade conflict (Choi, 2017). Additionally, different anti-whaling groups protest for the end of whaling, alleging the exposure of a high amount of mercury in whale meat and food poisoning (Choi, 2017; Cunningham et al., 2012), as surplus from whaling can be used as snacks in schools or as frozen supplies (Cunningham et al., 2012).

In addition to Iceland and Japan, Norway also maintains the practice of commercial whaling, although this country was not mentioned in the reviewed articles and, consequently, was not included in the map of ecosystem services. Norway, in particular, continues to hunt minke whales (*Balaenoptera acutorostrata*), justifying this activity as a cultural tradition and an important source of economic return (Carlarne, 2005; Ramakers and Tiili, 2017). Despite remaining a member of the International Whaling Commission (IWC), the country has implemented its own regulatory framework, claiming transparency and good practices in conducting whaling, under the premise of sustainability and responsible management (Ramakers and Tiili, 2017). Norwegian policy seeks to assert national sovereignty by following its own regulations. Despite the international ban, Norway has continued commercial whaling since the imposition of the moratorium in 1986, reporting annual catches of at least 400 individuals from 1997 to 2023, as reported by the official IWC website (IWC, 2024).

The traditional fishing market is seen as an alternative to hunting, as it is more economically profitable. In Disko Bay for example, the number of whalers has been decreasing and many have adapted to the traditional market (Cook et al., 2022). Another alternative has been adapting to observation tourism, such as minke whale watching in Iceland, which has become important to the local economy. However, as these industries are conflicting and occur in waters that are close to one another, it is necessary to evaluate the economic return of both practices in the long term (Bertuli et al., 2016; Cook et al., 2022).

3.2 – Cultural Services

Cultural ESs encompass observation tourism, entertainment through music and art, different forms of education, cultural and religious enrichment, the central roles of whales in community cohesion and cultural identity, as well as the aesthetic side and value of the very existence and legacy of these species (Malinauskaite et al., 2019; Ressurreição et al., 2022). Cultural service records appear to be grouped more in the Eastern and South-eastern Pacific Ocean and the North-eastern Atlantic Ocean at different latitudes (Fig. 3). This ES is likely the most documented as it has become an economic pillar for different coastal communities, for example in Solano Bay in Columbia, with humpback whale sightings (Antosova et al., 2019), in Faxaflói Bay in Southwestern Iceland with minke and fin whales (Cook et al., 2020a) and in Sri Lanka with blue whales (Buultjens et al., 2016).

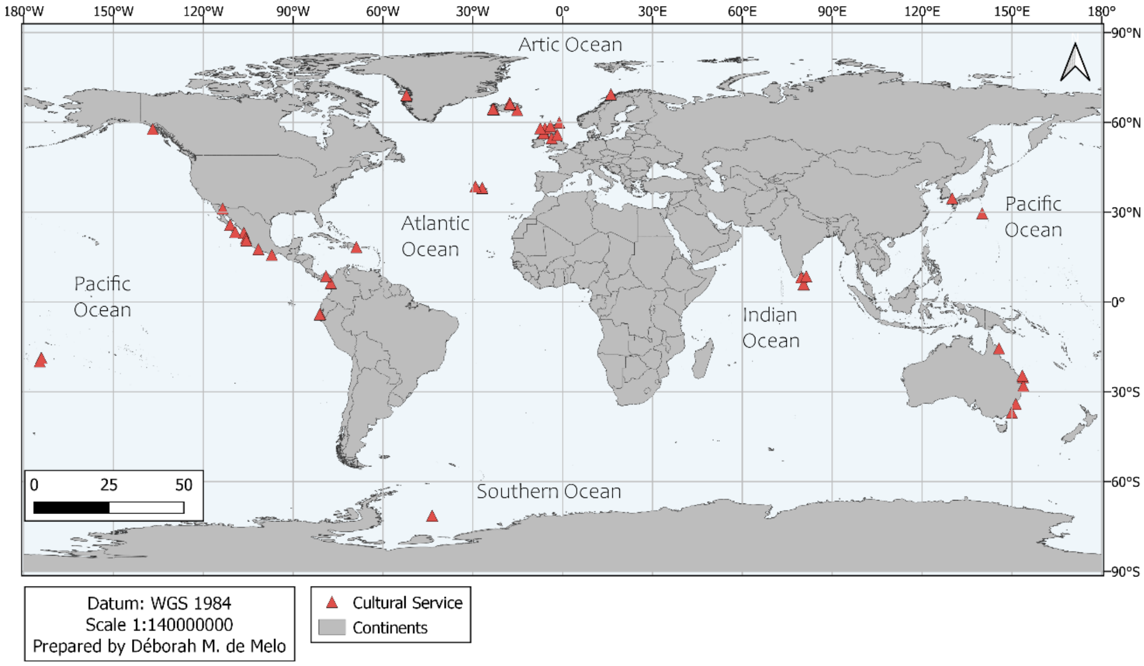

Fig. 3: Recording the distributions of articles that cited the cultural service of *Balaenoptera musculus, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera acutorostrata* and *Megaptera novaeangliae*.

In Portugal, this activity has focused on blue, fin and sei whales, generating jobs in different areas in both directly and indirectly. Furthermore, this activity generates an annual revenue, together with other marine tourism activities, of 56 million euros (Ressurreição et al., 2022). While in Scotland, minke whale tourism has reached around five million pounds (Cardenas et al., 2021; Cunningham et al., 2012, Ryan et al., 2018). Observation tourism, when well conducted, can be a tool for environmental conservation and protection, attracting tourist attention (García-Cegarra and Pacheco, 2017). Additionally, it can represent a form of economic recovery following periods of conflict as observed in Sri Lanka, post-war (Buultjens et al., 2016).

Beyond economic considerations, the presence of whales encompasses sociocultural values such as recreation and education, significantly impacting the well-being of the local community. They offer opportunities for education and environmental awareness, enriching the community's understanding of marine ecosystems and conservation efforts, as observed in Skjálfandi Bay, northern Iceland (Malinauskaite et al., 2021). Tourists visiting these communities can engage in additional educational experiences, such as at the Jangsaengpo Whale Museum in South Korea (Choi, 2017), contributing to community cohesion and identity and fostering a sense of belonging and connection among residents (Malinauskaite et al., 2021).

Although some whale-watching locations were not selected, the Brazilian coast is a key area for the annual migration of humpback whales to their breeding grounds. These whales exhibit strong site fidelity, particularly to the Abrolhos Bank region on the northeastern coast (Wedekin et al., 2010), which has led to a growing whale-watching industry (Cipolotti et al., 2005). Furthermore, the subpopulation migrating to Brazil has shown significant recovery since the historical exploitation of the species, expanding its breeding grounds to other parts of the Brazilian coast (Andriolo et al., 2023). With the expansion of both whale-watching locations and the activity itself, concerns about the well-being of the whales have also increased, as the activity can disrupt cetacean behavior, reducing resting and feeding time, especially for mothers and calves (Morete et al., 2023; Rossi-Santos, 2016). In this context, Morete et al. (2023) suggest that Brazilian legislation regarding best practices for whale-watching should be revised, recommending that boats maintain a safety distance of 300 meters instead of the current 100 meters. Additionally, they emphasize the importance of environmental education in the involved communities and reinforce the need for authorities to ensure adherence to best practices during whale-watching approaches.

Therefore, the industry must be regulated in a way that ensures the safety of the observed species, as well as of the tourists and vessel operators. As this is a coastal activity, it occurs in locations with intense vessel traffic. Furthermore, in some locations there are no good-conduct manuals, which can cause negative impacts on species and the sustainability of these activities (Kessler and Harcourt, 2012). Thus, regulation and monetary valuation need to be handled adaptively (Kessler and Harcourt, 2012) in order to accompany nature's dynamism and follow the temporal context, for example the industry's need to readapt due to the COVID-19 pandemic (Cook et al., 2020a; Cook et al., 2022; Richards et al., 2021).

3.3 – Regulation and Maintenance Services

Regulation and maintenance ESs refer to productivity and biodiversity enrichment, a role in nutrient cycling and evolutionary potential, in addition to their importance in climate regulation through direct and indirect carbon sequestration (Roman and McCarthy, 2010; Ratnarajah et al., 2014). Despite the importance of these services for ensuring biodiversity, evolutionary potential, and climate regulation (Cook et al., 2022), this topic is under-researched. Although it was well described by Roman et al. (2014), it seems to have gained scientific visibility only in 2022. The reviewed articles were performed in sub-tropical and polar regions, where whale-falls were recorded to occur only at the furthest points from the coast (Fig. 4). Of the reviewed articles, the approach of maintenance services for the increase in primary productivity used modelling for humpback, blue and fin whales as a tool of iron enrichment in the environment and consequent increase in productivity (Ratnarajah et al., 2016). Most of the articles involved studies on whale-falls and their associated communities and focused on direct and indirect carbon sequestration (Alava, 2009; Van Franeker et al., 1997).

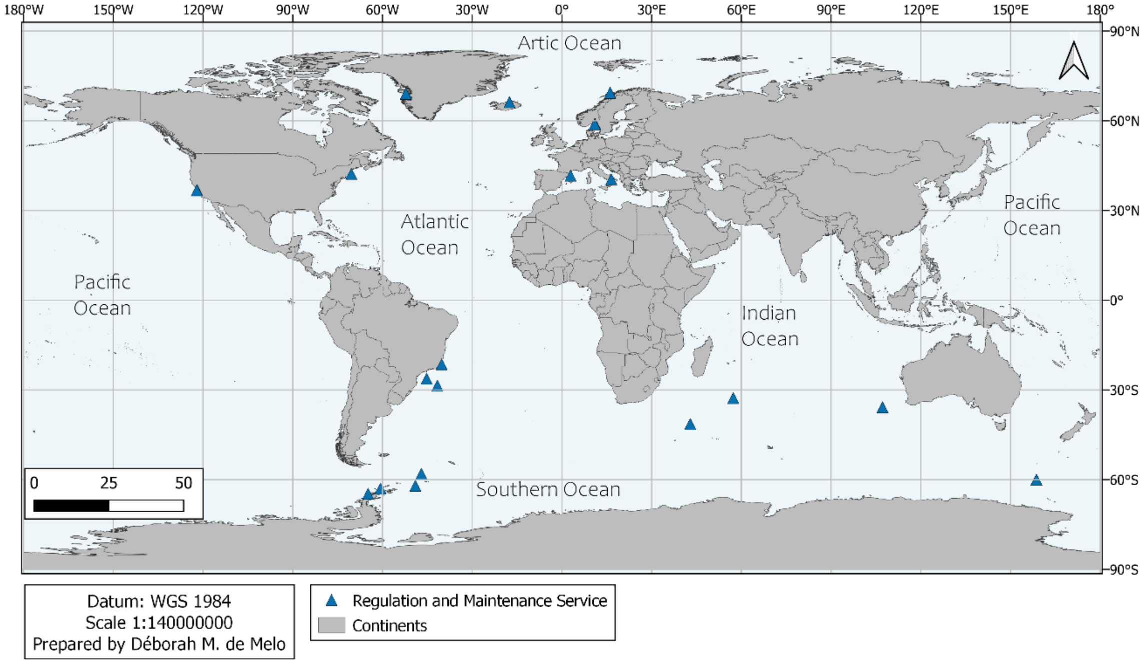

Fig. 4: Recording the distributions of articles that cited the regulation and maintenance service of *Balaenoptera musculus, Balaenoptera physalus, Balaenoptera borealis, Balaenoptera acutorostrata and Megaptera novaeangliae.*

Marine megafauna is responsible for redistributing the spatial patterns of nutrients and energy, influencing ecosystems and biodiversity (Estes et al., 2016; Roman et al., 2014). In feeding areas, species consume iron-rich resources such as krill (Jefferson et al., 2008; Roman and McCarthy, 2010; Roman et al., 2014). By moving vertically to feed and subsequently releasing faeces to the surface, whales return limiting and essential nutrients for primary productivity to the eutrophic zone. This concept was described by Roman and McCarthy (2010) as “whale pump” and acts as a fundamental element in iron cycling in the Antarctic Ocean (Nicol et al., 2010). Furthermore, when performing extensive migrations to breeding areas, they can be considered as ecosystem engineers (Hastings et al., 2007), as they horizontally fertilize the oceans through their excrement, placenta and milk which are rich in limiting and essential nutrients for primary productivity, increasing productivity at low latitudes (Allgeier et al., 2017; Lavery et al., 2010; Nicol et al., 2010; Roman et al., 2014).

This increase in productivity indirectly stimulates carbon fixation and sequestration, helping to mitigate climate change by regulating ecosystems (Lavery et al., 2010; Nicol et al., 2010; Roman et al., 2014). When great baleen whales die, tonnes of carbon can be sequestered in their bodies. For example, an adult can sequester an average of 33 tonnes of carbon to the ocean bed (Chami et al., 2019; Dufort et al., 2020; Pershing et al., 2010). Species can contribute to carbon sequestration in differently, for example, studies with blue and minke whales have concluded that they contribute more than other species (Dufort et al., 2020). Considering these important ecological functions, large marine mammals should receive more attention as potential biological pumps to mitigate the increase in atmospheric CO2, thus, providing a safer and more efficient solution to ocean fertilisation compared to costly and uncertain investments through the artificial addition of iron into the environment (Blain et al., 2007; Lavery et al., 2010).

Whale carcases are detrital reservoirs, representing sources of energy and nutrition for food chains and can affect the structure and dynamic of living species (Moore et al., 2004; Wilson and Wolkovich, 2011). Although they are stochastic and unpredictable, they heavily subsidise energy budgets which can increase food chain length and pass through several trophic levels before mineralising (Lea et al., 2018; Moore et al., 2004). The number of links can structure and stabilise an ecosystem, as it improves the food multi-channel by making resources available (Wilson and Wolkovich, 2011). Furthermore, carcases are food pulses which pass through different ontogenetic stages of decomposition, attracting a diversity of foragers (Fallows et al., 2013; Smith and Baco, 2003), forming islands of resources that resemble hydrothermal sources, vents and sinks (Alfaro-Lucas et al., 2018; Moore et al., 2004). They generate a mosaic of microhabitats that support assemblages with different levels of dependence on chemosynthetic environments, influencing the composition and structure of benthic communities and harbouring entire food chains whose effects can last for decades (Alfaro-Lucas et al., 2018; Amon et al., 2013; Danise et al., 2014; Dekas et al., 2018). They create biodiversity hotspots, ensuring spatial ecosystem complexity by modifying the physical structure of ecosystems and increasing consumer aggregations (Hastings et al., 2007; Holt, 2008; Moore et al., 2004; Smith and Baco, 2003).

At an evolutionary perspective, whale-fall occurs at different depths and may provide a path for specialisation, as described for polychaetes in a study by Danise et al. (2014) performed in Sweden with a minke whale carcass. The randomness of carcass distribution, unlike geological formations, could indicate whales as springboards for the evolution of different deep-sea species (Glover et al., 2005). This may have impacted the evolution of global marine ecosystems as suggested by Bianucci et al. (2019) in their study on a blue whale carcass during the Miocene era in Lake SanGiuliano – Italy. According to Malinauskaite et al. (2021), increasing biodiversity and evolutionary potential is the second most important role, after the value of the very existence of whales.

4. Loss of Ecosystem Services

The ecosystem services provided by rorquals may be underestimated, since populations were decimated and almost became extinct due to commercial hunting (Chami et al., 2019; Lavery et al., 2010; Roman et al., 2014,). The blue whale population, for example has been reduced to 3% of its original size (Chami et al., 2019). This drastic reduction in abundance and biomass can affect the nutrient dynamics of surface and deep environments, as well as decreasing carbon retention from living biomass and carbon sequestration to deep environments based on whale-fall (Butman et al., 1995; Lavery et al., 2010; Pershing et al., 2010).

Marine ecosystems have lower iron input, and they are storing less carbon, in addition to suffering from alterations in community dynamics and structure, biodiversity impoverishment (Cook et al., 2020b; Lavery et al., 2010; Moleon and Sanchez-Zapata, 2015) and trophic cascades (Roman et al., 2014). The effects on marine systems can be perpetuated over the long-term (Pershing et al., 2010, Wilson and Wolkovich, 2011), and can generate, for example, extinction debts of whale-fall specialists due to habitat loss caused by a decrease in carcasses on the sea floor (Smith et al., 2019). This issue may be intensified today by climate change, generating high temperatures which could, for example, change food availability, affecting migrations, reproduction and communities dependent on whales (Beasley et al., 2012; Hastings et al., 2007; Tulloch et al., 2019).

5. Marine Protected Areas and Ecosystem Services

The ESs mentioned in the reviewed articles were registered mainly in continental areas, across different latitudes and oceans (Fig. 5A) and close to the Exclusive Economic Zone (EEZ) which harbours an irreplaceable biodiversity (Sala et al.; 2021). Many ES areas identified in the articles are not inserted in Marine Protected Areas (MPAs) and based on the calculation of overlapping between ES areas and MPAs, it was possible to rank the most protected regions. The most overlapped area is located in the Great Barrier Reef – Australia. This area comprises different categories of national and international protection such as Marine Park, UNESCO Biosphere Reserve and World Heritage Site (Fig. 5D). This is followed by the Deep Mexican Pacific, Marietas Islands and Upper Gulf of California and the Colorado River Delta which are part of the Biosphere Reserve located in Western Mexico (Fig. 5B). The third most overlapped region was in a Marine Protected Area in the Inner Hebrides and the Minch in North-eastern Scotland (Fig. 5C).

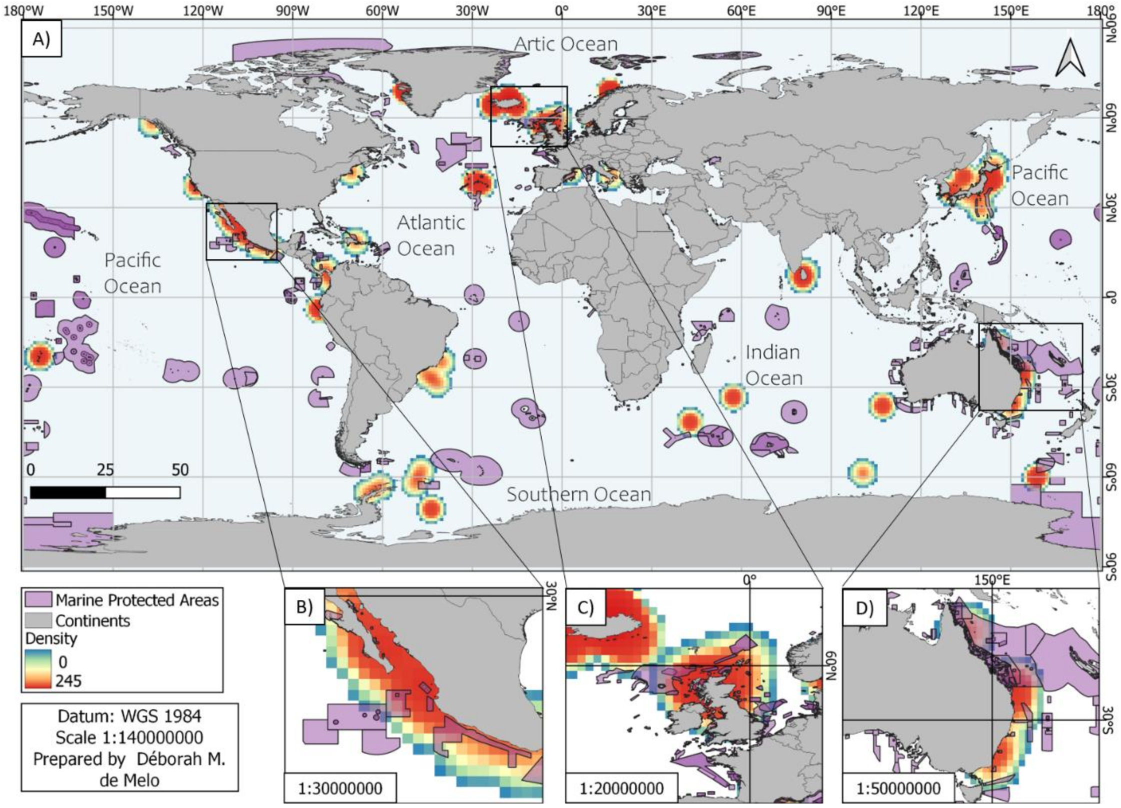

Fig. 5: A) Map showing the distribution of global Marine Protected Areas (MPAs) (in purple), with hotspots of ecosystem service density extracted from the article review; B – D) highlights of areas where the ecosystem services of *Balaenoptera musculus*, *Balaenoptera physalus*, *Balaenoptera borealis*, *Balaenoptera acutorostrata* and *Megaptera novaeangliae* overlap the most with MPAs.

Only 7% of the world's oceans are declared as Marine Protected Areas (MPAs), of these, only 2.7% are fully protected (MCI, 2022). These areas were created to ensure the protection and conservation of ecosystems and their associated services however, many priority areas are concentrated in the open ocean around submarine clusters, offshore plants, and unique biogeographic areas (Sala et al., 2021), which can make the management of these areas difficult and can interfere with the provisioning and efficiency of ESs. Urban and Vilória-Gómora (2021) observed differences in whale watching practices and surveillance in protected and unprotected areas in Mexico, showing the importance of efficiently managing protected areas. Another example is in Sri Lanka, where blue whales almost became extinct in 1997, however, following conservation initiatives and the creation of the Indian Ocean Sanctuary, this species has been recovering. Nonetheless, due to the poor management of tourist activities, together with high vessel traffic, negative impacts have arisen as result of these activities, making it is possible to observe changes in blue whale behaviour and area of occurrence (Anderson and Alagiyawadu, 2019).

Great baleen whales perform extensive migrations, connecting oceans and different latitudes and creating biological hotspots with their nutrient-rich faeces, in addition to forming regions of high primary productivity and aggregations of higher and diverse trophic levels (Estes et al., 2016; Roman et al., 2014). When prioritised, protected and well-managed, these regions can increase fishing yields, as they protect biodiversity (Sala et al., 2021), providing an ecological infrastructure and ensuring a variety of life supporting functions, as well as facilitating other services provided by whales (Cook et al., 2022).

6. Conservation and future prospects

Great baleen whales are key components of the marine system, influencing communities and the functioning of trophic webs (Estes et al., 1998; Nicol et al., 2010; Roman et al., 2014). Additionally, they can be used as bioindicators of tertiary productivity (Alava, 2009) and environmental sentinels (Bengston Nash et al., 2018). Therefore, investing in maintaining or recovering whale populations may be a long-term strategy for recovering fish stocks (Lavery and Roudnew, 2014; Roman and McCarthy, 2010). Additionally, whales offer a natural capital which is fundamental to all systems and relevant to the services that sustain human activities and life (Cook et al., 2022). The recovery of rorquals should be incorporated into cheap natural and ecologically sound solutions for carbon sequestration, helping to reach the aim of carbon neutrality and to mitigate and rebuild human resilience in face of climate change (Chami et al., 2019; Dufort et al., 2020; Hastings et al., 2007; Pershing et al., 2010).

Restoring populations can affect the economics of sustainable tourism, generate socioeconomic benefits, maintain biodiversity and conserve habitats (Dufort et al., 2020; Hastings et al., 2007). For a greater efficiency in service provision and positive returns to communities, governmental officials and decision makers need to view whales as a symbol of economic prosperity. Some strategies that implement a participatory approach can be adopted, together with the application of monetary and non-monetary valuation techniques which permit economic advances (Buultjens et al., 2016; Cook et al., 2020b; Malinauskaite et al., 2021). These strategies stimulate new mindsets regarding the dependence of human survival on natural systems (Chami et al., 2019).

It is also necessary to include ecosystem services when making decisions regarding management planning, spatial planning and the formation of conservationist policies (Cook et al., 2020a; Ressurreição et al., 2022), where it is necessary to maintain a pluralistic view on this topic. Good management using this approach, in addition to structuring protocols for identifying ecosystem services, in order to avoiding double-counting benefits, should also include different participants in decision making (Cook et al., 2020a; Fisher et al., 2009; Malinauskaite et al., 2021).

7. Summary and Conclusion

The numerous returns that great baleen whales provide to humans are indisputable, whether they are visible or not. But for this to continue, these species must be protected from anthropogenic impacts, thereby ensuring a healthy and balanced ecosystem. As such, regulations regarding environmental tourist practices must be implemented, in addition to intensifying access to good quality environmental education and the different means of communication to globalise and popularise the importance of conserving cetacean species. Government and private investments in scientific research are necessary, so that services such as regulation and maintenance can be better investigated and gaps can be filled, since this is the basis for the provision of other services and human and economic well-being. Additionally, short and long-term strategies should be created that improve the management of existing MPAs and expand them to areas that cover species' migration routes, areas of occurrence and the service hotspots highlighted here, forming corridors with connected priority areas.

The valuation of ecosystem services provided by whales is a crucial tool for making informed decisions in management planning, spatial planning, and conservation policy formulation. Therefore, this study underscores the urgent need for integrated and participatory policies that recognize and value the multiple ecosystem services provided by whales, ensuring a holistic and effective management approach. By promoting the conservation and recovery of cetacean populations, we can not only safeguard the health of marine ecosystems but also significantly contribute to long-term human well-being and economic sustainability. Great baleen whales are symbols of prosperity and identity in different cultures and maintaining healthy populations means having healthy marine life, including all ecosystems and living beings.

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CHAPTER 2

Tracing allochthonous nutrient pathways from whale carcasses to coral reef food webs: Experimental and stable isotope evidence

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Tracing allochthonous nutrient pathways from whale carcasses to coral reef food webs: Experimental and stable isotope evidence

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ABSTRACT

The presence of allochthonous nutrient sources derived from animal migrations can significantly alter the trophic structure of marine communities. This study investigated how the addition of a humpback whale (*Megaptera novaeangliae*) carcass pieces influences the reef community in the Abrolhos Bank, using stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Changes in the isotopic niche of individual species and in the trophic structure of the community were evaluated following the resource addition, along with an estimation of the carcass contribution to the diet of potentially consumer species. Primary producers and secondary consumers showed greater isotopic shifts toward the whale carcass stable isotope values and reductions in niche width. Other species responded differently: some exhibited niche contraction, suggesting specialization, while others expanded their isotopic niche, reflecting intraspecific plasticity. Despite methodological limitations, the results indicate that the allochthonous resource was assimilated through different trophic pathways, both directly and indirectly, highlighting the ecological role of whales as ecosystem vectors of nutrients. This research reinforces the importance of integrating punctual events, such as the death of large cetaceans, into the understanding of habitat connectivity and the conservation of reef ecosystems – this is particularly important in the face of the growing demand for marine management based on ecological processes.

Keywords: allochthonous input; energy flow; humpback whale; isotopic niche; trophic diversity; trophic structure;

INTRODUCTION

Coral reefs are highly biodiverse and productive ecosystems, characterized by rapid biogeochemical cycling and high accretion rates, which result in complex three-dimensional structures (Hatcher et al., 1997). This structural complexity supports niche diversification by providing shelter, spawning grounds, nurseries, and feeding habitats for a wide range of species (Newman et al., 2015; Woodhead et al., 2019). In addition, high decomposition rates minimize detritus accumulation, promoting efficient nutrient recycling (Hatcher et al., 1997; Nelson et al., 2023). However, due to their geographic location and the commercial value of many species, coral reefs are under increasing anthropogenic pressure, including eutrophication, overfishing, and climate change, which compromises their functionality through biotic homogenization and the loss of key species (Graham et al., 2020; Lesser, 2021; Donavon et al., 2021).

Reef food webs are complex and open systems, influenced by environmental connectivity that facilitates the transfer of energy and nutrients between ecosystems (Pozas-Schacre et al., 2021; Robinson et al., 2023). This connectivity is expressed through matter fluxes, defined as the pathways and rates by which essential elements move through trophic networks, shaping ecosystem functioning (Brandl et al, 2019; Skinner et al., 2021; Robinson et al, 2023). These fluxes comprise two of the eight pillars of reef ecosystem functioning proposed by Brandl et al. (2019): nutrient uptake and release, complementary processes of gain and loss through the introduction, retention, and reintegration of nutrients.

Reef functioning is regulated by both extrinsic factors (e.g., anthropogenic impacts, environmental conditions) and intrinsic ones (e.g., population dynamics, trophic structure) (Allgeier et al., 2014; Brandl et al., 2019; Robinson et al., 2023). While primary production fuels the base of energy pathways via photosynthesis, secondary production is largely driven by fish through biomass accumulation, excretion, and egestion (Allison and Ellis, 2001; Allgeier et al., 2013; Brandl et al, 2019; Robinson et al, 2023, Schiettekatte et al., 2023). Microorganisms also play a central role by remineralizing dissolved organic matter derived from both living organisms and detritus (Wilson et al., 2003; Ben-David and Flaherty, 2012), with the microbial loop channeling energy and supplying nutrients such as phosphorus and nitrogen to primary producers, protozoans, zooplankton, fish, and cetaceans (Pomeroy et al., 2007; Nelson et al., 2023).

Resource fluxes transport inorganic nutrients, detritus, reproductive organisms, and decomposing biomass across ecosystems, increasing resource availability in the receiving communities (Polis et al., 2004; Gounand et al., 2018). In reef environments, such spatial flows are mediated by passive abiotic mechanisms (e.g., currents, wind, upwelling) and active biotic ones (e.g., seasonal migrations, foraging, larval dispersal, life cycle movements) (Polis et al., 1997; Gounand et al., 2018; Brandl et al, 2019; Skinner et al., 2021; Dunn et al., 2025). This connectivity is critical to community and ecosystem functioning, and the meta-ecosystem framework provides a useful approach to understanding spatial coupling (Gounand et al., 2018).

Passive and active mechanisms, reef structural features, bathymetry, and interaction with surrounding seascapes, including proximity to terrestrial sources, shape reef structure and functioning (Williams et al., 2019). These factors differentiate tropical from temperate reefs, and coastal from oceanic ones, leading to variations in diversity, biomass, nutrient cycling efficiency, and food web length (Post 2002; Morais and Bellwood, 2019; Eddy et al, 2021; Brandl et al., 2025). Temperate reefs are more strongly affected by seasonal dynamics (Post, 2002), while tropical reefs, though nutrient-poor, benefit from high solar radiation supporting primary productivity (Sigman and Hain, 2012). Latitudinal gradients, as observed in Australia, directly influence the biomass, abundance, and richness of herbivores (Tebbett et al., 2024).

The dependence on allochthonous organic matter is particularly relevant in oceanic reefs, where pelagic subsidies may enhance the biomass of planktivores and piscivores (Sanchez-Piñero et al., 2000; Williams et al., 2019; Skinner et al., 2021). Although more turbid due to their proximity to land (Ferreira and Gonçalvez, 2006), coastal reefs benefit from energetic connectivity with sandy bottoms, seagrass beds, and mangroves (Davis et al., 2014). Coastal upwelling events may also increase their productivity (Sigman and Hain, 2012). In Moreton Bay, for example, mangrove connectivity increases the production of functional herbivores such as *Pseudolabrus guentheri* (Davis et al., 2014).

Detrital inputs such as carcasses, excreta, and plant material provide valuable energy subsidies of varying quality and residence time (Moore et al., 2004; Subalusky and Post, 2019). Upon entering the system, these materials may fall directly onto reefs or be assimilated through direct and indirect pathways, becoming new biomass, waste, or energy (Wilson et al., 2003; Moore et al., 2004; Benke, 2010; Eddy et al., 2021). Nutrients stored in biomass are then transferred through trophic networks (Allgeier et al., 2017). Events like whale falls create islands of high productivity on the seafloor, hosting specialized communities similar to those in hydrothermal vents (Amon et al., 2013; Danise et al., 2014; Alfaro-Lucas et al., 2018; Dekas et al., 2018). In contrast, the “whale pump” effect, driven by species such as humpback whales in feeding areas, transports nutrients like nitrogen and iron from deep to surface waters, enhancing primary production (Roman and McCarthy, 2010).

Stable isotope analysis is a powerful tool for tracing and quantifying allochthonous resource assimilation, enabling inferences about diet, trophic position, and nutrient source (Post, 2002; Fry, 2006; Ben-David and Flaherty, 2012). Tissue isotopic composition integrates dietary inputs over time and reflects environmental nutrient sources, functioning as a natural tracer of foraging behavior (Kim et al., 2012). Carbon stable isotope ratios ($^{13}C/^{12}C$, expressed by $\delta^{13}C$) indicates the basal carbon source and may reveal latitudinal differences and habitat use (Hobson 1999; Bird et al., 2018), while nitrogen stable isotope ratios ($^{15}N/^{14}N$, expressed by $\delta^{15}N$) increases with each trophic transfer (usually ~3–4‰ in marine food webs), making it widely use indicator of trophic level (De Niro and Epstein 1981; Layman et al., 2007). Nitrogen and carbon isotope ratios are commonly used due to their high availability in organic tissues and predictable enrichment between consumers and their sources, allowing researchers to characterize trophic niches at the individual and population levels (Fry, 2006; Layman et al., 2007).

The isotopic niche is a quantitative representation of the ecological niche, defined as the position a species or population occupies in isotopic space, providing insight into diet, trophic level, and resource origin (Newsome et al., 2007). To compare individuals, populations, or species, isotopic metrics can estimate diversity in energy pathways and trophic redundancy within food webs (Layman et al., 2007). For example, Kim et al. (2012) identified ontogenetic dietary shifts in white sharks (*Carcharodon carcharias*) in California, with broader niche widths at later life stages, reflecting generalist feeding strategies. These metrics also serve as indicators of anthropogenic impacts and can guide conservation efforts. For instance, unsustainable fishing pressure in unprotected reefs of the Abrolhos Bank reduce dietary diversity, leading to niche contraction and decreased trophic redundancy, which may compromise reef resilience (Leitão et al., 2023).

This approach is particularly relevant in tropical and coastal ecosystems such as the Abrolhos Bank, where biogenic reefs support high biodiversity and endemism (Leão, 1996; Leão, 2003), and multiple allochthonous nutrient sources contribute to local trophic dynamics. These include resuspended terrigenous sediments (Ferreira and Gonçalves, 2006) and nutrient inputs from seabird colonies nesting on the archipelagos. Such inputs, via guano or carcasses, are assimilated both directly and indirectly across all trophic levels, including coral reefs adjacent to the islands (Linhares and Bugoni, 2023).

In addition to these inputs, the seasonal movement of large vertebrates, such as humpback whales (*Megaptera novaeangliae*), represents a significant pathway of biological subsidization. The findings from the next chapter demonstrated that this species acts as an animal-derived subsidy within the Abrolhos reefs, with the potential to seasonally alter the structure and productivity of the reef fish community. Although these whales do not feed in the region, they transport nutrients from feeding grounds to breeding areas via placenta, sloughed skin, feces, and the carcasses of neonates and adults (Smith et al., 2019; Roman et al., 2025). This raises the hypothesis that such seasonal inputs are assimilated by the reef community, potentially causing trophic shifts detectable through stable isotope analysis.

In light of this, the present chapter investigated how the input of allochthonous nutrients derived from humpback whale carcasses can alter the trophic structure of the reef community and investigated the potential pathways for these nutrients at the Abrolhos Bank, using stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). The response of the reef community structure was assessed following the addition of this allochthonous resource, based on isotopic metrics (Layman et al., 2007) and the isotopic niche of individual species and the overall trophic organization of the community. The proportional contribution of the carcass to the diet of species that potentially utilized the resource was also estimated. It was expected that the presence of a high-quality, low-cost energy resource would result in a shift in species isotopic values toward those of the whale, via direct or indirect consumption.

In this context, we postulate and tested different scenarios for changes in community structure and species niche. At the community level, two scenarios are possible: if all species assimilate the resource in a homogeneous manner, all layman community metrics (Layman et al., 2007, see Methods section for a description of these metrics) will decrease and the community will become specialized on the allochthonous resource (Figure 1A); however, if all species utilize the resources in a more diversified manner, almost all metrics will increase, reflecting a generalist community in terms of resource acquisition (Figure 1B). Within each species, two situations are also possible: if only part of the individuals assimilate the resource, the isotopic niche will expand, suggesting greater intraspecific variability in resource uptake (Figure 1C-I); but if all individuals assimilate the resource, the isotopic niche space may contract, indicating specialization on the allochthonous resource (Figure 1C-II).

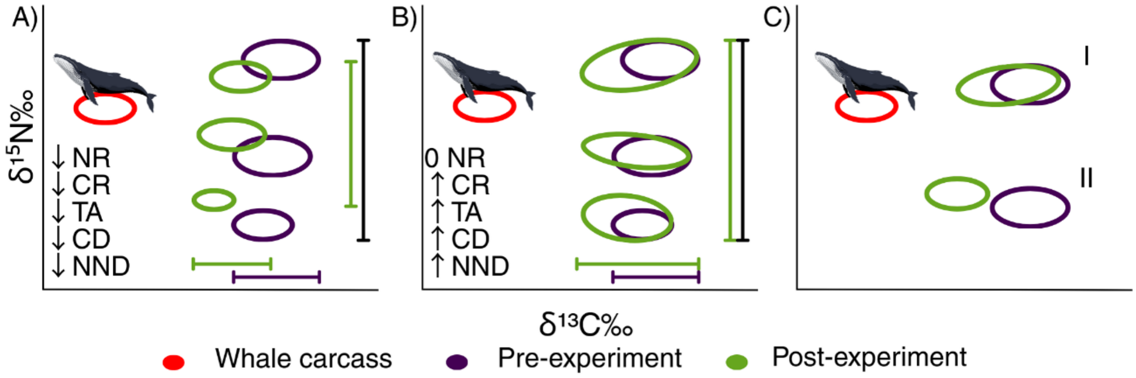

Figure 1: Hypothetical responses of the Abrolhos coral reef community following the addition of allochthonous nutrients derived from humpback whale carcasses. Different ellipses represent the isotopic niche of a particular species. The red circle denotes the isotopic position of the allochthonous resource, which has the most depleted carbon value. Some scenarios are proposed: all species use the resource homogeneously (A); species utilize resources in a more generalist fashion (B); part of the individuals assimilate the resource and the niche expands (C-I); or all individuals assimilate the resource and the niche contracts (C-II). The upward arrows, downward arrows, and "0" indicate changes in the metrics after resource addition – increase, decrease, or no change, respectively. NR (Nitrogen Range), CR (Carbon Range), TA (Total Area), CD (Centroid Distance); NND (Nearest-Neighbor Distance). The side bars indicate the ranges of NR and CR before and after the experiment.

Energy and nutrient fluxes in coral reefs determine organismal health and the provision of ecosystem services, ultimately influencing human well-being. Measurements of these fluxes can assist in guiding conservation and management of aquatic ecosystems (Robinson et al., 2023). Investigating these dynamics contributes to understanding the trophic effects of seasonal allochthonous subsidies in reef ecosystems and broadens the perspective on how large marine vertebrates – despite not feeding locally – can influence the structure and functioning of reef-associated communities that use these habitats seasonally.

METHODOLOGY

Study Area

The Abrolhos Bank region is located on the continental shelf between southern Bahia and northern Espírito Santo, Brazil (16°40′–19°40′S and 37°20′–39°10′W), encompassing an area of approximately 42,000 km². It comprises a complex reef system characterized by two main arcs, one closer to the coast and the other farther offshore, as well as volcanic-origin islands. These reefs form structurally diverse habitats with high benthic complexity and a notable proportion of endemic species (Leão, 1999; Moura et al., 2013). Composed of pinnacles at varying depths, the reef structure includes a combination of reef-building corals, crustose coralline algae, and encrusting bryozoans (Leão et al., 2003; Bastos et al., 2018). At the center of the region lies the Abrolhos Archipelago, consisting of five islands surrounded by fringing biogenic reefs, extensive live coral cover, and high fish biomass (Fainstein and Summerhayes, 1982; Leão and Kikuchi, 2001; Bruce et al., 2012). This reef complex stands out as one of the largest and most diverse in Brazil (Leão, 1999). Since 1983, the archipelago and approximately 880 km² of its surrounding waters have been protected as the Abrolhos Marine National Park (PARNA-Abrolhos) (Lodi and Borobia, 2013) (Figure 2).

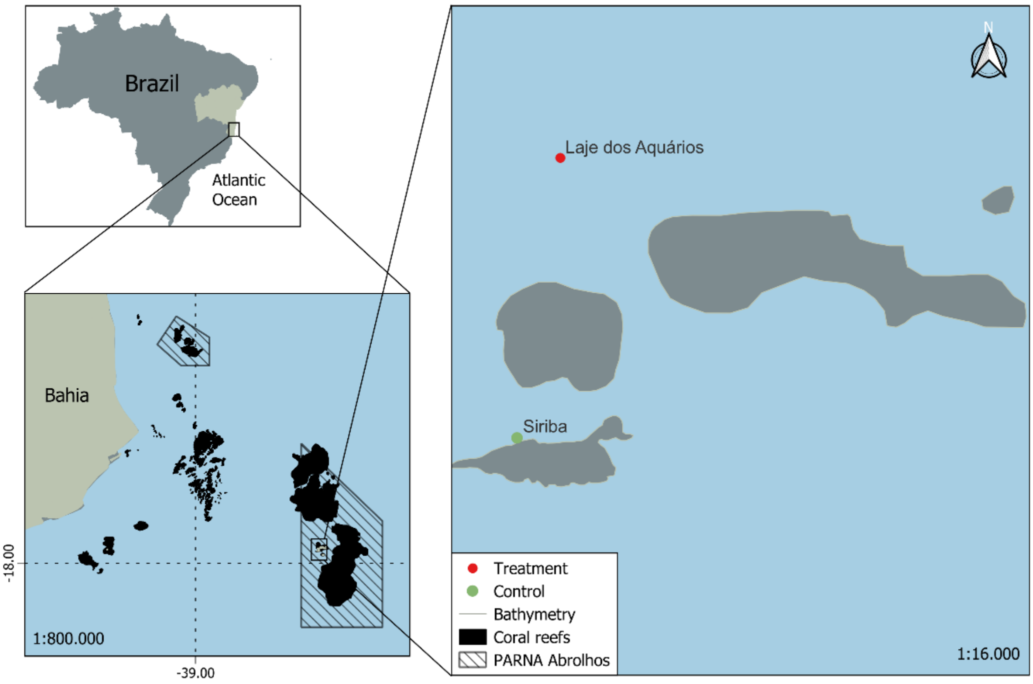

Figure 2: Location of the investigated coral reefs, the red dot refers to the location where the pieces of humpback whale muscles were inserted for the experiment; while the green dot refers to the control location for this addition.

During the austral winter, the Abrolhos Bank serves as a key breeding ground for humpback whales, hosting a high density of mother–calf pairs and functioning as an important nursery area for the species (Engel and Martin, 2009; Andriolo et al., 2010). These individuals belong to one of the seven recognized breeding stocks in the Southern Hemisphere and undertake annual migrations from feeding grounds in Antarctica to tropical waters off the Brazilian coast. They remain in the region between June and November, with peak abundance observed in August and September (Morete et al., 2008; Seyboth et al., 2023). Following the breeding season, the whales begin their return migration to the South Atlantic (Engel and Martin, 2009). The coastal zone of the Abrolhos Bank is also notable for the high number of whales strandings recorded between 2002 and 2019 – a total of 389 individuals – with the greatest concentration occurring along the mainland coast closest to the archipelago (da Cunha Ramos et al., 2024).

Data Collection

To understand how the seasonal arrival of this animal-derived subsidy may be assimilated into the trophic web of the region – and concomitant with the *in situ* experiment – specimens from different trophic levels were collected. The experiment was conducted on the shallow reefs of Laje dos Aquários (Figure 2), which were selected as the treatment site (T) for the deployment of humpback whale muscle tissue obtained from a stranding event during the 2023 breeding season, and which remained frozen until the time of the experiment. On this small reef, located approximately 280 meters from the main island of the archipelago, 17 muscle pieces of about 10 kg each were deployed, totaling an estimated 170 kg. The tissue was enclosed in iron cages (70 x 70 x 70 cm), each one was secured to the seafloor with two cement anchors (~50 kg each), forming five structural units (Appendix S1:FigureS1). The reef at Siriba Island was selected as the control site, where the same species were also collected. Both reefs were characterized by similar depths, ranging from three to eight meters, with an average temperature of 26 °C throughout the experimental period.

The experiment initiated in April 2024. Specimens were collected at both the treatment and control sites prior to the allochthonous resource addition, defining the pre-experiment period (P). After three months, algae, corals, and invertebrates were collected at the treatment site; and after six months, fish specimens were sampled from the same site – both representing the post-experiment period. For the post-experiment collection interval, the time of tissue isotopic turnover was considered, but mainly the logistics of returning to the collection site. Fish species selection was based on previous biodiversity surveys, with trophic level classifications retrieved from FishBase (Froese and Pauly, 2024) and subsequently validated through trophic level analysis of collected samples. According to the literature, *Acanthurus bahianus* and *Stegastes fuscus* are functionally categorized as herbivore (Ferreira and Gonçalves, 2006), occupying the trophic level of primary consumer. However, according to the isotopic values collected (see Results Section), they were regrouped in the present study as secondary and tertiary consumers, respectively.

Selected representatives included: Primary producers – *Dictyota sp.*; Turf – Epilithic algal matrix (turf); Mixotrophic corals – *Mussismilia harttii* and *Siderastrea* *stellata*; Primary consumers – hermit crab (Paguroidea), amphipods (Gammaridae), polychaetas (Nereididae), and *Echinometra lucunter*; Secondary consumers – *Malacoctenus zaluari* and *Acanthurus bahianus*; Tertiary consumers – *Stegastes fuscus*, *Haemulon aurolineatum*, *Haemulon plumierii* and *Lutjanus chrysurus*; and Quaternary consumer – *Mycteroperca bonaci*. The inclusion of *S. fuscus* occurred after the start of the experiment based on dietary interaction data observed in the literature. The post-experiment sampling inclusion of *H. aurolineatum* occurred due to the observed direct interaction (Table 1).

Table 1: Sampled species during the pre- and post-experiment periods of allochthonous resource addition. Columns represent the occupied trophic levels according to the respective estimated values based on $\delta^{13}C$ and $\delta^{15}N$ values of the samples; the number of samples collected in each treatment for $\delta^{15}N$ and $\delta^{13}C$ analysis; and the type of tissue sampled (ST). P – Producer; T – TURF; Mi – Mixotroph; 1Co - 1º Consumer; 2Co -2º Consumer; 3Co - 3º Consumer; 4Co - 4º Consumer; CS – Complete seaweed; SP – Soft part; M – Muscle.

				N sampled			
		Trophic level		**Treatment**		**Control**	
Species		**Pre**	**Post**	**Pre**	**Post**	**Pre**	**ST**
Dictyota sp.	P	1.3	1.9	5	5	5	CS
Turf	T	1.2	1.6	5	5	5	CS
Mussismilia harttii	Mi	2.2	2.3	5	5	5	SP
Siderastrea stellata	Mi	1.9	2.2	5	5	5	SP
Paguroidea – hermit crab	1Co	1.9	1.9	5	5	5	SP
Gammaridae – amphipod	1Co	1.9	1.9	6	2	4	SP
Nereididae – polychaeta	1Co	2	-	7	-	4	SP
Echinometra lucunter	1Co	2	2	5	5	5	SP
Malacoctenus zaluari	2Co	3.2	3.3	5	5	5	M
Acanthurus bahianus	2Co	3	2.9	5	5	5	M
Stegastes fuscus	3Co	-	3.6	-	5	-	M
Haemulon aurolineatum	3Co	-	3.6	-	8	-	M
Haemulon plumierii	3Co	3.8	4	5	5	5	M
Lutjanus chrysurus	3Co	3.8	3.8	5	6	6	M
Mycteroperca bonaci	4Co	4.2	4.1	5	2	5	M
Megaptera novaeangliae	-	-	-	8	-	-	M

For fish, muscle was the tissue of choice, always taken from the antero-dorsal region; for invertebrates and corals, all soft tissue was sampled; and for algae, the entire thallus was used, with one individual representing one sample. However, for polychaeta and amphipods, each sample consisted of a pool of individuals collected using a fine mesh. The turf, classified as an epilithic algal matrix and a primary producer, was treated as a separate category due to the presence of organic detritus that was not removed (Table 1). All samples were stored frozen until processing. In the laboratory, they were dried at 60°C for three days until fully dehydrated, then ground to a homogeneous powder. The resulting powder was placed into sealed, labeled tin capsules and stored in ELISA-type trays for further analysis. Lipids were extracted from *M. novaeangliae*, *E. lucunter* and corals tissues using the chloroform: methanol (2:1) method, as lipids are depleted in carbon and may bias incorporation rates and discrimination factors (DeNiro and Epstein, 1977; Ben-David et al., 2012). Following lipid extraction, samples underwent the same dehydration process.

All samples were sent to the Stable Isotope Center (CIE) at the Institute of Biosciences, São Paulo State University (UNESP). There, additional inorganic calcium carbonate extractions were performed on coral and turf samples via acidification with 20% HCl in silver capsules. The removal of inorganic carbonates is necessary due to their enriched carbon values and their non-dietary origin, which can distort isotopic results (Fry, 2006). Stable isotope analyses of carbon and nitrogen were conducted at CIE using an isotope ratio mass spectrometry system with an elemental analyzer (EA-IRMS, Flash 2000 - Delta V Advantage, Thermo Scientific, Germany). The system simultaneously determined the isotopic ratios $R(^{i}E/^{j}E)_{sample}$ for carbon and nitrogen, expressed as relative differences ($\delta^{i}E$) in per mil (‰) according to Coplen (2011):

$$\delta^{i}E_{(‰)} = (R(^{i}E/^{j}E)_{sample} / R(^{i}E/^{j}E)_{standard}) - 1,$$

where ^{i}E is the rare isotope, ^{j}E the abundant isotope, and $R(^{i}E/^{j}E)_{standard}$ are international standards VPDB and Air for $R(^{13}C/^{12}C)_{VPDB}$ and $R(^{15}N/^{14}N)_{Air}$, respectively. Results were normalized using certified reference standards USGS61, USGS62, USGS63, USGS90, and USGS91 (Paul et al., 2007; Schimmelmann et al., 2016, 2020). The analytical uncertainty was estimated at ±0.10‰ and ±0.15‰ for $\delta^{13}C$ e $\delta^{15}N$, respectively.

Data Analysis

To assess whether isotopic niches of species differed between sampling periods, $\delta\ ^{13}C$ and $\delta\ ^{15}N$ values were used to generate the Bayesian Standard Ellipse Area (SEA_B), a widely used proxy for core isotopic niche (Jackson et al., 2011), which resemble some characteristics of the wider ecological niche (Newsome et al. 2007). The functions "*siberMVN*" and "*siberEllipses*" were used with 20,000 iterations and burning out of the first 1,000 values and thin out factor of 10, fitting ellipses from a Bayesian multivariate normal distribution via JAGS and calculating SEA_B from posterior distributions, respectively, resulting in 4000 SEA_B simulations for each combination of treatments and periods.

To investigate whether SEA_B values differed for each species between periods, a multilevel Bayesian model was fitted using Stan to compare $\delta^{13}C$ and $\delta^{15}N$ values in samples collected at the carcass addition site (Bürkner, 2017). A Gaussian distribution with an identity link was used for $\delta^{13}C$ and $\delta^{15}N$ values. The model was run using four Markov Chain Monte Carlo (MCMC) chains to extract random posterior samples for

4000 iterations after a 1000 warm-up, using priors via the "*brms*" package (Bürkner, 2017). The model formula was:

$$SEA_B \sim period * SP,$$

where *period* refers to pre- or post-carcass addition, and *SP* refers to the species code. Model convergence and fit were evaluated by visual inspection of MCMC chains and checking if the Gelman-Rubin convergence statistic (^R) approached 1 (Gelman and Rubin, 1992; Bürkner, 2017). Estimates of predictor effects were obtained from the posterior distributions of the Bayesian model. To investigate variation in SEA_B between periods for each species, Log-Response Ratios (logRR) and their 95% credibility intervals were calculated. Evidence for an effect was determined based on the direction and magnitude of the posterior distributions, with effects considered significant when the 95% credible intervals did not cross zero (McElreath 2020).

To understand whether the isotopic values of sampled species became more similar to the whale's isotopic values after carcass addition, the Euclidean distance (a proxy for the proportion of the carcass derived nutrient consumption) of each sample point to the whale's isotopic centroid was calculated before and after the addition, using the formula (Ciancio et al., 2021):

$$ED = sqrt\ ((\delta^{15}N_{consumer} - mean\delta^{15}N_{whale})^{2} + (\delta^{13}C_{consumer} - mean\ \delta^{13}C_{whale})^{2}),$$

where ED is the Euclidean distance, and $\delta^{15}N_{consumidor}$ and $\delta^{13}C_{consumidor}$ are the nitrogen and carbon isotopic values of each sample. To identify species that shifted their isotopic position relative to the whale centroid, a linear model with interaction between period (pre and post) and species (SP) as fixed factors was fitted:

$$lm\ (DistWhale \sim period * SP),$$

where the response variable *DistWhale* is the Euclidean distance calculated previously. Temporal variation significance per species was assessed using marginal estimates from the model with the *emmeans* package, considering 95% credibility intervals.

Subsequently, to test whether species that became isotopically closer to the whale also showed reduced niche breadths, a regression analysis was performed between the difference in SEA_B values ($SEAB_{post} - SEAB_{pre}$) and the difference in Euclidean distances ($ED_{post} - ED_{pre}$), using the model:

$$lm\ (SEAB_{post\text{-}pre} \sim ED_{pós\text{-}pre}).$$

To understand community structure and whether it changed between the pre- and post-addition periods, Layman's metrics were calculated: *NR* (nitrogen range) – the distance between the species with highest and lowest $\delta^{15}N$values; *CR* (carbon range) – the distance between the most ^{13}C-depleted and ^{13}C-enriched species; *TA* (total area) – the area covered by all species in biplot space, representing total niche space; *CD* (centroid distance) – the average Euclidean distance of each species to the mean $\delta^{13}C$ and

δ^{15}N values; *NND* (mean nearest neighbor distance) – the mean Euclidean distance to the nearest neighbor in biplot space (Layman et al., 2007). Metrics were calculated using the *siber* package to create posterior distributions, followed by simulations with the "*bayesianLayman*" function, generating 4000 simulations per sampling period. Metric significance was assessed using Student's t-tests.

All species-level analyses were also applied to species grouped by trophic levels to assess how community trophic structure responded to resource addition. To confirm species trophic level, the formula proposed by Post (2002) was used:

$$TL = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{base}) / \Delta_n,$$

where TL is the trophic position of the consumer, λ is the trophic position of the baseline species, $\delta^{15}N_{consumer}$ is the δ^{15}N of the species of interest, $\delta^{15}N_{base}$ is the δ^{15}N of the baseline species, and Δ_n is the trophic enrichment factor. The sea urchin *Echinometra lucunter* was used as the baseline species, with $\lambda = 2$ and $\Delta_n = 3.4$ (Post, 2002) (Table 1).

In order to understand the impact of direct consumption of carcasses by scavenger fishes MixSIAR Bayesian mixing model was used to estimate the contribution of whale-derived input to consumer species (Stock et al., 2018). Selected consumers were *H. aurolineatum*, *L. chrysurus*, and *M. zaluari*, with the first two observed feeding directly on the carcass in video footage, and the latter suggested by stable isotope analysis. Literature on the diets of these species was reviewed to inform the mixing model (Pereira and Jacobucci, 2008; Fonseca, 2009; Limeira et al., 2022). Amphipods, polychaetas and whale carcass sampled during the experiment were used as resource items. Trophic discrimination factors used were 0.8 ± 0.4 ‰ and 3.4 ± 0.5 ‰ for δ^{13}C e δ^{15}N, respectively (Post, 2002). MCMC settings followed the "short" chain option (chain length = 50,000; burn-in = 25,000; thinning = 5 for three chains). Model convergence was evaluated using Gelman-Rubin and Geweke diagnostics (Stock and Semmens, 2016; Stock et al., 2018).

Data processing, statistical analyses, and visualizations were performed in R (R Core Team, 2024), using the packages *siber* (Layman et al., 2007; Jackson et al., 2011), *brms* (Bürkner, 2017), and *MixSIAR* (Stock & Semmens, 2016; Stock et al., 2018). Because *siber* package requires a minimum sample size in both pre- and post-treatment samples, amphipods, polychaetas, *S. fuscus*, *H. aurolineatum*, and *M. bonaci* were excluded from community-level metrics, ellipse area estimations, and the fitted model. Only species sampled in both periods were included for Euclidean distance to whale carcass calculations, excluding *S. fuscus* and *H. aurolineatum*. Species excluded from these analyses were also excluded from trophic groupings.

RESULTS

The treatment and control sites showed similar community structure (although the control site showed wider δ ^{13}C in the base of the food web), with investigated species showing similar values for δ^{13}C and δ^{15}N (Figure 3), validating the chosen site as "control".

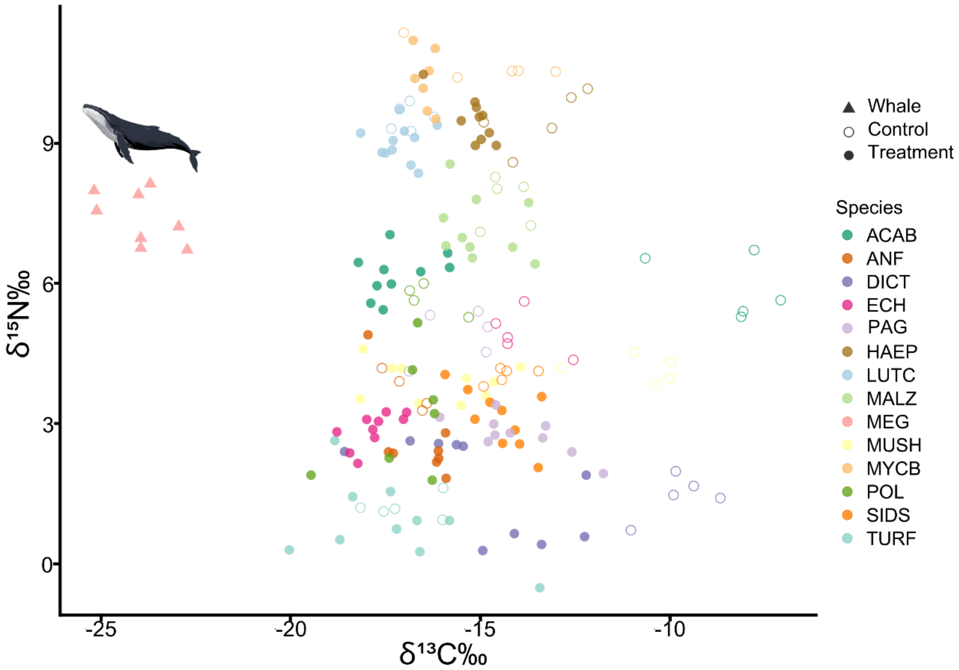

Figure 3: Stable isotope values of the species collected during the experiment in the treatment and control sites. ACAB – *A. bahianus*, ECH – *E. lucunter*; LUTC – *L. chrysurus*; MUSH – *M. harttii*; SIDS – *S. stellata*; ANF – Gammaridae; PAG – Paguroidea; MALZ – *M. zaluari*; MYCB – *M. bonaci*; TURF – epilithic algal turf; DICT – *Dictyota sp.*; HAEP – *H. plumierii*; MEG – *M. novaeangliae*; POL – Nereididae.

The community structure at the treatment site showed equal mean values of carbon range (CR) between the sampling periods (4.6 ± 0.7‰ SD). In contrast, the mean values of nitrogen range (NR) (9.4 ± 0.7‰ and 8.2 ± 0.7‰), total area (TA) (30.1 ± 3.9‰ and 23.9 ± 4.1‰), centroid distance (CD) (3.2 ± 0.1‰ and 2.8 ± 0.1‰), and nearest neighbor distance (NND) (1.78 ± 0.1‰ and 1.4 ± 0.2‰) showed higher values in the pre-experiment period. These reductions suggest that the community structure became more aggregated following the resource input. Except for CR, all metrics showed statistically significant differences in mean values between the experimental periods ($p < 0.05$) (Figure 4).

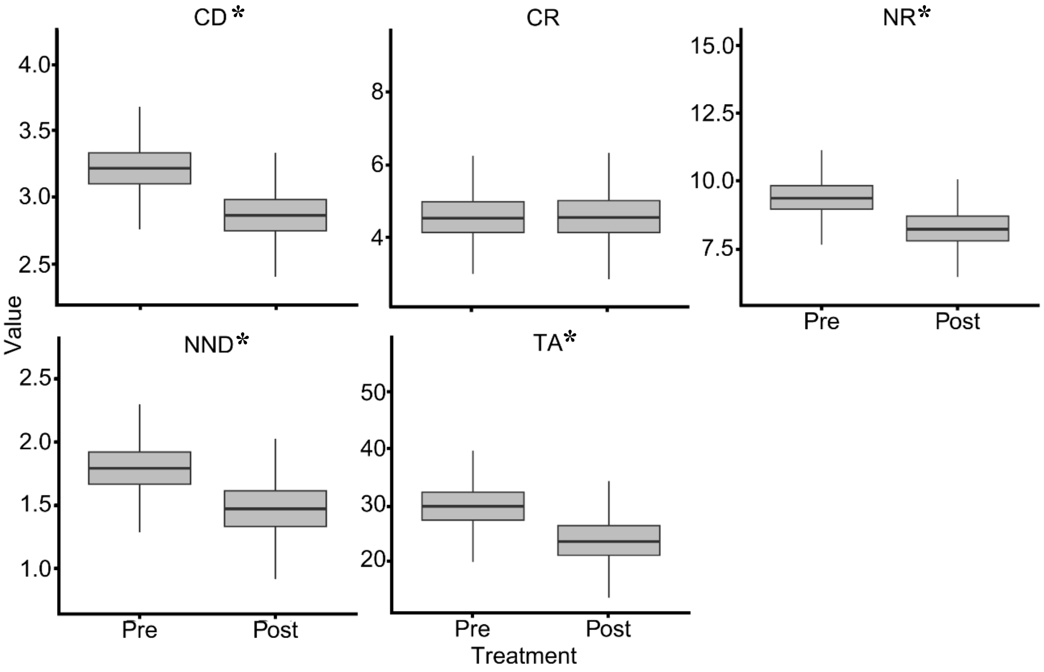

Figure 4: Layman's metrics estimated for community grouped by species from δ^{15}N and δ^{13}C values collected before and after the experiment at the treatment site. CD – Centroid distance; CR – Carbon range; NR – Nitrogen range; NND – Nearest Neighbor Distance; TA – Total Area. * Indicate significance differences between pre and post treatment ($p < 0.05$).

Studied species showed little isotopic niche overlap – Turf showed the highest SEA_B or isotopic niche values at the treatment site, with a mean of 4 ± 2.2‰^{2}sd, followed by *M. harttii* and *Dictyota sp*. (mean = 2.34 ± 1.3‰^{2}sd and 1.5 ± 0.8‰^{2}, respectively). In contrast, *E. lucunter* and *L. chrysurus* presented the smallest niche areas (0.6 ± 0.4‰^{2} and 0.7 ± 0.4‰^{2}, respectively) (Figure 5).

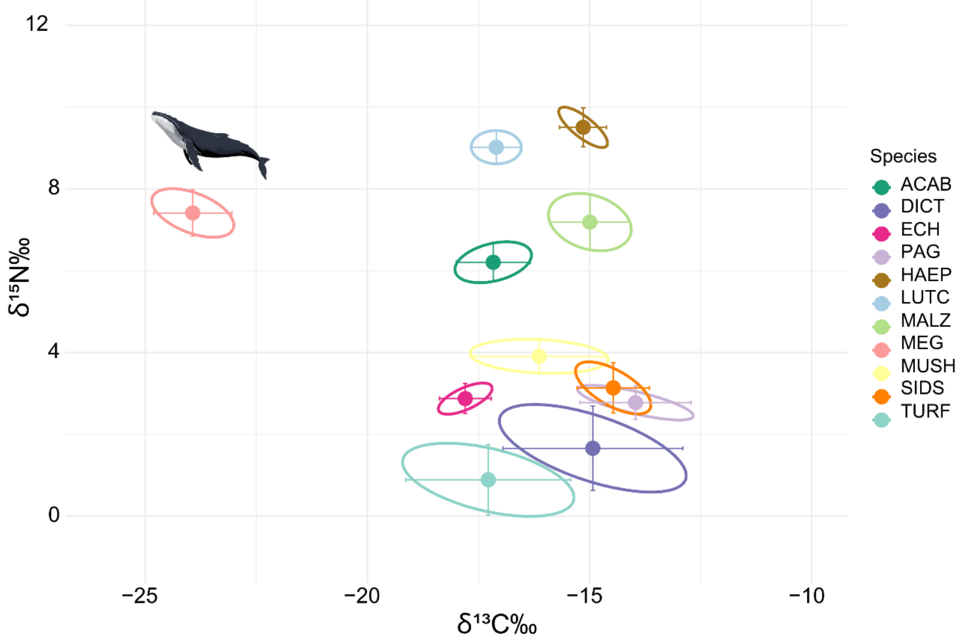

Figure 5: Standard Ellipse Area (SEA) or isotopic niche of species sampled during the pre- and post-addition periods together. ACAB – *A. bahianus*, DICT – *Dictyota sp.*; ECH – *E. lucunter*; PAG – Paguroidea; HAEP – *H. plumierii*; LUTC – *L. chrysurus*; MALZ – *M. zaluari*; MEG – *M. novaeangliae*; MUSH – *M. harttii*; SIDS – *S. stellata*; TURF – epilithic algal turf.

All species showed significant differences between pre and post addition of carcasses in SEA_B ($p < 0.05$). However, species responded differently: *Dictyota sp.*, *M. zaluari*, *A. bahianus*, and *L. chrysurus* showed lower values after the addition, reducing their niche areas by 2.24‰^{2}, 0.91‰^{2}, 0.74‰^{2}, and 0.12‰, respectively. In contrast, other species expanded their niche areas, especially *M. harttii*, *H. plumierii*, and Turf (1‰^{2}, 0.82‰^{2}, 0.79‰^{2}) (Figure 6A). Model results for SEA_B differences showed that the one-sided 95% credibility interval did not include zero for all species, showing significant effects. *Dictyota sp.*, *A. bahianus*, *M. zaluari*, and *L. chrysurus* stood out, with posterior effect estimates indicating smaller SEA_B values after the experiment compared to before. Conversely, the other species showed greater estimated SEA_B values following the resource addition (Figure 6B).

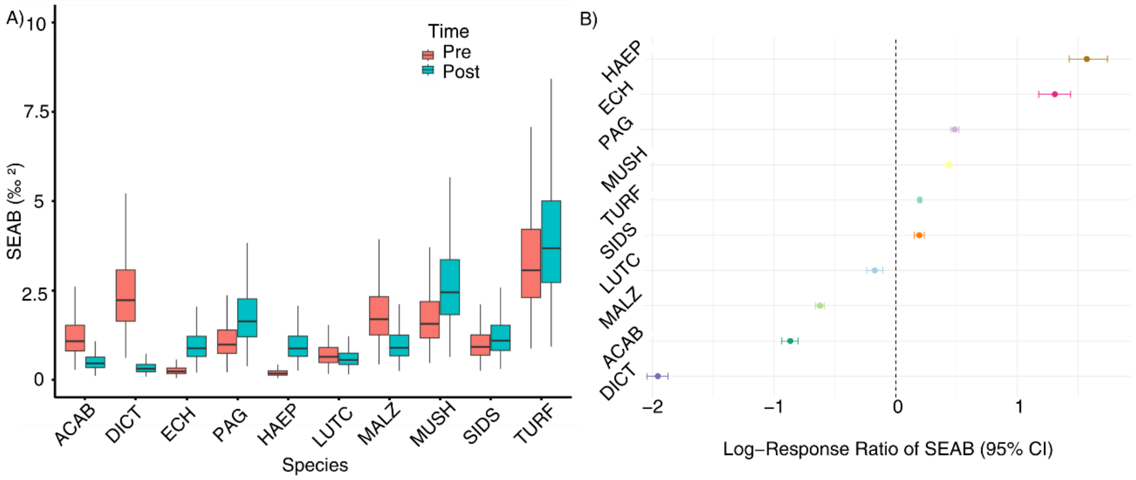

Figure 6: A) Posterior ellipses (SEA_B) of δ^{15}N and δ^{13}C values of sampled species. B) Log-Response Ratios (logRR) and 95% credibility intervals of posterior predictor effects (SEA_B) estimated from the BRMS model for the pre- and post-carcass addition periods. ACAB – *A. bahianus*, DICT – *Dictyota sp.*; ECH – *E. lucunter*; PAG – Paguroidea; HAEP – *H. plumierii*; LUTC – *L. chrysurus*; MALZ – *M. zaluari*; MUSH – *M. harttii*; SIDS – *S. stellata*; TURF – epilithic algal turf.

All species showed smaller Euclidian distances toward the whale carcass values after the carcass addition, except for Paguroidea (ERM), which showed a slightly greater post-pre difference (0.02‰). In contrast, *Dictyota sp.*, Turf, and *M. zaluari* showed significant differences ($p < 0.05$), with reduced distances of 3.61‰, 2.02‰, and 1.21‰ toward the allochthonous input, respectively (Figure 7A-B).

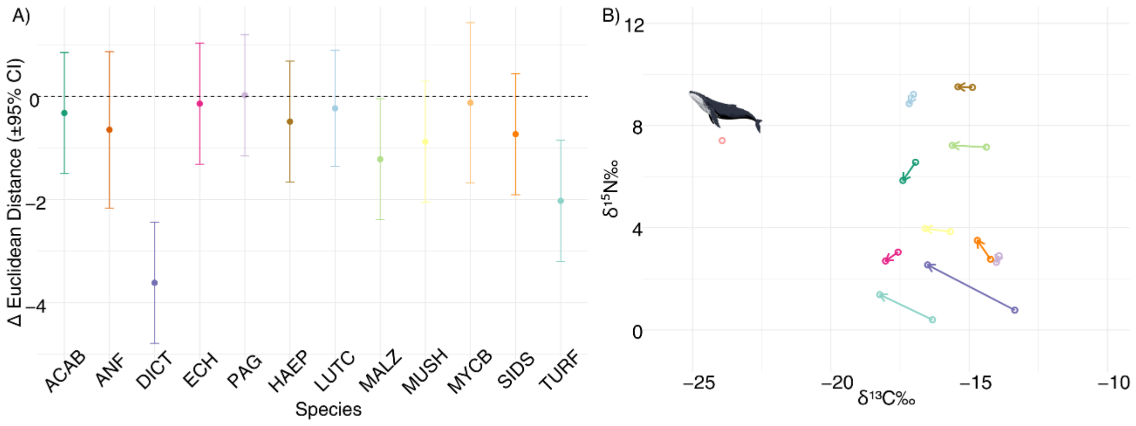

Figure 7: A) 95% credibility intervals based on marginal estimates adjusted from the linear model for the mean differences in Euclidean distances of each species relative to the whale centroid, comparing the pre- and post-resource addition periods. B) $\delta^{15}N$ and $\delta^{13}C$ values for each species with arrows indicating the post-addition period. ACAB – *A. bahianus*, ECH – *E. lucunter*; LUTC – *L. chrysurus*; MUSH – *M. harttii*; SIDS – *S. stellata*; ANF – Gammaridae; PAG – Paguroidea; MALZ – *M. zaluari*; MYCB – *M. bonaci*; TURF – epilithic algal turf; DICT – *Dictyota sp.*; HAEP – *H. plumierii*.

The regression analysis between the Euclidean distance and ellipse area between times showed no apparent relationship between the variables ($R^2 = 0.4$). Only *Dictyota sp.* stood out, indicating that the group not only approached the whale isotopically, but also reduced the amplitude (Figure 8).

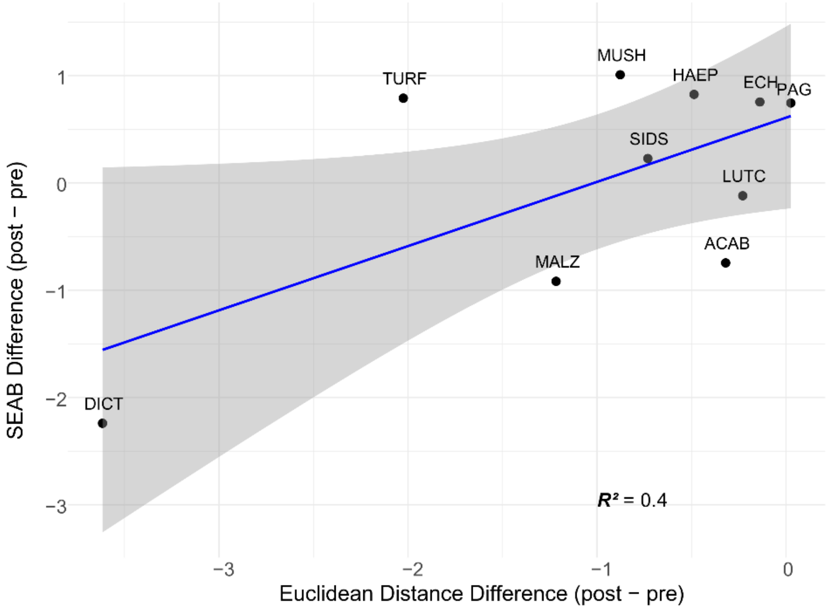

Figure 8: Regression of Euclidean distance in relation to SEA_B values

All Layman's community metrics decreased after the whale carcass addition on the reef for trophic groups: nitrogen range (NR) – mean = 9.1 ± 0.5‰ SD and 7.81 ± 0.6‰; carbon range (CR) – 3.12 ± 0.7‰ and 2.7 ± 0.6‰; total area (TA) – 13.97 ± 3.1‰ and 9.53 ± 2.3‰; centroid distance (CD) – 2.97 ± 0.1‰ and 2.54 ± 0.1‰; nearest neighbor distance (NND) – 2.05 ± 0.2‰ and 1.60 ± 0.2‰, for pre- and post-addition periods, respectively. All metrics were statistically significant ($p < 0.05$), and the lower values observed after resource addition suggest a more compact trophic community structure (Figure 9).

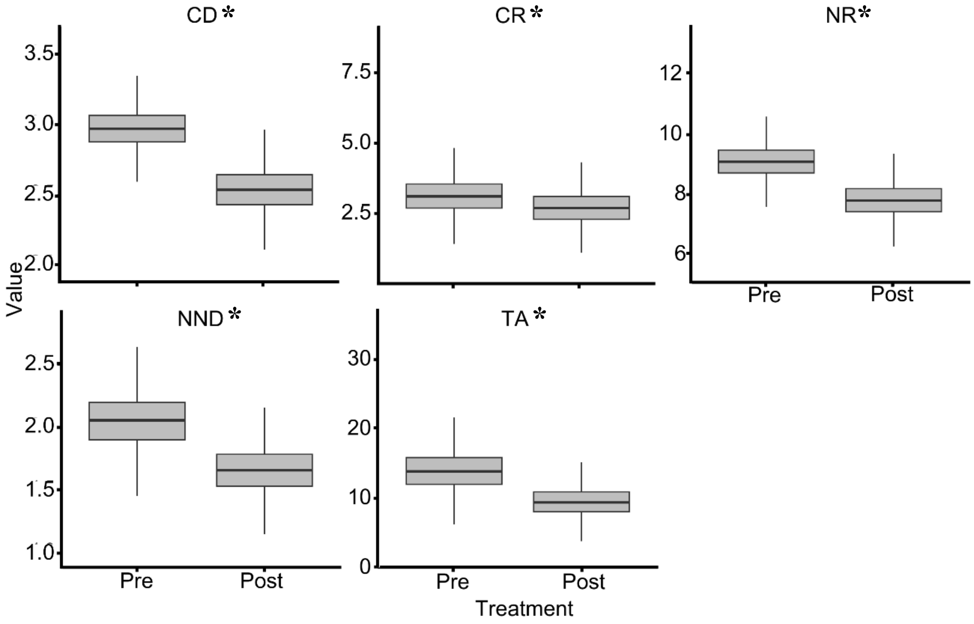

Figure 9: Layman's metrics estimated for community grouped by trophic level based on $\delta^{15}N$ and $\delta^{13}C$ values from pre- and post-experiment periods at the treatment site. CD – Centroid Distance; CR – Carbon Range; NR – Nitrogen Range; NND – Nearest Neighbor Distance; TA – Total Area. * Indicate significance differences between pre and post treatment ($p < 0.05$).

Stable isotopes captured the structure of the different trophic levels within the community and showed slight overlap between the isotopic niche of primary consumers, mixotrophs, and producers. As expected for marine food web, basal resources such as turf presented the largest SEA_B area, ranging from 0.66 – 41.02‰², followed by the primary producer (0.07 – 23.74‰²), while tertiary consumers had the smallest area, ranging from 0.62 – 7.83‰² (Figure 10).

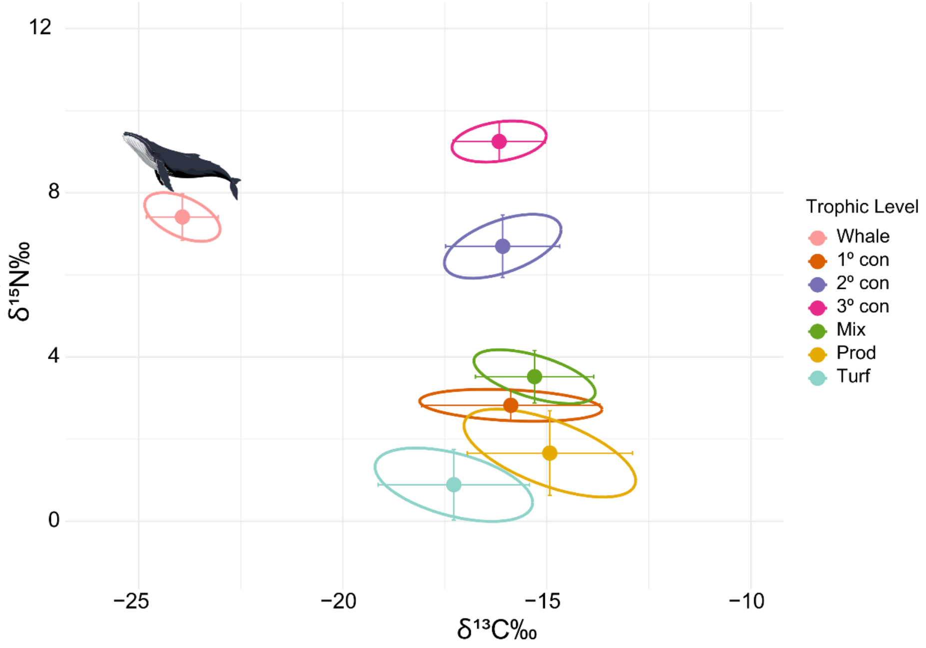

Figure 10: Standard ellipse areas (SEA) or isotopic niche of species sampled in the pre- and post-carcass addition periods together. Prod – Producer; Turf – epilithic algal turf; Mix – Mixotrophic; 1° Con – Primary consumer; 2° Con – Secondary consumer; 3° Con – Tertiary consumer.

All trophic levels showed significant differences between the pre- and post-addition periods in their SEA_B ($p < 0.05$). However, primary consumers and Turf increased their niche area after the addition by 1.42‰^{2} and 0.75‰^{2}, respectively; while producers, mixotrophs, and secondary consumers exhibited a reduction of 2.24‰^{2}, 0.40‰^{2}, and 0.32‰^{2}, respectively (Figure 11A). Model results also showed that the one-sided 95% credibility intervals did not include zero, indicating that trophic levels interacting with the sampling period exhibited significant effects. Primary producers, mixotrophs, and secondary consumers showed posterior estimates indicating smaller SEA_B values after the experiment compared to before. In contrast, the remaining groups showed higher estimated SEA_B values following the resource addition (Figure 11B).

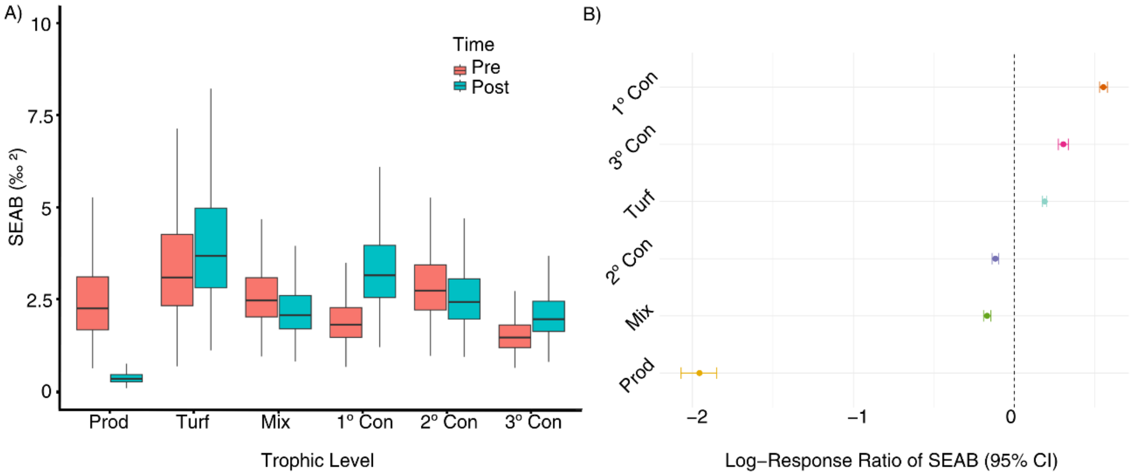

Figure 11: A) Posterior ellipses (SEA_B) of $\delta^{15}N$ and $\delta^{13}C$ values of sampled trophic levels. B) Log-Response Ratios (logRR) and 95% credibility intervals of the posterior predictor effects of SEA_B for each level estimated from the BRMS model, for the pre- and post-carcass addition periods. Prod – Producer; Turf – epilithic algal turf; Mix – Mixotrophic; 1° Con – Primary consumer; 2° Con – Secondary consumer; 3° Con – Tertiary consumer.

When examining Euclidean distance values for trophic levels across periods using marginal means from the linear model, most groups behaved similarly after the addition. However, the primary producer and Turf were the only ones to show significant differences ($p = 0.0001$ and 0.024, respectively), with lower values of 3.62‰ and 2.02‰ in the post-addition period. Although other groups also showed reduced distances, the differences were minor (Figure 12A). In addition to reducing the distance in biplot space in relation to the whale's $\delta^{15}N$ and $\delta^{13}C$ values, it is evident that the primary producer and Turf shifted toward the resource in the post-addition period. Mixotrophs also displayed a similar response. Even though Euclidean distance values increased for tertiary consumers, the direction of movement suggests a shift toward the whale values after the addition (Figure 12B).

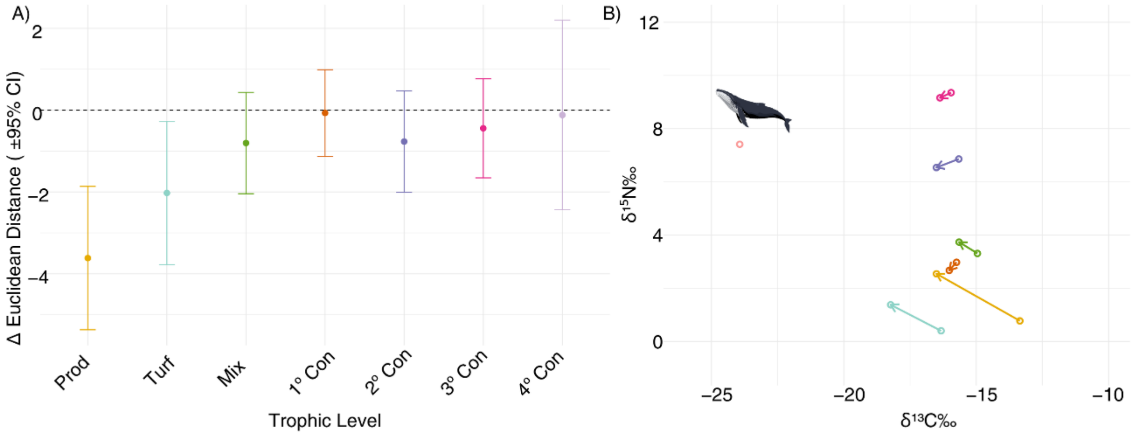

Figure 12: A) 95% credibility intervals based on marginal estimates adjusted from the linear model for the mean differences in Euclidean distances of each trophic level relative to the whale centroid, comparing the pre- and post-resource addition moments; B) $\delta^{15}N$ and $\delta^{13}C$ values of each trophic level with arrows indicating the post-addition moment. Prod – Producer; Turf – epilithic algal turf; Mix – Mixotrophic; 1º Con – Primary consumer; 2º Con – Secondary consumer; 3º Con – Tertiary consumer.

The isospace highlights a separation between the autochthonous food sources – amphipods and polychaetes – and the allochthonous whale resource, with the whale values being more enriched in $\delta^{15}N$ and more depleted in $\delta^{13}C$ compared to local sources. Which helps in making more reliable mixing models (Figure 13).

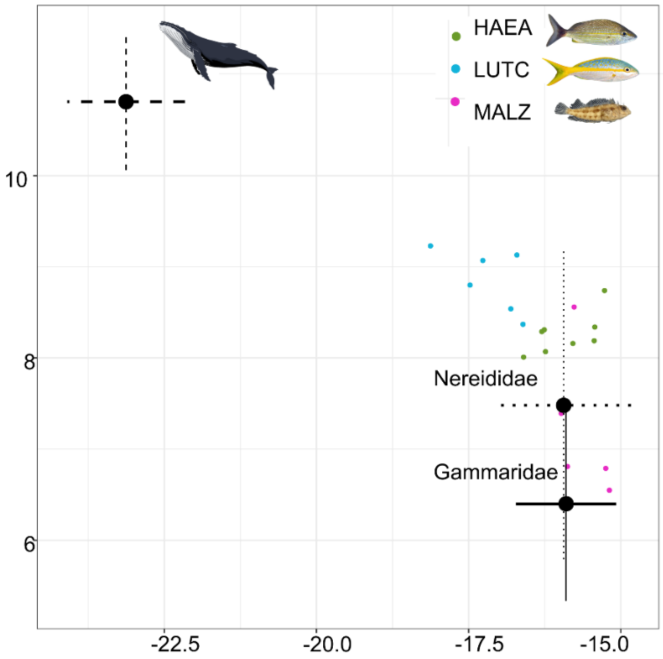

Figure 13: Isospace generated by MixSIAR using consumer data: HAEA – *Haemulon aurolineatum*; LUTC – *Lutjanus chrysurus*; MALZ – *Malacoctenus zaluari*; and resources: Gammaridae (amphipod), Nereididae (polychaeta) and humpback whale carcass.

The mixing model for *H. aurolineatum* indicated that the average contribution of whale-derived nutrients to the species' diet was 6% (mean = 0.065; sd = 0.074), with a 95% credible interval ranging from 0.03 – 26%. Polychaetas contributed the most to the diet (mean = 56%; CIs = 1 – 90%), followed by amphipods (38%; CIs = 3 – 81%) (Figure 14A). For *L. chrysurus*, the model indicated a higher global average contribution of whale matter to the diet (20%; mean = 0.201; sd = 0.082), with credible intervals ranging from 5 – 35%. Polychaetas contributed 55% (CIs = 14 – 85%) and amphipods 25% (CIs = 1 – 62%), indicating a slightly higher use of allochthonous resource compared to *H. aurolineatum* (Figure 14B). For *M. zaluari*, the model showed that whale-derived matter contributed 19% to the diet (mean = 0.192, sd = 0.252), with a 95% credible interval ranging from 0.03 – 61%. Amphipods had the highest contribution (43%; CIs = 2 – 86%) followed by polychaetas (36%; CIs = 1 – 80%) (Figure 14C). Among the three species, *L. chrysurus* exhibited the strongest signal for allochthonous resource use, the credibility of this estimation is supported by the narrow base of the posterior density distribution compared to the other species. All models showed good convergence, with ^R values close to 1.

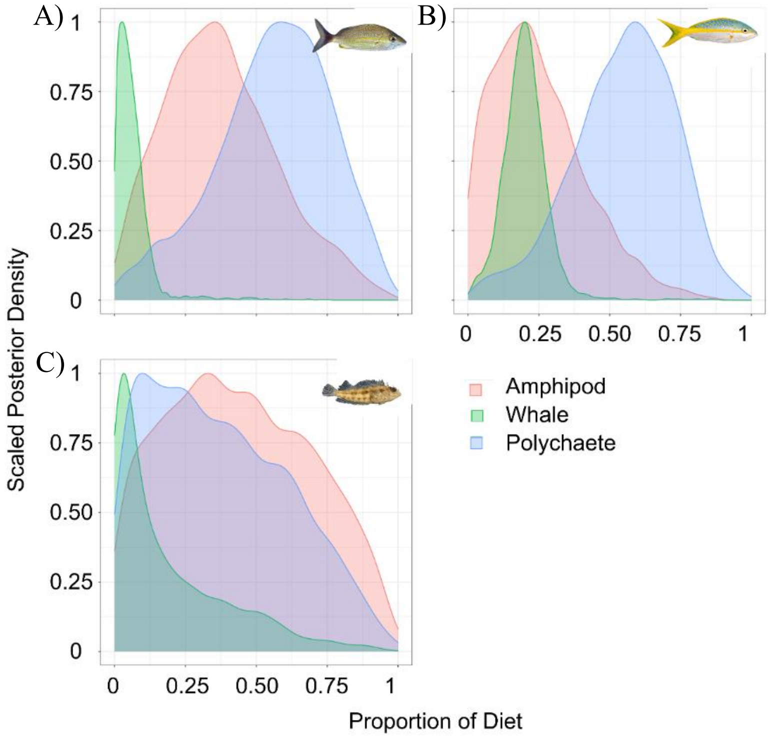

Figure 14: Proportional dietary contributions estimated in the MixSIAR model for each consumer: A) *Haemulon aurolineatum*, B) *Lutjanus chrysurus* and C) *Malacoctenus zaluari*.

DISCUSSION

The structure and functioning of tropical coastal environments, such as the reefs of the Abrolhos Bank, are sustained by strong connectivity with the surrounding seascape, composed of nutrient-rich ecosystems such as mangroves, rhodolith beds, sandy bottoms, and estuaries (Moura et al., 2013; Souza et al., 2013; Amado-Filho et al., 2017; Bastos et al., 2018; Lima et al., 2025). This connectivity, combined with structural complexity and constant light availability – even during periods of increased turbidity caused by sediment resuspension – favors high biodiversity and the complexity of local food webs (Leão and Kikuchi, 2005; Dutra et al., 2006; Ferreira and Gonçalves, 2006; Moura et al., 2013; Ferreira et al., 2020). Based on a multitrophic and ecosystem-based approach, this study revealed that punctual allochthonous inputs derived from the movement of large animals could affect many traits of reef communities and showed nutrients are incorporated into this complex food web by different pathways. Findings of this research indicate that this detrital resource may temporarily establish itself as a new basal source, increasing trophic diversity at the base of the web, with potential implications for functional redundancy, without altering the overall trophic length of the food chain (Layman et al., 2007).

The analysis of isotopic metrics revealed a general contraction in the trophic structure of the community after the introduction of the allochthonous resource, confirming the first prediction on the postulated scenario. When data were grouped by species, metrics such as NR, CD, NND, and TA were reduced, while CR remained stable. When grouped by trophic level, all metrics showed reductions. This aggregation in isotopic space suggests a decrease in the diversity of carbon sources being utilized. The difference when looking at community metrics by species or by trophic levels shows that, although the use of the basal resource was partially diluted in the species-level analysis – possibly due to intraspecific variation in resource use – grouping by trophic level revealed a collective specialization toward the allochthonous energy source.

The contraction of the community, evidenced by the reduction in total area and distances between consumers, suggests a convergence in feeding strategies – especially among certain groups – in response to assimilation of carcass-derived nutrients (Layman et al., 2007). Such trophic reorganization in response to resource availability shifts has also been documented in other systems. For example, in Argentine Patagonia, interannual fluctuations in forage fish abundances caused shifts in the isotopic niche of penguins (*Spheniscus magellanicus*), with niche expansion during years of lower prey abundance due to a more diverse diet (Ciancio et al., 2021). In savanna rivers in Africa, large terrestrial herbivores, such as hippopotamuses and cattle, provide substantial organic matter inputs via excretion and egestion. In these systems, elevated $\delta^{13}C$ values were observed, influencing the composition and dominance of aquatic guilds and promoting variation in trophic diversity and niche size (Masese et al., 2018).

Some species experienced contraction of isotopic niche, whereas others expanded their niches following resource addition. This heterogeneous response – contraction and expansion – toward the allochthonous resource confirms that both predictions may occur depending on the species trophic ecology. This differentiation may relate to optimal foraging theory, according to which consumers tend to select resources offering the highest energetic return (Werner and Hall, 1974). Hence, increased environmental productivity allows for the optimization of foraging, often resulting in narrower niches (Lesser et al., 2020). One example occurs in the surf zones of the Argentine continental shelf, where the influx of estuarine organic matter promotes greater diversity of carbon sources and, with abundance of the allochthonous resource, reduces overlap among benthic invertebrate niches (Carcedo et al., 2024). Conversely, the niche variation hypothesis (Van Valen, 1965) proposes that, in contexts of greater resource diversity, some populations tend to expand their niches, with individuals exploiting differentiated opportunities. Such a pattern was identified, for example, in *Salvelinus fontinalis* in pond environments (Baker et al., 2022).

Thus, the whale carcass represents both a resource that promotes environmental productivity (Chapter III) and a diversification of resources for the food webs. It constitutes an animal subsidy of high energetic quality, concentrating assimilated nutrients in highly productive regions – like iron-rich krill – retained in tissues to sustain the reproductive period (Estes et al., 2016; Subalusky and Post, 2019; Roman et al., 2025). Therefore, it is considered highly nutritious detritus, easily assimilated and energetically low-cost (Moore et al., 2004). More broadly, a punctual subsidy resulted in different observed patterns of intraspecific specialization or generalization in resource use. These divergent responses were reflected in a temporary reorganization of the reef community, promoting trophic aggregation, with inter- and intraspecific adjustments, in addition to indirect benefits at multiple levels of the food web.

Species such as *Dictyota sp.*, *A. bahianus* and *M. zaluari* exhibited reduced niche amplitude following the addition, contributing to a denser and more redundant community structure in the use of basal sources. In contrast, the wide niches of *M. harttii*, Paguroidea and *E. lucunter* suggest diverse intraspecific exploitation. These interspecific differences in amplitude may explain the constancy of CR in species-level analysis. However, when considering trophic-level groupings, mixotrophs and secondary consumers – with lower amplitudes post-experiment – contributed to the reduction of community CR. Almost all species showed some degree of isotopic shift toward the whale signal in the isotopic space, albeit subtly. *Dictyota sp.* and turf algae exhibited the largest shifts; they also had the most depleted $\delta^{15}N$ values before resource addition, and became enriched afterward – contributing to a decrease in NR. This result strongly suggests the incorporation of whale carcass nutrients via different pathways, altering the whole food web.

In aquatic environments, detritus can be assimilated through multiple direct and indirect pathways, moving across several trophic levels before being remineralized or deposited as sediment (e.g., Allgeier et al., 2014; Moore et al., 2004; Subalusky and Post, 2019; Nelson et al., 2023). Species that directly assimilate these resources demonstrate dietary plasticity – a trait that allows exploitation of punctual, high-efficiency energy sources, often associated with opportunistic consumers (e.g., Evangelista et al., 2014; Zorrozua et al., 2020). Such plasticity is a crucial adaptive strategy in dynamic coastal systems, enabling organisms to adjust their diets in response to spatiotemporal fluctuations in resource availability (e.g., Collins et al., 2016; Bartels et al., 2018; Pereira et al., 2015; Kliemann et al., 2019; Neves et al., 2023). In subtropical islands in the Bahamas, for example, exposure to extreme weather events leads to the accumulation of seaweed on land. This has caused a shift in the isotopic niche of the lizard *Anolis sagrei*, which began to consume marine detritivores as a substitute for terrestrial prey, demonstrating its dietary plasticity (Spiller et al., 2010).

In shallow environments such as the studied reef, the entire system remains within the photic zone, preventing the sinking and sequestration of nutrients, which are instead rapidly recycled (Sigman and Hain, 2012). Due to limited visibility and filming time, direct documentation of scavenging behavior on the reef was hampered, preventing clear identification of direct consumption pathways. Nevertheless, direct interaction with the carcass was observed in two species – *H. aurolineatum* and *L. chrysurus*. Both are reef-associated tertiary consumers that share similar feeding behaviors and migratory patterns, utilizing habitats such as macroalgal beds, seagrass meadows, and mangroves at different life stages (Cocheret de la Morinière et al., 2003; Pereira et al., 2010; Martínez-Juárez et al., 2024). These species have diets based on mobile invertebrates such as copepods, amphipods, polychaetes, and small fish, with ontogenetic variation associated with size or life stage (Pereira et al., 2015; Martínez-Juárez et al., 2024; Pelage et al., 2022; Brulé et al., 2023).

Stable isotope mixing models indicated a higher proportion of amphipod and polychaete consumption, with a lower direct contribution from the carcass in these species. Still, even in reduced proportions, assimilation of the allochthonous resource represents an additional energy source. Notably, *L. chrysurus* the species that showed the highest proportion of carcass in diet, displayed niche width contraction and a shift toward the whale's isotopic signal – a pattern not confirmed for *H. aurolineatum* due to a lack of pre-experiment data. This suggests that the high quality of the resource may have selectively influenced the diet of the sampled population. Both species play key ecological roles in regulating prey populations and vectoring nutrients across habitats (Appeldoorn et al., 2009; Araujo et al., 2018; Zapelini et al., 2020; Limeira et al., 2022), indicating that even punctual carcass consumption may have been propagated to adjacent habitats.

M. zaluari, a poorly documented cryptobenthic species, was also analyzed due to its pronounced niche width contraction and isotopic shift toward the carcass. The sampled population showed high proportions of amphipod and polychaete consumption and low levels of direct carcass assimilation. Although detailed ecological information about the species is scarce, records from congeners suggest similar feeding habits, consuming mobile invertebrates whose composition varies with microhabitat (Pereira and Jacobucci, 2008; Pimentel et al., 2018). There are also reports of members of the same family feeding on detritus, bacteria, and diatoms associated with turf algae (Randall, 1967; Wilson et al., 2003). As fast-growing cryptobenthic species with high vulnerability to predation, they play a critical role in energy transfer within reefs (Depczynski and Bellwood, 2006; Depczynski et al., 2007; Morais and Bellwood, 2019; Brandl et al., 2019, 2025), suggesting that *M. zaluari* may act as a key link in the assimilation and redistribution of nutrients from the carcass.

A. bahianus, classified here as secondary consumers, also showed marked niche width contraction and a shift toward the allochthonous resource. Even though it is a species functionally categorized as a roving herbivore, moving across coral reefs in search of algae (Longo et al., 2018; Pimentel et al., 2018; Leitão et al., 2023). In Abrolhos, it is known for its high consumption of organic detritus associated with turf algae, playing an important functional role in regulating algae that compete with corals (Ferreira and Gonçalves, 2006; Leitão et al., 2023). Species with such detritivorous habits channel productivity to higher trophic levels (Allgeier et al., 2017), and, being itinerant, may serve as trophic connectors between habitats (Tebbett et al., 2022). Thus, it is plausible that nutrients from the carcass were indirectly absorbed via detritus deposited in turf algae, with *A. bahianus* acting as an important vector in nutrient propagation.

Overall, primary consumers exhibited little change in niche width or isotopic displacement after carcass addition. Nevertheless, they remain fundamental links in the food web. *E. lucunter*, for example, is a sea urchin abundant on tropical coastal reefs (Labbé-Bellas et al., 2016), with a diet based on algae and detritus, though it occasionally consumes metazoans (Rodríguez-Barreras et al., 2020). In addition to shaping benthic communities through bioerosion, its grazing activity promotes leaching, fragmentation, and initiates saprophytic decomposition processes (Koike et al., 1987; Labbé-Bellas et al., 2016). In seagrass beds, urchin feces contributed ammonium to primary production and nutrient transfer to the water column and detritivores (Koike et al., 1987). In the present study, *E. lucunter* exhibited an increase in niche width after carcass addition, indicating intraspecific plasticity and an active role in redistributing allochthonous energy both upward in the food web and through detritus deposition in the benthos.

Among all groups, primary producers showed the most pronounced changes, with sharp reductions in niche width and displacement toward nutrients derived from the carcass. Dictyota sp., one of the most abundant fleshy macroalgae in Abrolhos (Paula et al., 2003; de Oliveira Figueiredo et al., 2008; Francini-Filho et al., 2013), demonstrated high use of nutrients of the resource. Macroalgae are important assimilators of carbon, and their exudates represent significant flows of organic matter into the food web (Nelson et al., 2023). Thus, primary producers not only support ecosystem productivity but also contribute to biological retention and recycling of particulate and dissolved nutrients (Karl et al., 2003; Lønborg et al., 2021). Additionally, dissolved organic matter released by macroalgae may stimulate microbial respiration, as observed in Caribbean reefs (Thobor et al., 2024). Therefore, the interaction with this herbivorous epifauna and incorporation into the microbial loop can facilitate the assimilation of allochthonous nutrients by different trophic levels.

Turf algae, in turn, were considered in this study as an epilithic matrix composed of organic detritus, sediments, microalgae, and microorganisms (Wilson and Bellwood, 1997). Its composition can vary according to hydrodynamic factors and the substrate to which it attaches (Crossman et al., 2001; García-Seoane et al., 2023), even reflecting the decay of suspended organic matter (Wilson et al., 2003). The expansion of the isotopic niche and the shift toward the carcass signal suggest direct nutrient absorption via primary production, or the influence of material egested by fish and/or invertebrates. Turf is abundant and highly productive in coral reefs (Tebbett and Bellwood, 2021), including in Abrolhos (Francini-Filho et al., 2013), acting as a key link between the base and secondary consumers (Wilson et al., 2003), with high nutritional value (Choat et al., 2002; Crossman et al., 2005).

The two studied coral species, *M. harttii* and *S. stellata*, showed similar responses, with increased niche width and reduced isotopic distances. Both are abundant reef-building corals in Abrolhos (Leão and Kikuchi, 2001), and being mixotrophic, they obtain energy both autotrophically via endosymbiotic zooxanthellae and heterotrophically by assimilating dissolved organic and inorganic compounds (Houlbrèque and Ferrier-Pagès, 2009). Such dietary plasticity helps explain the evolutionary and ecological success of symbiotic corals (Grottoli et al., 2006; Frankowiak et al., 2016; Wiedenmann et al., 2023). The intraspecific variability observed may occur in spatially proximate colonies, as found for other species (e.g., Fox et al., 2019; Sturaro et al., 2021), and may result from morphological differences, for example in polyp size, allowing exploitation of distinct feeding reservoirs (e.g., Luu et al., 2025). Thus, mixotrophic corals represent important pathways optimizing foraging to assimilate punctual allochthonous sources such as humpback whale carcasses.

The greatest isotopic shifts toward the carcass were observed in species that utilize autotrophic pathways to absorb nutrients from dissolved or particulate organic matter. Which suggests this new nutrient area made available for primary producers. Although microorganisms responsible of processing this surplus of biomass were not analyzed, their role in the microbial loop and remineralization making nutrients like ammonium and nitrate available is widely acknowledged (e.g., Pomeroy et al., 2007; Gertler et al., 2015). During decomposition, nitrogen isotopic fractionation occurs, whereby the lighter isotope (^{14}N) is preferentially lost via volatilization, resulting in relative enrichment of the heavier isotope (^{15}N) (Mizutani et al., 1985). Thus, even if the $\delta^{15}N$ values of these species are lower than those of the carcass, their increase relative to the baseline indicates indirect incorporation of allochthonous nutrients. In addition to supplying nutrients such as nitrogen and phosphorus for primary production (Pomeroy et al., 2007; Nelson et al., 2023), they represent essential links in heterotrophic recycling pathways. For example, heterotrophic bacteria transform and consume detritus, making it digestible to corals, metazoans, and invertebrates (Alongi et al., 1989; Pomeroy et al., 2007; McNally et al., 2017; Nelson et al., 2023).

Since this experiment was conducted in a natural environment, where environmental and confounding variables are less controllable, the results must be interpreted with caution. Species that were not included in the analysis (e.g. microbial loop) may also play key roles in the energy and nutrient flow of the local food web. Furthermore, logistical and temporal limitations may have affected the results, such as the interval between resource addition and sampling, or the removal of parts of the carcass by reef fishes that was recorded on the same monitoring day. Still, this study shows that coral reefs are highly detritivorous systems (Mumby and Stener, 2018), with multiple biological compartments participating in the assimilation and redistribution of nutrients. Fish and invertebrates play a fundamental role by ingesting, metabolizing, and redistributing nutrients via excretion and egestion (Allgeier et al., 2014; Schiettekatte et al., 2023), with both interspecific and interindividual variations reflecting the trophic complexity of the community.

Humpback whales arrive in reproductive areas in large numbers, and was estimated that their presence in Abrolhos may release around 3,715 kg of nitrogen per day through urea and detritus (Roman et al., 2025). Carcasses, in turn, represent many tons of high-quality resource pulses with the potential to stimulate secondary productivity in shallow reefs, as demonstrated in the next chapter (Chapter III). Understanding the energy and nutrient flows resulting from allochthonous inputs is essential to deepening our knowledge of the connectivity between the open ocean and reef environments. Coral reefs provide a wide range of ecosystem services that directly influence human well-being (Robinson et al., 2023). The assimilation of nutrients by ecologically, economically, and socially relevant species – such as *H. plumierii*, *H. aurolineatum*, and *L. chrysurus* – reinforces the importance of considering these interactions in fisheries management and conservation strategies (Pereira et al., 2015; Pelage et al., 2022; De Melo et al., 2020; Zapelini et al., 2020). These findings also raise questions about the potential impacts of detrital pulses in other coastal and pelagic environments, such as beaches, mangroves, vegetated bottoms, rhodolith beds, reefs, or even in open ocean areas prior to whale falls.

The movement of these large mammals transfers energy and materials horizontally and vertically between migration areas. Additionally, they accumulate carbon in their bodies over their lifespan, rendering it unavailable to the atmosphere upon death, and thereby indirectly stimulating carbon storage within the food webs of receiving regions (Estes et al., 2016; Pearson et al., 2023; Roman et al., 2025). This study reinforces the role of humpback whales as mobile ecological vectors, connecting distinct ecosystems through the transport and release of nutrients. Even if sporadic, these energy and nutrient pulses have the potential to temporarily modify local trophic structure, benefiting key species that contribute to reef ecosystem productivity. Such evidence highlights the need for integrated marine management that considers migratory routes, ecologically important areas, and the protection of functional species, whether emblematic or not. More than reinforcing the ecological value of whales, the results emphasize the importance of conservation strategies that integrate science, management, and public awareness. By protecting species with critical functional roles, such as large cetaceans and reef fishes, we promote the resilience and stability of coastal ecosystems, as well as the well-being of the human populations that depend on them.

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CHAPTER III

Nutrients from the giants, whale carcasses improve secondary productivity in coral reefs

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Whale's carcasses as allochthonous subsides that increase secondary productivity in coral reefs.

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ABSTRACT

Coral reefs are dynamic and open ecosystems that rely on both internal nutrient recycling and external, often pulsed, allochthonous inputs to sustain productivity. Yet, the role of large marine vertebrates as episodic nutrient vectors in these systems remains underexplored. Humpback whales (*Megaptera novaeangliae*), which migrate seasonally from high-latitude feeding areas to tropical breeding grounds, may provide an ecologically relevant, animal-derived resource pulse in shallow reef environments. In this study, we tested how the arrival of whale-derived detritus affects the structure and functioning of reef fish communities in the Abrolhos Bank, the largest and most biodiverse coral reef system in the South Atlantic. We conducted an in-situ experiment by adding humpback whale muscle tissue to a reef site and monitored fish biomass, abundance, diversity, secondary productivity, and trophic structure across three time points. A Before-After-Control-Impact (BACI) design was employed, complemented by regression tree analyses to identify functional group responses. The resource pulse led to temporary shifts in community composition, particularly attracting herbivore-detritivores and mobile invertivores – groups that play key roles in energy transfer and nutrient cycling in reef systems. Notably, the impacted assemblage returned to near-baseline conditions over time. Our findings highlight how episodic, animal-mediated inputs can momentarily boost secondary production and reorganize trophic interactions in reef systems, even in nutrient-efficient tropical environments. As humpback whale populations continue to recover from historical exploitation, their role as ecosystem engineers may become increasingly relevant in shaping nearshore ecosystem processes through both direct and indirect nutrient pathways. This study underscores the ecological significance of marine megafauna subsidies in reef food webs and adds to the growing understanding of how spatially and temporally heterogeneous inputs regulate biodiversity, productivity, and resilience in coastal systems. Recognizing and incorporating these episodic processes is critical for understanding the broader functioning of coral reef ecosystems and for guiding conservation strategies that include mobile, cross-ecosystem nutrient fluxes.

Keywords: allochthonous nutrient pulse; coral reef productivity; nutrient flow; reef fish; trophic interactions;

INTRODUCTION

Resource subsidies are nutrient flows originating in a donor ecosystem that are transferred to a recipient ecosystem, altering the dynamics of local consumer assemblages. These subsidies, also known as *inputs*, vary in quality, quantity, seasonality, and duration (Subalusky & Post, 2019). Such flows can influence food web structure either directly or indirectly, by enhancing nutrient availability in the recipient systems (Polis & Strong, 1996; Huxel et al., 2002; Baxter et al., 2005). These allochthonous inputs can modify recipient ecosystem functioning by promoting changes in productivity rates (Naiman et al., 2009; Marcarelli et al., 2011; Subalusky et al., 2018). Pelagic-derived subsidies, for instance, may boost productivity in coastal recipient systems (Morais & Bellwood, 2019), with consumers playing a crucial role in the capture, storage, and transfer of this biomass through trophic interactions (Allgeier et al., 2017). Heterotrophic organisms, in particular, are key agents of nutrient cycling in marine ecosystems, serving as important nutrient reservoirs and contributing significantly to production in coral reefs (Allgeier et al, 2017; Robinson et al., 2023). Despite their importance, the effects of subsidies on heterotrophic communities remain underexplored in part because anthropogenic impacts have disrupted these natural systems (Benkwitt et al. 2021).

It is well established that allochthonous nutrient inputs transported by animals can increase productivity in natural systems. However, these cross-boundary transfers between habitats and ecosystems are difficult to quantify due to high temporal and spatial variability (Robinson et al. 2023). Well know examples illustrate how these inputs function: in streams of North America and Asia, salmon carcasses directly increase primary productivity and indirectly accelerate the decomposition of leaf litter, further enhancing productivity (Yanai & Kochi, 2005). This surplus of biomass and nutrients even support terrestrial food webs, populations of predators such as wolf or bears depend on this resource (Hilderbrand et al., 1999) and riparian trees of rivers that support salmon runs show larger growth (Helfield & Naiman, 2001). Another example is the nutrient transfer from vegetated and sandy habitats (e.g., seagrass beds and macroalgal banks) to coral reefs, where reef fishes forage in these habitats and return to reefs for shelter. Through daily migrations, they contribute directly to coral nutrition via feces and egesta during their resting period on the reef (Meyer & Schultz, 1985; Dunne et al. 2023; Collins et al. 2024). Whale falls, discovered in recent decades, are also a striking example of nutrient transfer between ecosystems, providing critical resources to deep-sea benthic communities and supporting temporary community production (Baco & Smith, 2003; Holt, 2008).

Coral reefs are exemplary ecosystems where nutrient dynamics are strongly mediated by consumers. The composition of fish communities directly influences nutrient storage and supply rates and ratios (DeAngelis et al., 1992; Allgeier et al., 2014; Van Wert et al., 2023), making coral reefs among the most productive ecosystems due to the efficiency of nutrient recycling among biomass reservoirs (Hatcher, 1990). Although coral reefs are highly productive and biodiverse, with complex and open food webs

(Robinson et al., 2023), they depend on both internal recycling processes and external allochthonous inputs to sustain productivity rates (DeAngelis et al., 1989; Morais & Bellwood, 2019). Assessing secondary productivity in such environments provides valuable insight into ecosystem structure and functioning and serves as a tool for evaluating biological integrity, resistance, and resilience (Dolbeth et al., 2012). Thus, it is a robust metric for detecting environmental changes and guiding the management of reef resources and ecosystem functions (Morais & Bellwood, 2020).

Among the agents that connect vast oceanic areas and serve as vectors for allochthonous input into coastal ecosystems, humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) stand out. Their presence in reef environments during the breeding season (Oviedo & Solís, 2008; Smith et al., 2012; Lodi & Borobia, 2013; Garrigue et al., 2020) raises questions about their role in reef productivity dynamics. Humpbacks are known for their annual migrations between feeding and breeding grounds, potentially driving biological resource flows through the release of metabolic and reproductive byproducts (Allgeier et al., 2017; Gounand et al., 2018; Subalusky & Post, 2019). As such, marine megafauna connects ecosystems at large spatial scales, contributing to ecosystem dynamics (McCauley et al, 2012). Their horizontal movements can transport limiting nutrients and essential materials to lower-latitude regions, supporting mobile predators, scavengers, microorganisms, and benthic invertebrates, and seasonally enhancing productivity (Roman et al., 2014; Roman et al., 2021; Roman et al., 2025).

Whale carcasses represent the largest form of carrion in marine environments (Baco & Smith, 2013). Their decomposition supports entire food webs, as the material is consumed across multiple trophic levels before full mineralization (Moore et al., 2004). Carrion consumers play an important role in nutrient redistribution within ecosystems (Payne & Moore, 2006). Whale falls, in particular, generate episodic food pulses upon reaching the ocean floor, introducing nutrients and sustaining deep-sea biodiversity and communities (Baco & Smith, 2003, Holt, 2008, Danise et al., 2014). However, little is known about the influence of whale carcasses in shallow habitats, such as coral reefs located in breeding areas. The annual migration of humpbacks to lower latitudes results in a significant number of carcasses (Meynecke & Meager, 2016; Giardino et al.,2024; da Cunha Ramos et al., 2024; Toro et al., 2025). These seasonal mortality events, involving numerous individuals, generate substantial carrion pulses (Baxter et al., 2005; Uno & Power, 2015), which can create biodiversity hotspots, increase landscape heterogeneity, and enhance spatial ecosystem complexity (Smith & Baco, 2003).

Although these events are stochastic and unpredictable, they may significantly contribute to the energy budgets of various consumers (Fallows et al, 2013; Lea et al, 2018). It is therefore essential to investigate the impact of such low-cost, allochthonous food sources in shallow environments, especially considering direct detrital nutrient inputs (Figure 1 – general introduction). Understanding how these inputs influence the structure and functioning of reef assemblages during the breeding season may shed light on the role of whales as ecosystem engineers in reef environments. Such knowledge can support habitat conservation, reinforce understanding of ecosystem services, and inform strategies for the recovery and maintenance of fishery stocks.

Thus, we hypothesize that the annual migration of humpback whales affects the structure and functioning of coral reefs in breeding areas by altering the secondary productivity of reef fish assemblages. These migrations represent massive biomass transport and enable allochthonous nutrient inputs through the release of biological derivatives – such as excretion, egestion, gametes, or carcasses (Allgeier et al., 2017). Specifically, this study aims to identify the effects of the annual input of biomass and nutrients derived from humpback whale carcasses on structural aspects of fish assemblages, including abundance, biomass, taxonomic diversity, trophic group structure, and secondary productivity.

METHODOLOGY

Study Area

The Abrolhos Bank is a broad extension of the continental shelf approximately 200 km long along the eastern coast of Brazil (16°40′–19°40′S e 37°20′–39°10′ W), covering an estimated area of about 42000 km². It consists of two shallow reef arcs – one coastal and the other offshore – as well as volcanic-origin islands, protected by a mosaic of marine protected areas (MPAs) (Moura et al. 2013). In 1983, the Abrolhos Marine National Park (PARNA-Abrolhos) was established, encompassing the islands and offshore reef arc, covering approximately 880 km² (Lodi & Borobia, 2013). Considered one of the largest and most diverse coral reef systems in Brazil, the archipelago is characterized by fringing reefs formed by the accretion of corals, algae, and encrusting organisms, with diverse reef morphologies and a high number of endemic species (Leão, 1999; Leão & Kikuchi, 2001; Bastos et al., 2018). The connectivity with the surrounding seascape, combined with habitat quality and structural complexity, results in highly abundant and diverse fish assemblages (Lima et al., 2024). These assemblages are closely associated with extensive rhodolith beds – intense producers of calcium carbonate that harbor specific microbiomes involved in biomineralization processes – which are particularly important for the early life stages of reef fishes (Moura et al., 2013; Amado-Filho et al., 2017; Lima et al., 2025) (Figure 1).

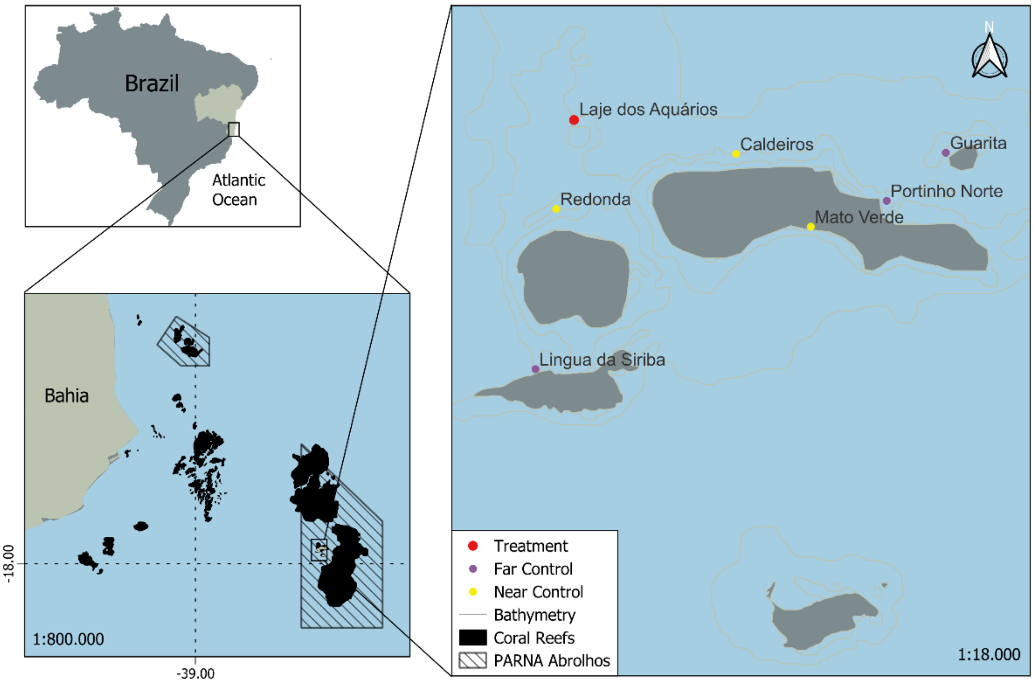

Figure 1: Location of the treatment, near-control, and far-control sites selected for the experiment.

The Abrolhos Bank is also renowned for the high seasonal abundance of humpback whale, serving as a nursery ground for the species due to the large number of mother-calf pairs observed in the region. It also constitutes a key migratory route to the lower latitudes of the Brazilian coast (Andriolo et al., 2010; Lodi & Borobia, 2013). The population occurring along the Brazilian coast belongs to one of the seven primary breeding stocks in the Southern Hemisphere. These whales migrate from feeding grounds in Antarctica, arriving in the region during the winter, around June, with a peak in abundance between August and September (Morete et al., 2008; Engel & Martin, 2009; Seyboth et al., 2023). Return migration to the Southern Ocean begins in November (Morete et al., 2008; Engel & Martin, 2009).

Sampling design and data collection

To investigate the influence of humpback whale carcass-derived nutrient input on the structure of reef fish assemblages, an *in-situ* experiment was conducted using a beyond-BACI (Before-After-Control-Impact) design (Underwood, 1992). The treatment was defined with a two-level fixed factor (T x C). The treatment site (T) was Laje dos Aquários, a small reef located approximately 280 meters from the main island of the archipelago (Figure 1). At this site, pieces of humpback whale muscle tissue – originating from a stranded adult individual during the 2023 breeding season – were placed in iron cages (70 x 70 x 70 cm) and anchored to the seafloor using two cement blocks per cage (50 kg each). A total of five cage sets were deployed, containing 17 muscle pieces of approximately 10 kg each, totaling 170 kg of whale biomass.

Six additional reefs were simultaneously monitored as controls sites, subdivided into control-near sites (Caldeiros reef; Ilha Redonda reef; Mato Verde reef), and control-far sites (Siriba Island; Guarita Island; Portinho Norte reef) (Figure 1). The selection of control sites was based on environmental factors and structural habitat similarity (Ferreira and Gonçalves, 2006), as these elements directly influence fish assemblage structure (Chabanet et al., 1997; Hackradt et al. 2011; Hackradt et al. 2020). Therefore, sites (S) are included as a random factor with seven levels.

The experimental framework considered the carcass addition as a localized nutrient input, aiming to assess temporal responses of reef fish assemblages in the impacted area compared to controls. The experiment began in April 2024 when carcasses were deployed, with three monitoring periods: period one, according to the beyond-BACI framework - was categorized as "before" carcass deployment (December 2023); period two - three months "after" deployment (July 2024); period three - six months "after" deployment (October 2024). While periods forming a fixed factor with three levels (P), according to the BACI framework (Underwood 1992; Benedetti-Cecchi 2001) (Appendix S1:Figure S1).

At each site, six stationary underwater visual censuses were conducted, with a four-meter radius and a five-minute observation period per census (cf. Minte-Vera et al., 2008). All species within the radius were recorded, and individuals were assigned to geometric abundance classes, with body sizes estimated in two-centimeter intervals (cf. Hackradt et al., 2011). Censuses were performed at three distances from the carcass in geometric progression (4, 16, and 64 meters), constituting a random distance factor (D) with three levels. Each reef was surveyed in two different directions, totaling six fixed-point observations per reef, considered as the samples for each location (Appendix S1:Figure S2). Altogether, 126 visual censuses were conducted during the monitoring.

Visual censuses provide two key ecosystem functioning metrics: species abundance and size structure. These allow the estimation of essential indicators and calculation of productivity (Robinson et al., 2023). This approach may reveal biomass increases around carcass-deployed reefs, either via actual biomass addition or fish attraction, potentially indicating enhanced secondary productivity. Standing biomass is a straightforward metric for assessing resource availability in coral reefs (Nash & Graham, 2016), while secondary productivity integrates both static and dynamic aspects of population ecological performance, offering insights into ecosystem dynamics (Dolbeth et al., 2012).

DATA ANALYSIS

Calculation of biomass, abundance, diversity, and trophic groups

For each fish species observed during visual censuses, biomass was estimated using species-specific Bayesian length-weight regression parameters obtained from FishBase (Froese & Pauly, 2024). Biomass estimation or standing biomass at a given time point was considered as the sum of the body mass of surviving individuals in a community, within a taxonomic unit per unit of surveyed area (Morais & Bellwood, 2020). The calculation accounted for a survey radius of four meters for individuals equal to or larger than 20 cm, and two meters for individuals smaller than 20 cm.

Additionally, we calculated taxonomic diversity indices for each sample, using the effective number of species based on Hill numbers (Hill, 1973). This approach provides an understanding of diversity by weighting species abundances: q^0 reflects absolute diversity, where species abundance is disregarded, favoring rare species; q^1 corresponds to Shannon entropy and emphasizes evenness, giving weight to common species; and q^2, favoring dominant species and assigning greater weight to abundance (Jost 2006). Diversity indices were calculated using the *entropart* package in R (Marcon & Herault, 2015).

Observed species were also categorized into trophic groups based on their diets, allowing investigation of how trophic structuring of communities responds to resource addition. This classification followed Morais and Bellwood (2018) and dietary information available from FishBase (Froese & Pauly, 2024). Diets were grouped as follows: herbivores/detritivores (HERDET), herbivores/macroalgae feeders (HERMAC), omnivores (OMNI), planktivores (PLKT), sessile invertebrate feeders (INVSES), mobile invertebrate feeders (INVMOB), and fish and cephalopod predators (FISCEP).

Productivity estimation

Productivity was calculated based on the approach proposed by Morais and Bellwood (2018), which combines taxonomic identity, body size, and species abundance to estimate biomass production derived from somatic growth of individuals within a community over a given time interval. To describe average body size increments over time, we applied the Von Bertalanffy Growth Model (VBGM) (Morais & Bellwood, 2020). This required combining species' morphological and behavioral traits (diet, size, and reef association) with temperature data to estimate the standardized growth parameter (K_{max}), which reflects how close individuals would approach the species' asymptotic length if they grew to maximum size (Morais & Bellwood 2018). Reef-association categories followed the same classification used for diets and were defined as: bentho-pelagic associated (BtPlAs), bentho-pelagic dwelling (BtPlDw), benthic associated (BnthAs), benthic dwelling (BnthDw), pelagic associated (PelgAs), and pelagic dwelling (PelgDw) (Morais & Bellwood, 2018; Froese & Pauly, 2024).

Natural mortality over time was also incorporated into productivity estimates using a size-based mortality rate, acknowledging that mortality tends to decline as body size increases (Gislason et al., 2010). This was applied stochastically using a Bernoulli distribution. Since productivity is a time-dependent rate based on observed biomass, time intervals were aligned with experimental monitoring events. Because no visual census was conducted at the exact time the carcass was deployed, the census from December 2023 (1 = before) was used to estimate productivity up to March 2024 (carcass deployment), defined as period one. Period two (2 = after) represented the difference in productivity from December 2023 to June 2024 minus the period one estimate. For period three (3 = after), the productivity was estimated from June to October 2024, using data from the June visual census. Additionally, productivity at period four (4 = after) was estimated from October 2024 to January 2025, based on the October visual census data. Each time interval spanned approximately 90 days.

Productivity was then calculated as the average biomass gained per day in each monitoring period, based on 1,000 bootstrap simulations and accounting for losses due to mortality. Fisheries mortality was considered insignificant because the experiment area was a well enforced MPA. All calculations were performed using the *rfishprod* package (Morais & Bellwood, 2018, 2020).

Statistical analyses

To assess the effect of allochthonous nutrient supply on reef fish assemblages, a null model was employed. Null models are pattern-generating frameworks based on the randomization of ecological data or random sampling from a known or hypothetical distribution (Gotelli & Graves, 1996). These models generate expected distributions of a response variable in the absence of causal processes (Paes & Blinder, 1995), simulating communities as they would occur without a specific mechanism, where the null hypothesis assumes that no effect has occurred (Gotelli & Graves, 1996). The null model tested the hypothesis of equality between treatment and control (T x C) and period (P), representing "B x A", for the following response variables: *Abundance* – to assess the effect of the carcass on the number of individuals; *ii Biomass* – to evaluate potential aggregative effects of species; *iii Productivity* – to detect differences in somatic growth; and *iv Taxonomic diversity* – to identify potential structural changes in the assemblage. A simplified null model was constructed using the formula:

$$\textit{response variable} \sim \textit{period} + (1 \mid \textit{Site}),$$

while adhering to the experimental hierarchy, with fixed factor for period (P) and random intercepts for sites (S). Due to low explanatory power, the distance factor (D) was excluded from all models.

A more complete model was also tested:

$$\textit{response variable} \sim T \times C * \textit{period} + (1 \mid \textit{Site}),$$

in which fixed effects of treatment (T x C) interacted with period (P), and site (S) as a random effect, accounting for potential before-after differences between impact and control sites. Both models were built as Generalized Linear Mixed Models (GLMMs), testing for differences in abundance, biomass, productivity, and diversity. GLMMs are well-suited for complex ecological datasets with repeated or grouped observations (Schielzeth et al., 2020), and they require specification of fixed and random effects, response distribution, and residual variance-covariance structure to ensure normality and homoscedasticity (Fitzmaurice & Laird, 2014). An Analysis of Variance (ANOVA) was conducted between the null and full GLMMs to evaluate whether differences between models were statistically significant and whether factor interactions improved model fit. Models were implemented using the *lme4* package and the *lmer* function (Bates et al, 2015; R Core Team, 2024).

Lastly, a Regression Tree Analysis (RTA) was performed to investigate changes in trophic structure of the fish communities in response to the carcass. This method predicts variation in a continuous response variable based on one or more explanatory variables – in this case, treatment (T x C), period (P), and the seven trophic groups. RTA is particularly suitable for ecological data due to its ability to handle missing values, nonlinear relationships, and high-order interactions, while producing easily interpretable graphical outputs (De'ath & Fabricius, 2000). The analysis was conducted using the *rpart* package in R (Therneau et al., 2017; R Core Team, 2024).

RESULTS

In total, 71 fish species were identified: 51 in period one, 58 in time two, and 49 in time three. At the treatment site, 22 species were recorded in period one, 29 in period two, and 22 in period three. *Haemulon aurolineatum* was the most abundant species across all sampling points during the first two time periods, later replaced by *Abudefduf saxatilis*. A similar pattern was observed at the experimental site for the first two periods, with *H. aurolineatum* replaced by *Haemulon parra* in time three.

Regarding total biomass, *Scarus trispinosus* showed the highest values across all three period at the control-near site (1264 ± 29.3 g/m²; 844 ± 20.2 g/m²; 2347 ± 29.2 g/m², respectively). At the control-far site, *S. trispinosus* dominated in period one, but was replaced by *H. parra* in subsequent samplings (2347 ± 31.7 g/m²; 917 ± 14.4 g/m²; 2847 ± 9.83 g/m², respectively). At the treatment site, *Acanthurus coeruleus* was initially dominant but was replaced by *H. parra* in the last two monitoring periods (287 ± 5.78 g/m²; 1408 ± 16.1 g/m²; 1054 ± 6.40 g/m², respectively).

The mean daily productivity of the fish assemblage at the control-far site was 517 ± 17 g/m²/day in period one, 744 ± 24 g/m²/day in period two, 276 ± 10 g/m²/day in period three, and 342 ± 22 g/m²/day in period four. At the control-near site, daily productivity averaged 286 ± 11 g/m²/day in period one, 430 ± 17 g/m²/day in period two, 319 ± 15 g/m²/day in period three, and 343 ± 14 g/m²/day in period four. The treatment site consistently showed lower daily values: 59 ± 7 g/m²/day, 85 ± 10 g/m²/day, 134 ± 14 g/m²/day, and 65 ± 12 g/m²/day for periods one through four, respectively.

The trophic groups with the highest species richness across sites over time were INVMOB and FISCEP (22 and 15 species, respectively), while PLKTIV comprised only three species. At the carcass site, INVMOB and HERDET were the most representative groups (10 and 9 species, respectively). Regarding total biomass, HERDET had the highest value in period one, later surpassed by INVMOB in subsequent periods (5811 ± 14.7 g/m²; 2355 ± 6.76 g/m²; 3761 ± 9.74 g/m², respectively). At the control-near site, HERDET consistently exhibited the highest biomass (2201 ± 15.6 g/m²; 3022 ± 10.6 g/m²; 4133 ± 16.1 g/m², respectively), while INVMOB dominated at the treatment site (548 ± 2.74 g/m²; 2426 ± 9.21 g/m²; 1390 ± 9.98 g/m², respectively).

All null models generated for the tested variables were significant (Table 1), rejecting the hypothesis that observed patterns were similar to natural conditions without resource addition. Thus, carcass addition has induced temporary changes in the reef fish assemblage at Abrolhos reefs, so we use the full models to better understand where these variations occurred.

Table 1: Null models for abundance, biomass, estimated productivity, and diversity indices (q^0, q^1, q^2) of fish sampled at treatment, control-near, and control-far points across the three monitoring periods. P1: first period; P3: third period; P4: fourth period. Boldface values indicate statistically significant differences.

		Abundance			
	Estimate	**SE**	**df**	**t**	**p**
Intercept	1.28	0.11	14.87	11.94	**5.07E-09**
P3	-0.05	0.11	117	-0.40	0.6897
P1	0.00	0.11	117	0.00	0.9992
		Biomass			
Intercept	5.57	0.19	17	29.16	**8.646E-16**
P3	0.06	0.21	117	0.30	0.7665
P1	-0.04	0.21	117	-0.21	0.8356
		Productivity			
Intercept	7.57	0.19	12	38.96	**2.1E-14**
P3	-0.46	0.18	158	-2.58	**0.0107**
P4	-0.50	0.18	158	-2.84	**0.0051**
P1	-0.40	0.18	158	-2.26	**0.0249**
q0		***Diversity***			
Intercept	2.64	0.07	10	35.80	**5.18436E-12**
P3	-0.04	0.06	117	-0.65	0.5149
P1	-0.14	0.06	117	-2.31	**0.0224**
q1					
Intercept	1.82	0.07	17	27.42	**8.74889E-16**
P3	0.07	0.07	117	0.88	0.3823
P1	0.03	0.07	117	0.38	0.7019
q2					
Intercept	1.45	0.07	25	21.10	**1.20659E-17**
P3	0.14	0.09	117	1.56	0.1215
P1	0.11	0.09	117	1.30	0.1955

Abundance

A marked increase in total abundance was observed at the treatment site between periods one and two, followed by a decline in period three. Control sites did not show similar changes (Appendix S2:Figure S1). The GLMM revealed significant interaction between treatment and period one (p = 0.0068; estimate = -0.91), indicating lower pre-treatment abundance (Figure 2). A significant interaction was also found for treatment and time three (p = 0.0201; estimate = -0.78), showing that differences persisted six months post-treatment, although at a lower magnitude than in period two (Figure 2). Comparing the completed to the null model we found significantly differences between than ($p < 0.05$), indicating that total abundance was influenced by the applied design in the experiment (Table 2).

Table 2: Full model and ANOVA test between the null and full models based on fish abundance data collected at treatment, control-near, and control-far points across the three monitoring periods. P1: first period; P3: third period; Cn: control-near; Tr: treatment. Boldface values indicate statistically significant differences.

Complet Model GLMM

	Estimate	SE	df	t	p
Intercept	1.29	0.18	7.58	7.08	**0.0001**
Cn	-0.16	0.26	7.58	-0.64	0.5412
Tr	0.44	0.36	7.58	1.22	0.2607
P3	-0.07	0.17	113	-0.41	0.6809
P1	0.16	0.17	113	0.97	0.3330
Cn X P3	0.31	0.23	113	1.34	0.1829
Tr X P3	-0.78	0.33	113	-2.36	**0.0201**
Cn X P1	-0.07	0.23	113	-0.30	0.7620
Tr X P1	-0.91	0.33	113	-2.76	**0.0068**

ANOVA

	npar	AIC	logLik	deviance	x^2	df	p
Null Model	5	206.73	-98.37	196.73			
Complet Model	11	203.95	-90.98	181.95	14.78	6	**0.022**

Model predictions showed a peak in abundance at time two for the treatment site, followed by an abrupt drop, suggesting a transient response to the nutrient pulse. Far-control predictions reflected expected patterns in the absence of carcass addition (Figure 2).

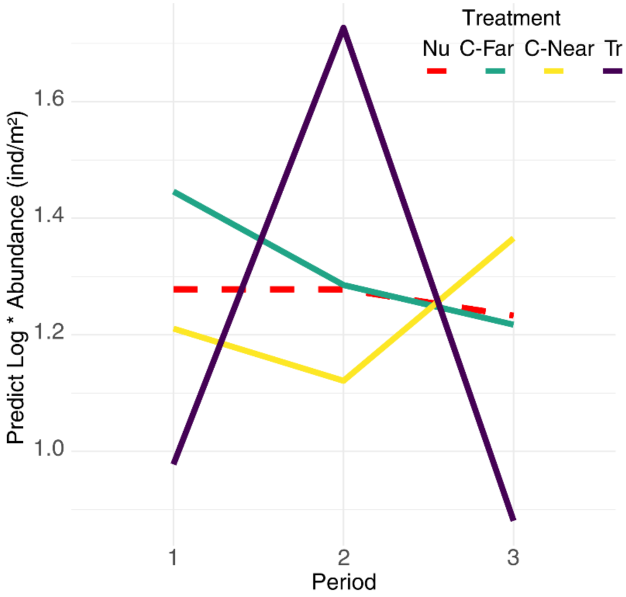

Figure 2: Predicted log-transformed abundance (ind/m²) from the models built for the treatment, near-control, and far-control points across the three monitoring periods.

Biomass

Patterns for biomass were similar to those observed for abundance. Biomass increased at the treatment site in period two and declined in period three, unlike control sites (Appendix S2:Figure S2). The interaction between treatment and time one was significant ($p = 0.0001$), showing lower biomass prior to resource input. The full model was significantly different from the null ($p < 0.05$), confirming that the combined effects of the investigated factors explained the observed biomass variation (Table 3).

Table 3: Full model and ANOVA test between the null and full models based on fish biomass data collected at treatment, control-near, and control-far points across the three monitoring periods. P1: first period; P3: third period; Cn: control-near; Tr: treatment. Boldface values indicate statistically significant differences.

Complet Model GLMM					
	Estimate	SE	df	t	p
Intercept	5.50	0.29	9	18.90	**7.48E-09**
Cn	-0.02	0.41	9	-0.04	0.9712
Tr	0.49	0.58	9	0.84	0.4216
P3	0.003	0.30	113	0.01	0.9924
P1	0.70	0.30	113	2.33	**0.0218**
Cn X P3	0.40	0.42	113	0.93	0.3529
Tr X P3	-0.77	0.60	113	-1.28	0.2035
Cn X P1	-0.93	0.42	113	-2.19	**0.0308**
Tr X P1	-2.41	0.60	113	-4.01	**0.0001**

ANOVA							
	npar	AIC	logLik	deviance	x^2	df	p
Null Model	5	363.89	-176.95	353.89			
Complet Model	11	352.25	-165.13	330.25	23.64	6	**0.0006**

Predictions indicated an increase in biomass three months after carcass addition, followed by a decline at six months, though still above initial levels. No significant changes were found in the control sites (Figure 3). Size class distributions (Appendix S2:Figure S3), showed a progressive increase over time at the treatment site, suggesting a nutrient-driven shift favoring larger individuals.

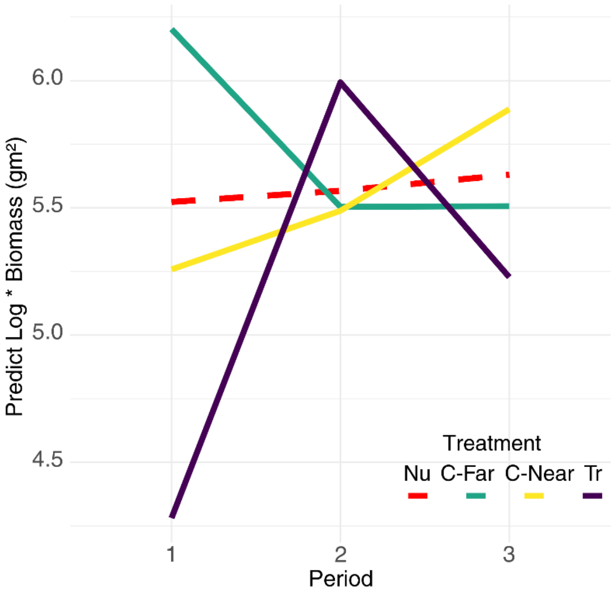

Figure 3: Predicted log-transformed biomass (g/m²) from the models built for the treatment, near-control, and far-control points across the three monitoring periods.

Productivity

The full model showed a significant positive effect of treatment for both period three and four ($p = 0.0006$, estimate = 1.79; $p = 0.0794$, estimate = 0.91, respectively). The model was significantly different from the null ($p < 0.05$), confirming that nutrient addition contributed to increased productivity (Table 4).

Table 4: Full model and ANOVA test between the null and full models of estimated productivity over four monitoring periods, based on fish data collected at treatment, control-near, and control-far points. P1: first period; P3: third period; P4: fourth period; Cn: control-near; Tr: treatment. Boldface values indicate statistically significant differences.

			Complet Model		
	Estimate	SE	df	t	p
Intercept	8.06	0.27	9	29.63	**2.97E-10**
Cn	-0.65	0.38	9	-1.70	0.1235
Tr	-1.46	0.54	9	-2.68	**0.0253**
P3	-1.00	0.26	152	-3.91	**0.0001**
P4	-0.98	0.26	152	-3.81	**0.0002**
P1	-0.37	0.26	152	-1.43	0.1541
Cn X P3	0.68	0.36	152	1.88	0.0626
Tr X P3	1.79	0.51	152	3.49	**0.0006**
Cn X P4	0.81	0.36	152	2.23	**0.0270**
Tr X P4	0.91	0.51	152	1.77	0.0794

Cn X P1	-0.04	0.36	152	-0.11	0.9160
Tn X P1	-0.11	0.51	152	-0.21	0.8378

ANOVA							
	npar	AIC	logLik	deviance	x²	df	p
Null Model	6	426.29	-207.15	414.29			
Complet Model	14	416.27	-194.14	388.27	26.02	8	0.0010

Pre-treatment productivity was lower than post-treatment, as evidenced by model predictions showing a marked increase at the treatment site (Figure 4). Although generally less productive than control sites, the addition of allochthonous nutrients at the treatment site led to a transient increase in secondary productivity that remained above baseline levels by the end of the experiment.

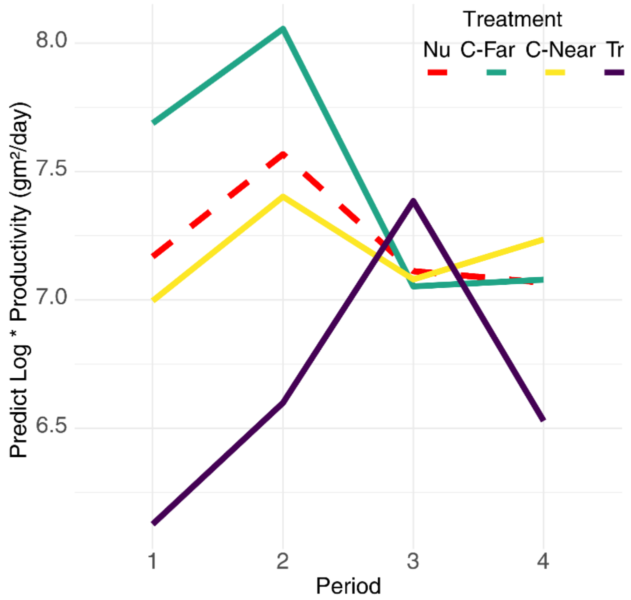

Figure 4: Predicted log-transformed productivity (g/m²/day) from the models built for treatment, control-near, and control-far points across the four monitoring periods.

Diversity

Among the taxonomic diversity indices, species richness (q^0) followed the expected pattern, with the highest richness at the treatment site during the second monitoring. Indices q^1 and q^2 showed no clear difference among sites, although all indices increased following carcass addition (Appendix S2:Figure S4). Full models confirmed a significant interaction between treatment and period one for q^0 ($p = 0.0009$; estimate = -0.61). Although less apparent, q^1 and q^2 were also significantly different at the far-control site in period one ($p = 0.0097$ and $p = 0.0063$, respectively). All three diversity models explained significantly more variance than their null counterparts ($p < 0.05$), indicating a treatment effect on reef diversity (Table 5).

Table 5: Full model and ANOVA test between the null and full models for diversity indices (*q0, q1, q2*) based on fish data collected at treatment, control-near, and control-far points across the three monitoring

periods. P1: first period; P3: third period; Cn: control-near; Tr: treatment. Boldface values indicate statistically significant differences.

			Complet Model GLMM		
q0	**Estimate**	**SE**	**df**	**t**	**p**
Intercept	2.70	0.09	9	29.51	**5.25028E-10**
Cn	-0.12	0.13	9	-0.91	0.3880
Tr	-0.05	0.18	9	-0.26	0.8036
P3	-0.03	0.09	113	-0.35	0.7284
P1	-0.04	0.09	113	-0.40	0.6880
Cn X P3	0.11	0.13	113	0.84	0.4044
Tr X P3	-0.38	0.18	113	-2.12	**0.0362**
Cn X P1	-0.04	0.13	113	-0.34	0.7322
Tr X P1	-0.61	0.18	113	-3.40	**0.0009**
q1					
Intercept	1.75	0.09	15	19.01	**5.52515E-12**
Cn	0.22	0.13	15	1.72	0.1067
Tr	-0.14	0.18	15	-0.75	0.4659
P3	0.16	0.11	113	1.46	0.1481
P1	0.26	0.11	113	2.31	**0.0229**
Cn X P3	-0.23	0.16	113	-1.46	0.1461
Tr X P3	0.01	0.22	113	0.06	0.9552
Cn X P1	-0.42	0.16	113	-2.63	**0.0097**
Tr X P1	-0.36	0.22	113	-1.60	0.1127
q2					
Intercept	1.32	0.10	21	13.41	**9.15397E-12**
Cn	0.34	0.14	21	2.44	**0.0238**
Tr	-0.09	0.20	21	-0.44	0.6667
P3	0.28	0.13	113	2.13	**0.0354**
P1	0.38	0.13	113	2.94	**0.0040**
Cn X T3	-0.34	0.18	113	-1.86	**0.0660**
Tr X T3	0.04	0.26	113	0.15	0.8846
Cn X T1	-0.51	0.18	113	-2.78	**0.0063**
Tr X T1	-0.34	0.26	113	-1.32	0.1883

			ANOVA				
q0	npar	AIC	logLik	deviance	x^2	df	p
Null Model	5	58.88	-24.44	48.88			
Complet Model	11	49.68	-13.84	27.68	21.20	6	**0.0017**
q1							
Null Model	5	101.68	-45.84	91.68			
Complet Model	11	99.65	-38.83	77.65	14.03	6	**0.0293**
q2							
Null Model	5	135.69	-62.84	125.69			
Complet Model	11	133.51	-55.75	111.51	14.18	6	**0.0277**

Based on predictions, the treatment site initially had lower diversity than controls, but diversity indices reached similar levels post-treatment. The q^0 index increased in period two, suggesting a rise in rare species, followed by a decrease in period three.

Indices q^1 and q^2 remained stable, showing a slight increase over time, suggesting an accumulation of common species. A marked increase in q^2 in period three suggests growing dominance at that stage (Figure 5).

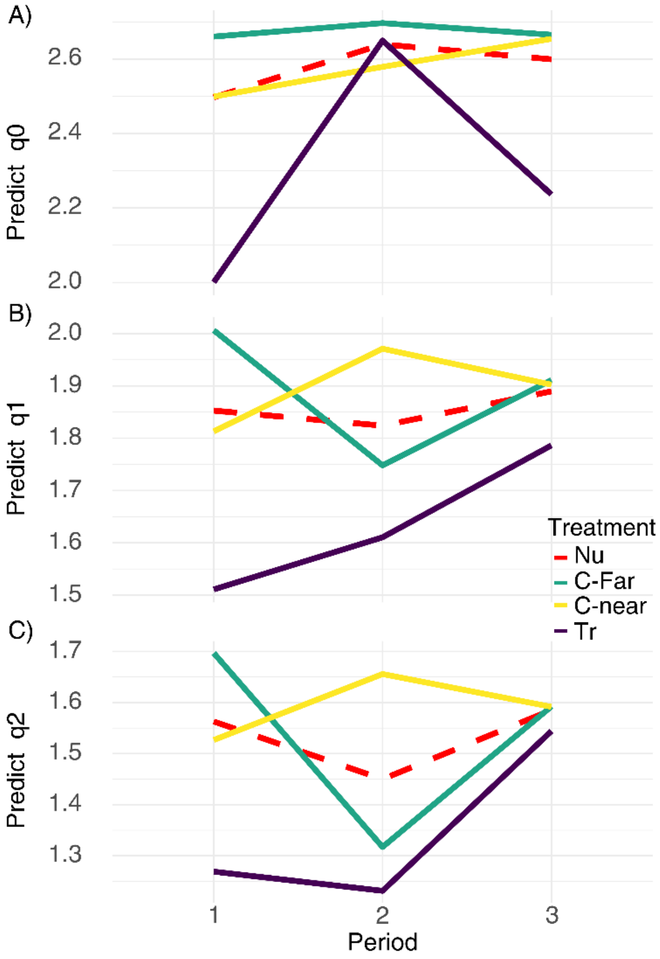

Figure 5: Predicted taxonomic diversity indices from the models built for the experimental sites across the three monitoring periods. A) q^0 indicates species richness. B) q^1 weights richness by species abundance and is equivalent to Shannon entropy. C) q^2 gives greater weight to abundance, highlighting species dominance.

Trophic Structure

To complement the analyses, we evaluated the trophic structure of fish communities across sites and periods, grouping response variables by trophic group (TG). Overall abundance patterns did not show the expected increase in the treatment site during the second monitoring, though some temporal changes were noted for INVMOB (Figure 6).

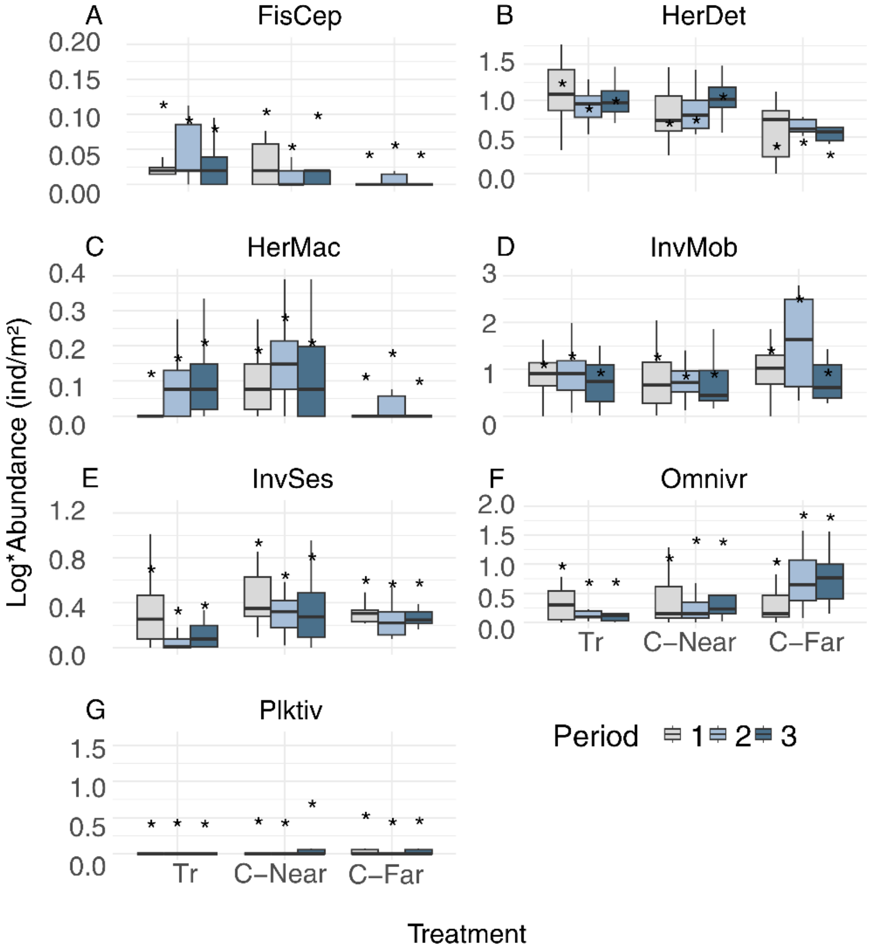

Figure 6: Log-transformed abundance (ind/m²) of trophic groups based on observed data during the experiment at treatment, control-near, and control-far points across the three monitoring periods. Herbivores/detritivores (HERDET), herbivores/macroalgae feeders (HERMAC), omnivores (OMNI), planktivores (PLKT), sessile invertebrate feeders (INVSES), mobile invertebrate feeders (INVMOB), and fish and cephalopod predators (FISCEP).

The regression tree generated to test these data indicates that the FISCEP, HERMAC, INVSES, OMNIV, and PLKTIV groups varied naturally across the studied communities, accounting for nearly 50% of the observed variation. The tree split suggests that the trophic group abundances at the site where the carcass was added already varied naturally, and those differences in the control sites were primarily associated with the INVMOB and HERDET groups (Figure 7A).

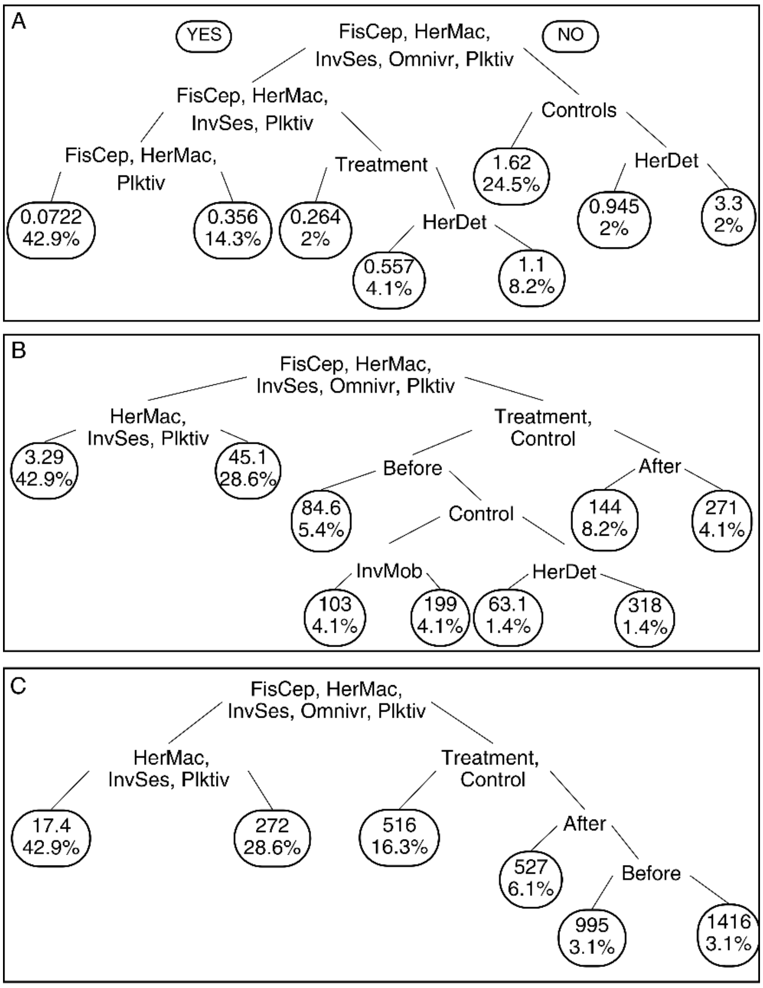

Figure 7: Regression Tree based on observed abundance (A), biomass (B) and estimated productivity (C) data during the experiment at treatment, control-near, and control-far points across the three monitoring periods. Herbivores/detritivores (HERDET), herbivores/macroalgae feeders (HERMAC), omnivores (OMNI), planktivores (PLKT), sessile invertebrate feeders (INVSES), mobile invertebrate feeders (INVMOB), and fish and cephalopod predators (FISCEP).

As observed in the abundance data, the biomass of trophic groups also did not show changes in the treatment site between monitoring periods; in fact, a decrease over time was observed for most groups. Additionally, PLKTIV biomass was nearly absent in the treatment site and present in the controls (Figure 8). This pattern aligns with the regression tree structure, which mirrored the patterns observed for abundance, indicating that the biomass of the groups structuring the community was not affected by the nutrient addition. However, the tree split differed in the treatment divisions, where the carcass site appears to have been influenced by the resource addition, suggesting an effect of the treatments and monitoring periods on the INVMOB and HERDET groups (Figure 7B).

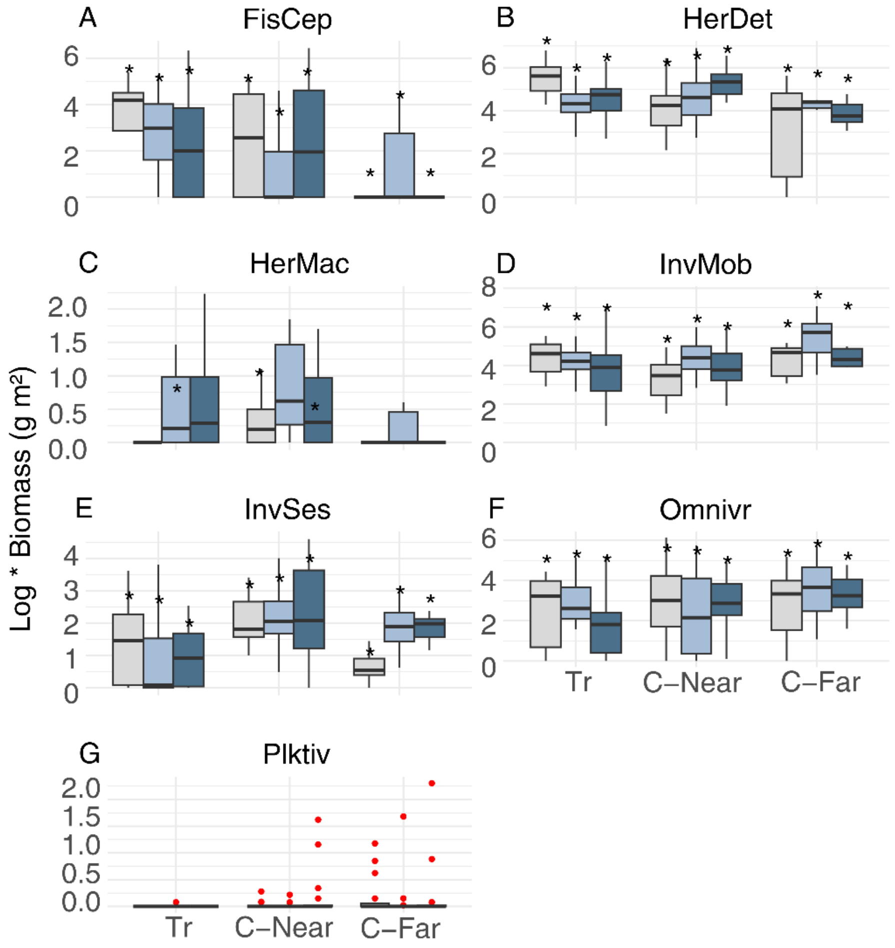

Figure 8: Log-transformed biomass (g/m²) of trophic groups based on observed data during the experiment at treatment, near-control, and far-control points across the three monitoring periods. Herbivores/detritivores (HERDET), herbivores/macroalgae feeders (HERMAC), omnivores (OMNI), planktivores (PLKT), sessile invertebrate feeders (INVSES), mobile invertebrate feeders (INVMOB), and fish and cephalopod predators (FISCEP).

Regarding productivity, the results indicate that regardless of the experimental conditions, the groups FISCEP, HERMAC, INVSES, OMNIV, and PLKTIV influence the trophic structure of the community. Among these, HERMAC, INVSES, and PLKTIV account for nearly 50% of the structural variation, which appears to be independent of the nutrient addition. Meanwhile, 16% of the productivity variation was explained by the treatments and 6% by the post-impact monitoring periods, indicating that these were relevant factors in structuring the community. The absence of INVMOB and HERDET in the initial nodes of the tree suggests that these groups influenced the data variation over time at the different locations, indicating that they are trophic groups potentially affected by the input of allochthonous nutrients (Figure 7C).

The observed changes in biomass and productivity of INVMOB and HERDET in the treatment site over period, combined with the natural variation in abundance, may suggest a possible increase in somatic growth for these groups rather than an actual aggregation at the experimental site. These results are consistent with those obtained from the abundance, biomass, productivity, and species richness models, indicating a structural difference in the communities due to the nutrient input. By observing the trophic structure, it is possible to conclude that there is natural variation among groups, but also that the treatment has an effect on that variation.

DISCUSSION

Humpback whales utilize the "great whale conveyor belt," which refers to the migratory corridors between feeding and breeding grounds (Pearson et al., 2022). Bortolotto et al. (2021), based on modeling approaches, estimated the southwestern Atlantic humpback whale population at 21878 individuals, indicating a recovery to approximately 93% of pre-exploitation levels. In addition, the subpopulation migrating to the Brazilian coast has been expanding its range both northward and southward along the coastline (Ristau et al., 2020; Morete et al., 2022). However, despite this population recovery, the species still faces multiple threats, including bycatch, entanglement in fishing gear, underwater noise, ship strikes, and the impacts of climate change and ocean warming (Pearson et al., 2022; von Hammerstein et al., 2022). The species' life history, characterized by long migrations sustained by lipid reserves, coupled with anthropogenic pressures, increases its vulnerability to mortality, leading to the frequent deposition of whale carcasses (Subalusky & Post, 2018; Pearson et al., 2022; von Hammerstein et al., 2022; Giardino et al., 2024). These events result in significant pulses of organic matter in shallow reef systems within breeding areas.

Based on the experimental findings, whale carcasses reaching tropical regions could be considered allochthonous nutrient input pulses, that influence many traits of shallow reef ecosystems. Initially, the carcass benefits the local assemblage through direct consumption, promoting individual aggregation and an increase in abundance and diversity. As this detrital input is assimilated into the food web, the biomass of the local assemblage increases, suggesting that the receiving system effectively utilizes the nutritional *input*, enhancing productivity via secondary production in addition to the biomass of immigrant opportunistic fish attracted by the carcass. These effects led to a temporary shift in community structure, particularly in trophic organization. This response primarily involved groups capable of directly consuming the resource, such as detritivorous herbivores, as well as indirect consumers – namely, mobile invertebrate-feeding fish. The experiment demonstrated that the presence of whales introduces nutrients that could be used both directly and indirectly by local fish assemblages, with their spatially heterogeneous distribution potentially creating localized productivity hotspots.

The aggregative response, evidenced by increased fish abundance, may indicate nutrient storage and recycling by the assemblage. The carcass seemingly created a localized nutrient-rich patch, altering the community composition. Over time, conditions reverted to pre-addition states, suggesting resilience of system components and a trend toward local stability (DeAngelis et al., 1989), with community structure resembling the initial configuration. However, it is important to note that such stability may reflect a response to a one-time experimental perturbation, and may not represent the long-term effects of naturally recurring events on a broader scale. In cases where allochthonous inputs occur more frequently, they could sustain or even enhance productivity and induce longer-lasting changes in community structure (e.g., Payne & Moore, 2006; Nishijima et al., 2015). Thus, the present findings highlight both the high nutrient recycling efficiency of autochthonous sources (DeAngelis et al., 1989; Huxel et al., 2002) and the system's capacity to incorporate and utilize allochthonous resources, albeit temporarily.

The treated reef assemblage appeared to exhibit low species diversity in the absence of supplemental food resources. However, following the addition of the subsidy, there was a significant increase in taxonomic diversity, followed by the dominance of a few species. This pattern indicates that mobile consumers were initially attracted from surrounding areas and aggregated locally. Subsequently, only the most common and abundant species remained, and the system returned to its original state. This suggests that individuals dispersed to adjacent patches, potentially carrying the ingested nutrients with them, thereby affecting neighboring communities (Holt, 2008). Resource pulses may sustain species diversity, but their effect depends on the magnitude and duration of the pulse (Holt, 2008). In this case, the carcass-derived pulse in the shallow reef was not long-lasting, likely due to the limited amount of input combined with the rapid consumption of detritus in reef environments (Rassweiler & Rassweiler, 2011; Nelson et al., 2023). This provided a short-lived and accessible resource for microorganisms, benthic invertebrates, fish, and mobile predators (Fallows et al., 2013). This dynamic contrasts with what occurs in deep-sea environments, where whole carcasses can form rich organic islands capable of supporting specialized communities through multiple successional stages (Lundsten et al., 2010; Sumida et al., 2016; Onishi et al., 2018; Smith et al., 2015).

The resource addition also resulted in increased biomass over time, followed by a decline, although values remained higher than initial levels. Combined with productivity data, these results suggest that allochthonous inputs enhance secondary production in the receiving reef ecosystem via the detrital pathway. When the resource is of high quality, consumers exhibit greater assimilation efficiency, which directly influences growth rates and nutrient retention (Elser et al., 2008; Wilson & Wolkovich, 2011). Consequently, the energy contained in the consumed biomass is channeled through various trophic pathways, potentially stimulating the growth and biomass production of the recipient community (Brandl et al., 2019). Therefore, the structure of fish assemblages is influenced by the rates and proportions of nutrient supply and storage within reef ecosystems (Allgeier et al., 2014).

Fish contribute to secondary production through their biomass (Allison & Ellis, 2001), and serve as useful indicators of how populations and communities functionally respond to environmental changes (Dolbeth et al., 2012). The arrival of subsidies can either enhance or reduce secondary productivity in the recipient ecosystem (Anderson et al., 2008; Marcarelli et al., 2011). The experimental reef was initially characterized by low productivity compared to nearby reefs, and the resource input was fundamental in altering this condition. The results indicate that nearly a year after the carcass addition, productivity values decreased but remained higher than baseline levels. This suggests that even in productive ecosystems, where nutrient recycling is efficient, allochthonous organic matter inputs play an important role in maintaining elevated productivity.

The temporary increase in secondary production promoted by the resource input was evident in the responses of herbivorous-detritivorous and invertivorous fish populations. These groups are abundant along the Brazilian coast and particularly prominent in the Abrolhos Bank region (Ferreira et al., 2004; Longo et al., 2019). In the experimental site, HERDET species – including scrapers and excavators – primarily consume detritus, turf algae, and macroalgae (Ferreira et al., 2004), acting as key channels for energy transfer in the food web (Allgeier et al., 2017). These consumers also feed on large quantities of microbial biomass and associated meiofauna (Ferreira & Gonçalves, 2006), while INVMOB species consume mobile benthic invertebrates such as crustaceans, mollusks, and polychaetas (Ferreira et al., 2004). A rapid response to fish carcass addition has also been documented in benthic predators such as crabs, lobsters, and sea stars in the marine lake of Lough Hyne, Ireland (Davenport et al., 2021). In the present experiment, this primary attraction may have acted as a stimulus for the aggregation of mobile invertivorous fish.

However, unlike the trophic groups emphasized in this study, other research has identified omnivores and carnivores as the main facultative scavengers (Nowlin et al., 2008; Wilson & Wolkovich, 2011; Davenport et al., 2021). The pattern observed here may be related to the form in which the resource was made available and to the local dynamics, wherein detritus – consisting of decomposing organic fragments – is initially processed by microorganisms and invertebrates (Moleón & Sánchez-Zapata, 2015). This decomposition increases its digestibility and facilitates assimilation by other consumer groups (Cross et al., 2007; Sitters et al., 2015), thus functioning as a trophic bridge among invertebrates, detritivores, and predators (Hall et al., 2000). Therefore, the identified patterns reflect specific responses to the experimental enrichment but offer valuable insights into how localized nutrient inputs may influence trophic structure in reef systems, especially under environmental change and varying inputs of organic matter.

Among the interspecific interactions that occur in various ecosystems, facilitation arises when species modify the environment in ways that favor the establishment of other species, even causing physical changes in the habitat (Connell & Slatyer, 1977). In this experiment, the resource pulse generated by the whale carcass appeared to act as a facilitator, temporarily altering the structure of the local community. Resource pulses can promote competitive coexistence in variable environments (Holt, 2008), and aggregations in space and time may give rise to biological productivity hotspots or "hot moments" within biogeochemical cycles (Paine & Moore, 2006; McIntyre et al., 2008). While such dynamics are less commonly documented in shallow reef habitats, they are well established in deep-sea ecosystems, where whale falls create sulfidic conditions similar to chemosynthetic habitats, facilitating the radiation and dispersal of local fauna (Roman et al., 2014).

Animal-mediated changes in community structure have been documented elsewhere as well. For example, on islands in the Gulf of California, Mexico, secondary productivity of terrestrial consumers increased following nutrient input from seabird guano on local vegetation (Sánchez-Piñero & Polis, 2000). Nutritional subsidies have also been shown to enhance reef recovery mechanisms, promoting coral resilience by increasing growth rates in the Chagos Archipelago in the Indian Ocean (Benkwitt et al., 2023), and improving calcification rates in fast-growing branching corals (Lange & Benkwitt, 2024). In Abrolhos, the presence of migratory seabirds was considered an allochthonous subsidy that influenced not only the terrestrial island communities but also adjacent reef corals (Linhares & Bugoni, 2023).

Within this context, the humpback whale carcass stands out as an animal-derived subsidy, capable of influencing material flows, species diversity, and physical habitat conditions. In the donor ecosystem, the species primarily consumes krill, which acts as a floating reservoir of iron – an essential and limiting element for all life forms. The excretion of unassimilated iron feeds back into feeding areas (Nicol et al., 2010; Lavery et al., 2014; Roman et al., 2014; Dufort et al., 2020). During reproductive migrations, carcasses entering recipient ecosystems carry nutrients accumulated for reproduction (Subalusky & Post, 2018), since mammals can only lose iron through blood or milk production (Lavery et al., 2014). Thus, nutrient-rich donor ecosystems can increase the nutritional quality of recipient systems (Subalusky & Post, 2018). However, the quantity of this resource may vary intra-specifically, temporally, and spatially (Dufort et al., 2020), and the duration of migration and the location of death can affect carcass quality due to fat reserve depletion (Tiegs et al., 2011; Roman et al., 2014; Sitters et al., 2015), while detrital chemical composition may change over time (Moore et al., 2004).

Given their size and the number of individuals arriving in the region each year, these large marine mammals are considered important vectors for the transport of organic matter (Estes et al., 2016; Allgeier et al., 2017; Subalusky & Post, 2018). They influence recipient ecosystems through the persistence of the pulse and the response capacity of consumers, which may manifest as either aggregative or reproductive responses (Yang et al., 2008; Yang et al., 2010). Even when such resource pulses occur infrequently and for brief durations, they can be characterized by high magnitude. They may promote facultative scavenging and attract predators in high numbers (Lea et al., 2018), functioning as a multichannel food web (Odum & Beiver, 1984; Polis & Strong, 1996). Although not always inducing direct effects on the ecosystem, these pulses can drive demographic changes in populations and temporarily alter the strength of trophic interactions (Wilson & Wolkovich, 2011). Therefore, it is essential to observe the system's reactivity to the resource pulse and the peak amplification before returning to equilibrium (Holt, 2008).

Thus, the population size of humpback whales, which has been steadily recovering in recent decades, is a key factor driving the magnitude of this allochthonous input. In the year 2000, an estimated 3871 individuals were using the Abrolhos Bank as a breeding ground (Freitas et al., 2004), a figure that requires updating given the significant population increase over the years. By 2012, estimates suggested approximately 20389 individuals migrating between Rio Grande do Norte (~5°S) and Rio de Janeiro (~23°S) (Bortolotto et al., 2017). Complementarily, monitoring data on strandings between 2002 and 2019 recorded 389 stranded individuals along the coast between ~16°S and ~20°S, with a higher concentration near the municipality of Caravelas (da Cunha Ramos et al., 2024). These records reinforce the occurrence of mortality events that may represent important pulses of organic matter entering the shallow reefs of the region.

Pelagic-derived inputs provide critical energy subsidies to reef systems, and fish productivity is directly linked to standing biomass accumulation (MacNeil et al., 2015; Morais & Bellwood, 2019). However, the coastal reefs of the Abrolhos Bank appear not to be directly sustained by such pelagic routes, as reflected, for example, in the low abundance of planktivorous species (e.g., Francini-Filho & Moura, 2008; Bruce et al., 2012). Nevertheless, being coastal systems, these reefs are highly connected to other components of the seascape, such as mangroves, terrestrial inputs, sandy bottoms, and rhodolith beds (Lima et al., 2024; Moura et al., 2021). Seasonal migrations between habitats for nursery use by reef fish species have also been documented (Lima et al., 2025). The whale carcass, however, represents a sporadic input that temporarily alters community structure and affects key groups such as herbivores. This trophic guild generally dominates standing biomass and influences biomass turnover and nutrient production in reefs. An increase in these populations may sustain fishable biomass in adjacent areas (Robinson et al., 2023). Therefore, maintaining or restoring whale populations may represent a long-term strategy for the recovery of fish stocks (Lavery et al., 2014), contributing to food security in fishing communities.

Measurements of secondary production provide direct information about the food supply derived from an ecosystem and hold significant socioeconomic relevance (Pinto et al., 2010). However, while estimates of secondary productivity offer important insights, Cusson and Bourget (2005) highlight the limitations of empirical models under non-equilibrium conditions. These models may overlook imbalances or deviations from a steady state that could lead to negative annual production estimates. Additionally, the biomass of carcass used in the experiment may have been insufficient to simulate the magnitude of disturbance that a full whale fall could cause in the recipient community (e.g., Sumida et al., 2016; Smith et al., 2019; Ibrahim et al., 2025). It is also essential to understand how the benthic community is being affected, whether these nutrients are being assimilated by organisms, and through which trophic levels incorporation occurs (see Chapter II to discussion).

Humpback whales directly store carbon in their bodies, and due to their long lifespans, they may constitute one of the largest and most stable living carbon reservoirs in the pelagic ocean (Pershing et al., 2010; Pearson et al., 2022). It is estimated that an adult humpback whale at the end of its life may weigh around 27 tons and sequester approximately 2782 kg of carbon to the ocean floor (Roman et al., 2025). Indirectly, they stimulate carbon storage in food webs by increasing local productivity through detrital pathways, with carbon being recycled by organisms in the recipient ecosystem (Pearson et al., 2023). Therefore, when a whale dies in shallow waters, it may not sequester carbon in the same way as in a deep-sea whale fall, but the carbon accumulated in its body over its lifetime is absorbed and recycled via the detrital pathway, rendering it unavailable to return to the atmosphere (see Chapter II to discussion). Moreover, whales enhance carbon storage in multiple ecosystem compartments by stimulating primary and secondary productivity through the release of placenta, milk, sloughed skin, and carcasses (Roman et al., 2025). Recent estimates suggest that a female whale may produce ten calves over her lifetime, performing at least 20 migrations and releasing approximately 77 kg of nitrogen per journey – totaling around 774 kg of nitrogen throughout her life – which could support the fixation of 4391 kg of carbon in low-latitude regions (Roman et al., 2025).

In this context, the establishment of the South Atlantic Whale Sanctuary, as well as the creation, expansion, or improved management of Marine Protected Areas (MPAs) that encompass the whales' ecosystem service zones, including feeding and breeding sites and migratory corridors, are fundamental for species conservation and the maintenance and enhancement of their ecosystem services (de Melo et al., 2024). MPAs are globally recognized for their biodiversity conservation benefits, and their expansion into priority areas could protect threatened and critically endangered species as well as biogeographic provinces (Sala et al., 2021). Moreover, well-managed MPAs can increase the abundance and biomass of fish within their boundaries (Mumby et al., 2021), with adjacent areas benefiting from the spillover of adult fish and larvae (Hackradt et al., 2014). Consequently, the accumulation of large, commercially valuable individuals may enhance fisheries yields outside conservation zones (Sala et al., 2021; Seguin et al., 2022).

This study highlights the role of humpback whales as important allochthonous subsidies to the shallow reefs of the Abrolhos Bank and underscores the ecological relevance of organic matter inputs to the region. These nutrients can temporarily alter community structure and support nutrient recycling in this highly productive ecosystem. The study also reinforces the species' contribution to the ecosystem service of climate regulation via carbon sequestration, and to biodiversity maintenance through nutrient enrichment. The recovery of fish and whale stocks can be considered analogous to carbon sequestration initiatives, while the conservation of healthy whale populations enhances ecosystem resilience and promotes local productivity. Understanding the function and value of these ecosystem services is essential to guide strategic decisions regarding spatial planning, conservation policy development, and assessments of trade-offs linked to economic development.

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Permissions

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CONCLUSÕES GERAIS

Os ecossistemas marinhos são moldados e conectados pelo fluxo de matéria, energia e organismos, e a teoria de metaecossistemas fornece um arcabouço importante para compreender tais processos (Loreau et al., 2003; Gounand et al., 2018). A movimentação animal entre distintos habitats pode introduzir nutrientes alóctones a partir de gametas reprodutivos, excretas ou carcaças, e afetar a dinâmica da comunidade receptora, sendo conhecidos como subsídios de recurso (Gounand et al., 2018; Subalusky e Post, 2019; Robinson et al., 2023). Como, por exemplo, as movimentações verticais de grandes mamíferos em áreas de alimentação ("whale pump"), e as extensas migrações anuais entre as áreas de alimentação e de reprodução (Roman e McCarthy, 2010; Lodi e Borobia, 2013).

As baleias de barbatanas (Balaenopteridae) estão entre os maiores mamíferos marinhos, distribuídas ao longo de diferentes latitudes em todos os oceanos. A baleia jubarte, cuja recuperação e expansão populacional é emblemática após séculos de sobrexploração (Bortolotto et al., 2021; Morete et al., 2022), conecta áreas polares e tropicais, fertilizando horizontalmente os oceanos e potencialmente afetando as comunidades receptoras (Roman et al., 2025), como os ecossistemas recifais diversos e altamente produtivos (e.g. Henderson et al., 2022; Andrews-Goff et al., 2023; Robinson et al., 2023). Nesses locais, além dos aportes orgânicos reprodutivos, o crescente número de carcaças pode atuar como importantes pulsos de nutrientes e energia (Subalusky e Post, 2019; da Cunha Ramos et al., 2024).

O funcionamento dos recifes de corais é resultado da dinâmica do carbonato de cálcio estruturando os habitats, da obtenção da energia e matéria a partir da produção primária e secundária e da eficiente ciclagem dos nutrientes (Brandl et al., 2019). São locais de elevada produtividade e eficiente reciclagem interna de nutrientes, que possibilitam uma estrutura de comunidade com teias alimentares complexas formadas por diferentes compartimentos biológicos (DeAngelis et al, 1989; Allgeier et al, 2017). Contudo, pouco se sabe sobre o efeito da chegada de carcaças de baleias jubarte nesses ambientes costeiros. Assim, a pergunta central desta tese foi investigar se a baleia jubarte atua como pulso de recurso e subsídio animal em recifes de corais rasos, que pode ser assimilada por diferentes vias e influenciar a estrutura e o funcionamento da comunidade recifal.

A investigação foi estruturada em três eixos complementares. Em escala global investigou-se as lacunas de serviços ecossistêmicos de espécies da família Balaenopteridae. Ao mapear os serviços, demonstrou-se que as grandes baleias são fonte concreta de produção e disseminação de serviços ecossistêmicos ao longo de suas áreas de ocorrência. Destacando-se o serviço cultural como elo essencial para a valorização social e econômica de comunidades costeiras (Antošová et al., 2019; Ressurreição et al., 2022). Embora fundamentais, permanecem subdocumentados, sobretudo devido à dificuldade inerente em investigá-los e quantificá-los. Observa-se uma função ecológica clara das baleias, atuando como vetores verticais no transporte de nutrientes entre a zona fótica e afótica dos sistemas marinhos, sustentando comunidades receptoras e promovendo a biodiversidade em ecossistemas profundos (associados ao “whale fall”). Contribuem com o sequestro do carbono acumulado em seus corpos ao longo da vida, aprisionando-os em leitos oceânicos profundos quando morrem. Entretanto, a análise espacial revelou que muitos desses serviços ocorrem fora de Áreas Marinhas Protegidas, evidenciando a necessidade de estratégias de gestão que incorporem corredores migratórios e hotspots de serviços ecossistêmicos.

No entanto, seu papel no transporte horizontal dos nutrientes ao cruzarem os oceanos, ainda carece de evidências empíricas. Sendo assim, por meio de um experimento *in situ*, utilizaram-se os recifes de Abrolhos como modelo ecológico de ecossistema receptor do aporte alóctone proveniente da carcaça de baleia jubarte. Buscou-se compreender, por meio da análise de isótopos estáveis de carbono e nitrogênio, a existência de um fluxo trófico promovido pela presença da carcaça, e como esses nutrientes podem estar sendo assimilados ao longo da teia alimentar. Evidenciou-se a assimilação por diferentes níveis tróficos, destacando-se produtores primários, como macroalgas e corais, bem como consumidores secundários. O consumo por espécies funcionalmente importantes, que se movimentam entre distintas paisagens e que são importantes para a pesca, indica que, mesmo de forma episódica, a chegada de nutrientes alóctones serve como aporte de nutrientes para a cadeia trófica local. Com relevância funcional para os recifes e comunidades costeiras.

Por fim, investigou-se como essa entrada pode afetar a estrutura e o funcionamento da comunidade recifal, analisando os efeitos sobre as assembleias de peixes. Observou-se que esse aporte promoveu uma resposta temporária, mas consistente, na assembleia de peixes. A abundancia, diversidade e biomassa aumentaram inicialmente e, embora tenham diminuído depois, permaneceram acima dos níveis prévios ao aporte, indicando um efeito de atração da carcaça sobre a ictiofauna. Entretanto, as taxas de produtividade calculadas, indicam que existem claramente um aumento da produção secundária da comunidade no tratamento do experimento. Assim, inputs desse tipo têm o potencial de gerar hotspots de produtividade em ambientes recifais de baixa profundidade, com efeitos que podem se prolongar no tempo. O estudo, portanto, oferece uma contribuição inédita para a compreensão do papel das baleias em ecossistemas recifais tropicais, historicamente pouco explorados nesse contexto.

A tese percorre desde a compreensão da importância das baleias nos ecossistemas, passando pela análise da incorporação de seu aporte nutricional pelo ecossistema receptor e possíveis entradas diretas e indiretas, até os efeitos de sua presença na comunidade recifal. Assim, ao integrar abordagens ecológicas, experimentais e espaciais, a pesquisa confirmou a hipótese central de que a carcaça de baleias jubarte atua como pulso de recurso e subsídio animal, que pode ser assimilada por diferentes vias tróficas, influenciando temporariamente a estrutura da comunidade recifal, e impulsionando a produtividade secundária. Os resultados reforçam a relevância ecológica das baleias jubarte na conectividade dos ecossistemas antárticos e tropicais, no suporte à biodiversidade e na ciclagem de nutrientes, com efeitos na produtividade dos recifes de corais rasos. Confirmando não apenas o papel da espécie no serviço ecossistêmico de manutenção da biodiversidade, mas também na regulação climática. Visto que, houve a assimilação e a transferência do carbono detrítico proveniente da carcaça da baleia por diferentes vias tróficas, indisponibilizando-o para retornar à atmosfera.

Essas evidências ressaltam a necessidade de regulamentar as práticas de turismo ambiental, ampliar as pesquisas científicas e aprimorar as AMPs. De modo a incluir corredores de migração e áreas de hotspots dos serviços ecossistêmicos. A gestão deve reconhecer essas baleias como parte integral de sistemas ecológicos mais amplos, vinculando sua função à manutenção da biodiversidade e ao bem-estar humano. Ao conectar o fluxo de nutrientes da megafauna aos recursos pesqueiros, este estudo evidencia o valor da proteção dos processos ecológicos que sustentam tanto a vida marinha quanto os meios de subsistência costeiros.

Finalmente, esta pesquisa abre novos caminhos para investigação. Questões emergentes incluem: Quais espécies têm maior probabilidade de se beneficiar da presença de carcaças em ambientes recifais? Qual o efeito das carcaças de baleias flutuantes na produtividade anual da pesca? E como esses aportes detríticos ricos em nutrientes influenciam grandes predadores marinhos que interagem com os sistemas recifais? Além disso, a recuperação de outras populações de baleias de barbatana pode ter efeitos semelhantes, reforçando sua importância para o funcionamento de ecossistemas receptores. Em síntese, este trabalho aborda lacunas críticas de conhecimento em ecologia trófica marinha e fornecem evidências valiosas para apoiar políticas de conservação marinha fundamentadas na ciência ecológica. Demonstrando que as baleias não são apenas símbolos da megafauna carismática, mas agentes dinâmicos que conectam processos oceânicos, sustentam a resiliência costeira e influenciam diretamente sociedades humanas.

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ANEXOS

Chapter I: Great Baleen Whales, Great Services

SM. 1: Complete lists of the bibliographic references of the reviewed articles on the ecosystem services provided by *Balaenoptera musculus*, *Balaenoptera physalus*, *Balaenoptera borealis*, *Balaenoptera acutorostrata* and *Megaptera novaeangliae*, along with the study locations.

Specie	**CICES classification**	**Service**	**Locality**	**Bibliographic reference**
Blue	Cultural	Tourism	Sri Lanka, Iceland, Mexico, Portugal	Anderson and Alagiyawadu (2019); Buultjens et al. (2016); Malinauskaite et al (2021); Ressurreição et al. (2022); Urbán and Viloria-Gómora (2021)
		Educational	Iceland	Cook et al. (2022); Malinauskaite et al (2021)
		Aesthetics	Iceland	Cook et al. (2022); Malinauskaite et al (2021)
		Community cohesiveness and cultural identity	Iceland	Cook et al. (2022); Malinauskaite et al (2021)
		Music and arts	Iceland	Cook et al. (2022); Malinauskaite et al (2021)
		Existence/Bequest	Iceland	Cook et al. (2022); Malinauskaite et al (2021)
	Regulation and maintenance	Enhanced biodiversity and evolutionary potencial	Italy; Iceland; USA; Australia; Southern Ocean	Bianucci et al. (2019); Cook et al. (2022); Dekas et al. (2018); Ratnarajah et al. (2014); Ratnarajah et al. (2016)
		Climate regulation	Iceland	Cook et al. (2022)
Fin	Provisioning	Food products (meat, blubber, skin and intestines)	Greenland; Japan; Iceland	Cook et al. (2022); Cunningham et al. (2012)

	Cultural	Tourism	Mexico; Iceland; Portugal	Malinauskaite et al. (2019); Ressurreição et al. (2022); Urbán and Viloria-Gómora (2021);
		Educational	Iceland	Malinauskaite et al. (2021)
		Aesthetics	Iceland	Malinauskaite et al. (2021)
		Community cohesiveness and cultural identity	Iceland; Greenland	Cook et al. (2022); Malinauskaite et al. (2021)
		Music and arts	Iceland	Malinauskaite et al. (2021)
	Regulation and maintenance	Enhanced biodiversity and evolutionary potencial	Australia; Southern Ocean	Ratnarajah et al. (2014); Ratnarajah et al. (2016)
		Climate regulation	Southern Ocean	Van Franeker et al. (1997)
Humpback	Provisioning	Food products (meat, blubber, skin and intestines)	Greenland	Cook et al. (2022)
	Cultural	Tourism	Greenland; Colombia; Argentina; Panamá; Finland; Iceland; Australia; Japan; Southern Ocean; Peru; Mexico; Tonga; Alaska; Dominican Republic	Antosova et al. (2019); Bailey (2012); Cardenas et al. (2021); Cook et al. (2022); Cunningham et al. (2012); Deininger et al. (2016); García-Cegarra and Pacheco (2017); Guidino et al. (2020); Kessler and Harcourt (2012); Kessler and Harcourt (2013); Lopez and Pearson (2017); Malinauskaite et al. (2021); Mitra et al. (2019); Orams (2002); Orams (2013); Parsons and Draheim (2009); Richards et al. (2021); Stamation et al. (2007); Thiele (2018); Tkaczynski and Rundle-Urbán and Viloria-Gómora (2021)

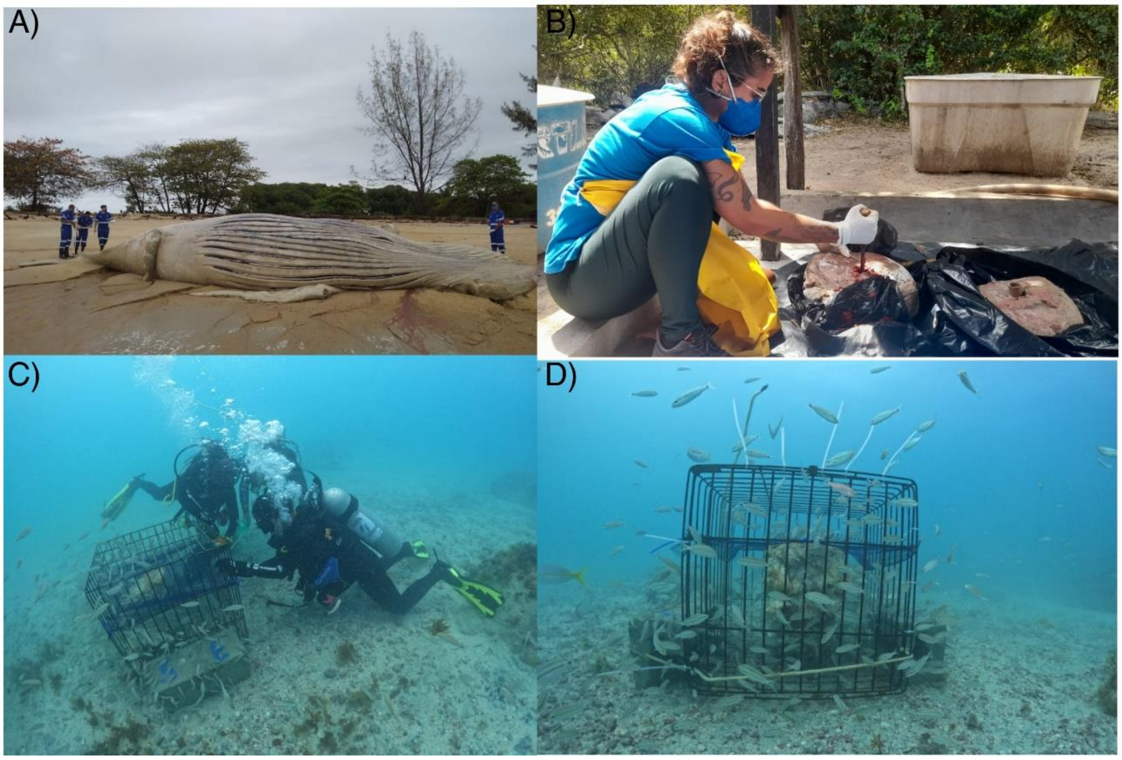
		Educational	Panama; Finland; Iceland; Greenland	Cardenas et al. (2021); Cook et al. (2022); Malinauskaite et al. (2021)
		Aesthetics	Finland; Iceland; Greenland	Cook et al (2022); Malinauskaite et al. (2021)
		Community cohesiveness and cultural identity	Finland; Iceland; Greenland	Cook et al (2022); Malinauskaite et al. (2021)
		Music and arts	Finland; Iceland; Greenland	Cook et al (2022); Malinauskaite et al. (2021)
		Existence/Bequest	Finland; Iceland; Greenland	Cook et al (2022); Malinauskaite et al. (2021)
	Regulation and maintenance	Enhanced biodiversity and evolutionary potencial	Southwest India; Finland; Iceland; Greenland; Brazil; Southern Ocean; Anvers Island; EUA	Amon et al (2017); Cook et al. (2022); Pereira et al. (2020); Ratnarajah et al. (2016); Ratnarajah et al. (2017); Roman and McCarthy (2010); Shimabukuro and Sumida (2019)
		Climate regulation	Finland; Iceland; Greenland	Cook et al. (2022)
Minke	Provisioning	Food products (meat, blubber, skin and intestines)	Iceland; South Korea; Greenland; Japan	Bertuli et al. (2016); Choi (2017); Cook et al. (2022); Cunningham et al. (2012); Endo and Wakamatsu et al. (2022); Yamao (2006)
	Cultural	Tourism	Iceland; South Korea; Finland; Greenland; Southern Ocean; Australia; Scotland	Bertuli et al. (2016); Choi (2017); Cook et al. (2022); Cunningham et al. (2012); Deininger et al. (2016); Farr et al (2014); Malinauskaite et al. (2019); Parsons et al. (2003); Ryan et al.

				(2018); Woods-Ballard et al. (2003)
		Educational	Finland; Iceland; Greenland; South Korea	Choi (2017); Cook et al. (2022); Malinauskaite et al. (2021)
		Aesthetics	Finland; Iceland; Greenland	Cook et al. (2022); Malinauskaite et al. (2021)
		Community cohesiveness and cultural identity	Finland; Iceland; Greenland	Cook et al (2022); Malinauskaite et al. (2021)
		Music and arts	Finland; Iceland; Greenland	Cook et al (2022); Malinauskaite et al. (2021)
		Existence/Bequest	Finland; Iceland; Greenland	Cook et al (2022); Malinauskaite et al. (2021)
	Regulation and maintenance	Enhanced biodiversity and evolutionary potencial	Brazil; Southwest India; Finland; Iceland; Greenland; Sweden; Spain; Southern Ocean	Amon et al (2017); Alfaro-Lucas et al. (2018); Cook et al. (2022); Danise et al. (2013); Glover et al. (2005); Taboada et al. (2020); Van Franeker et al. (1997); Wiklund et al. (2009)
		Climate regulation	Finland; Iceland; Greenland; Southern Ocean	Cook et al. (2022); Van Franeker et al. (1997)
Sei	Provisioning	Food products (meat, blubber, skin and intestines)	Japan	Cunningham et al. (2012); Endo e Yamao (2006)
	Cultural	Tourism	Iceland; Portugal	Cook et al. (2022); Ressurreição et al. (2022); Ressurreição and Giacomello (2013)
	Regulation and maintenance	Enhanced biodiversity and evolutionary potencial	Iceland	Cook et al. (2022)

	Climate regulation	Iceland	Cook et al. (2022)

Chapter II: Tracing allochthonous nutrient pathways from whale carcasses to coral reef food webs: Experimental and stable isotope evidence

Appendix S1



FigureS1: Humpback whale muscle tissue obtained from a stranding event during the 2023 breeding season (A-B); the tissue enclosed in iron cages, secured to the seafloor with two cement anchors (C-D).

Chapter III: Whale's carcasses as allochthonous subsides: increase secondary productivity in coral reefs

Appendix S1

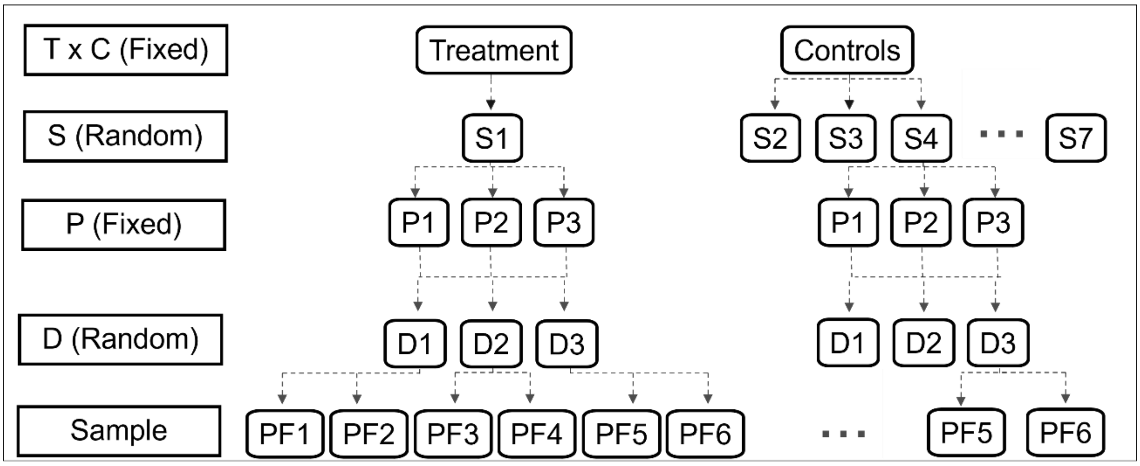


Figure S1: Experimental sampling design following the hierarchy of factors. The letters T, C, P, S, D, and PF represent: treatment, control, period, site, distance, and fixed point, respectively. PFs one through six represent the visual censuses. Period is equivalent a BACI framework. P1: "before"; P2 and P3: "after".

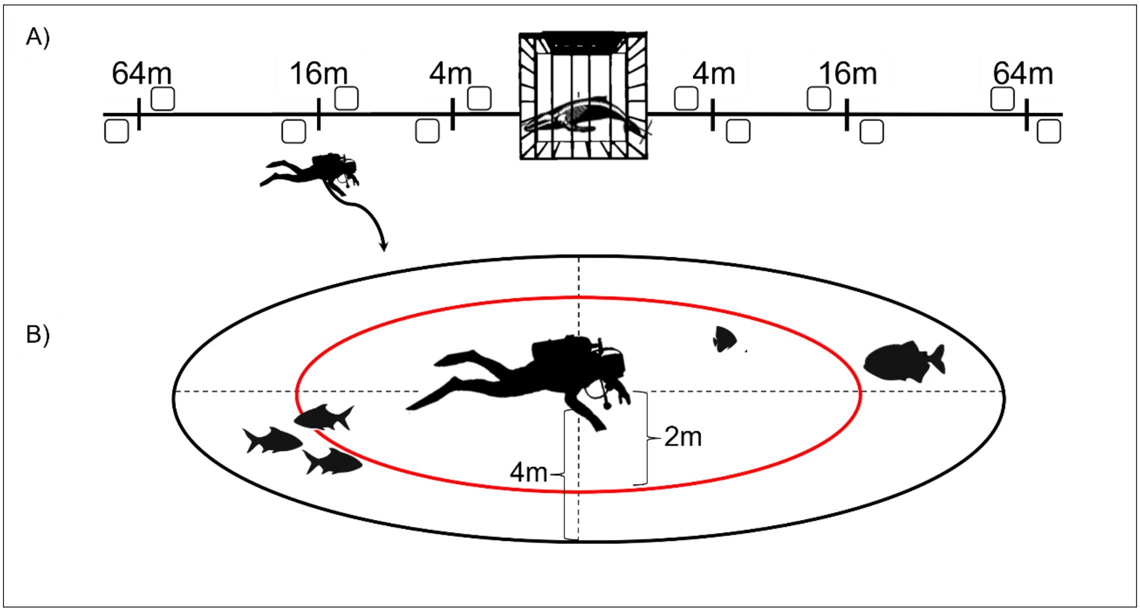


Figure S2: A) Illustrative diagram of the positioning of stationary visual censuses conducted at each sampled reef, totaling six fixed points. B) The diver positioned at the center records fish equal to or larger than 20 cm within a four-meter radius (black circle) and fish smaller than 20 cm within a two-meter radius (red circle) over five minutes.

Appendix S2

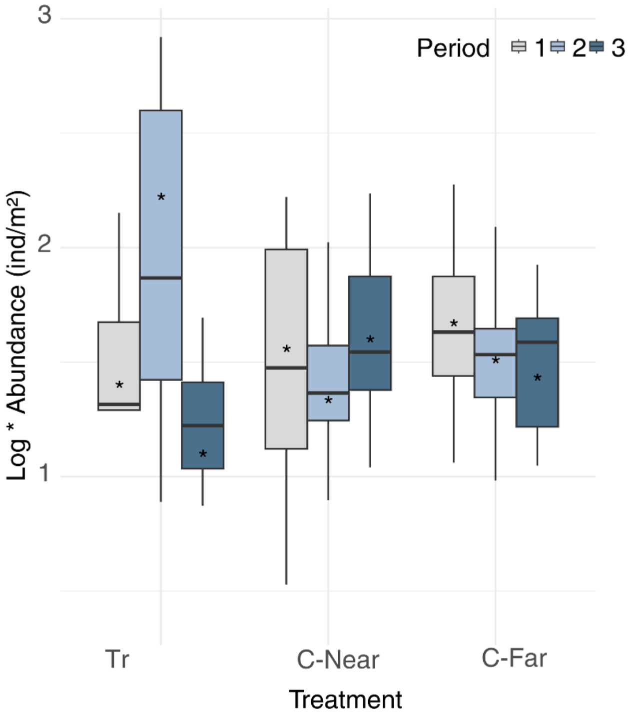


Figure S1: Log-transformed abundance (ind/m²) of observed data throughout the experiment at treatment, near-control, and far-control points across the three monitoring periods.

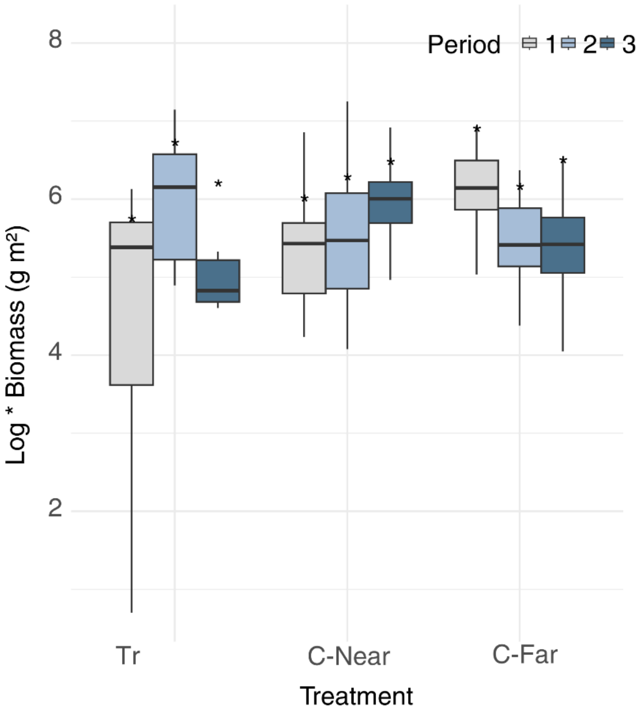


Figure S2: Log-transformed biomass (g/m²) of observed data throughout the experiment at treatment, near-control, and far-control points across the three monitoring periods.

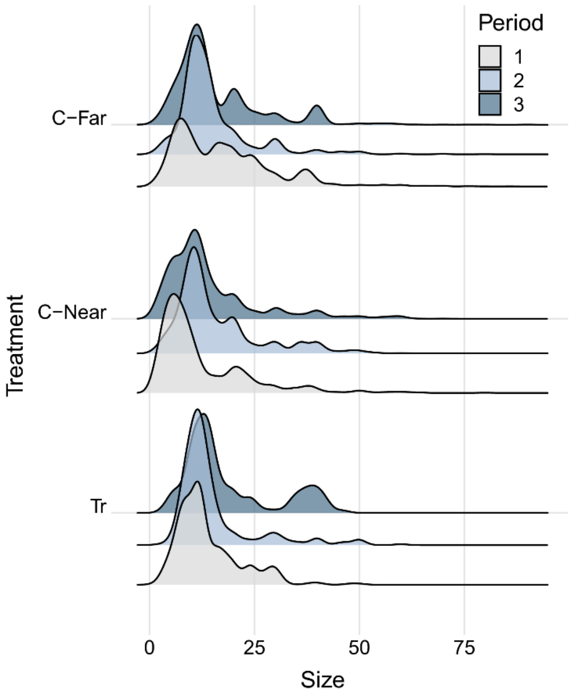


Figure S3: Growth curves for individuals observed during the experiment at treatment, near-control, and far-control points across the three monitoring periods.

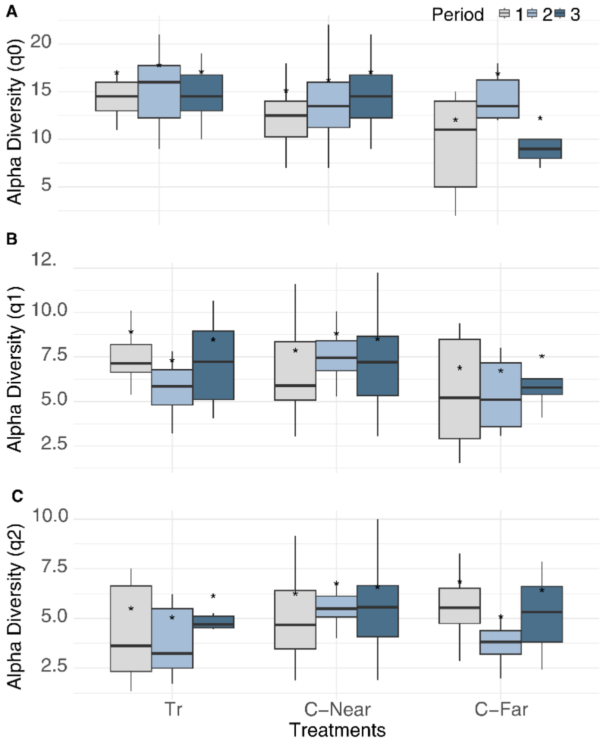


Figure S4: Taxonomic diversity indices from data collected during the experiment at treatment, control-near, and control-far points across the three monitoring periods. A) q0 indicates species richness. B) q1 weights richness by species abundance and is equivalent to Shannon entropy. C) q2 gives greater weight to abundance, highlighting species dominance.