UNIVERSIDADE FEDERAL DE ALAGOAS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos

MORGANA MARIA MACEDO

EFEITO DA SAZONALIDADE SOBRE O FLUXO DE RECURSOS EM META-ECOSSISTEMAS COSTEIROS TROPICAIS

MACEIÓ - ALAGOAS
Maio/2022

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Tese apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde. Universidade Federal de Alagoas, como requisito para obtenção do título de Doutora em CIÊNCIAS BIOLÓGICAS, área de concentração em Conservação da Biodiversidade Tropical.

Orientadora: Profa. Dra. Nidia Noemi Fabré
Co-orientador: Prof. Dr. Ronaldo Angelini

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DEDICATÓRIA

Dedico essa tese ao criador, sobretudo por reunir, em um ponto reduzido do espaço, formas de vida tão grandiosas que fascinam e intrigam aqueles capazes de perceber a dinâmica da vida à sua volta. A minha mãe, Maria Neide, pela dedicação, abdicação e amor incondicional. Ao meu esposo e a toda a minha família, pelo suporte emocional e parceria.

AGRADECIMENTOS (incluir apenas na versão final, PREVISTO PARA 2 PÁGINAS)

Texto sem itálico

“Há homens que lutam um dia e são bons.

Há outros que lutam um ano e são melhores.

Há os que lutam muitos anos e são muito bons.

Porém, há os que lutam toda a vida.

Esses são os imprescindíveis."

Bertolt Brecht

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SUMÁRIO

1 APRESENTAÇÃO

A eficácia da conservação ambiental está pautada na compreensão de padrões e processos ecológicos que governam a estrutura e o funcionamento dos ecossistemas. Entretanto, há expressivas distinções entre a ecologia tradicionalista e a ecologia moderna quanto aos pilares teóricos que fundamentam os estudos ecossistêmicos. Tal fato deve-se a divergências quanto à interpretação de conceitos importantes, como é o caso de estabilidade ecossistêmica e seus pilares: resistência e resiliência, bem como as perspectivas de autorregulação e independência ecossistêmica. Diante dessa problemática, torna-se necessário rever os processos estruturais e funcionais de muitos ecossistemas, sob bases teóricas robustas e atualizadas, dentre eles, os ecossistemas costeiros tropicais, que são usualmente considerados complexos e de difícil compreensão, em virtude das frequentes flutuações ambientais e interferência de ordem natural ou antrópica sob as quais estão sujeitos. Dessa forma, utilizamos a modelagem ecotrófica como ferramenta para compreender as relações que se estabelecem entre grupos funcionais tróficos de diferentes ecossistemas costeiros tropicais, por meio da conectividade existente entre esses ecossistemas, bem como as perturbações sazonais que influenciam estas relações. Para tanto, iniciamos o primeiro capítulo apresentando as bases conceituais que fundamentaram as ideias descritas nos capítulos posteriores. No segundo capítulo, avaliamos a conectividade trófica dos ecossistemas estuarino, nerítico e oceânico, a partir do fluxo de peixes e partindo da premissa de funcionalidade metaecossistêmica. Especificamente testamos a hipótese de similaridade espaço-temporal na distribuição da biomassa de diferentes grupos funcionais. Este capítulo subsidiou a definição de grupos para a montagem dos modelos tróficos analisados no capítulo subsequente, além de validar os modelos criados a partir do software Ecopath com Ecosim. No terceiro capítulo avaliamos o efeito da conectividade, comandada pela sazonalidade, sobre as propriedades e os principais indicadores da maturidade ecossistêmica da zona nerítica e estuarina. Neste capítulo investigamos especificamente como a variação sazonal afetava a produtividade, a ascendência, a energia de reserva e o fluxo energético dos ecossistemas em questão, sob a premissa de conectividade inter-ecossistêmica. Tudo isso para compreender como a conectividade, comandada pela sazonalidade, subsidia a dinâmica de fluxos interecossistêmicos locais que permitem a persistência e a evolução do meta-ecossistema em nível regional. Ao final, apresentamos uma discussão geral deste trabalho, mas procurando não entrar em particularidades que a discussão de cada capítulo intermediário apresentou.

2 REVISÃO DA LITERATURA

2.1 Concepções de Ecossistema

O paradigma clássico da ecologia tradicional consiste na perspectiva de que os ecossistemas seriam unidades autorreguladas, que seguiriam uma trajetória linear de desenvolvimento em direção a uma estabilidade, denominada, clímax (Fiedler *et al.* 1997). Essas metáforas de equilíbrio, linearidade e estabilidade ganharam força na ecologia de ecossistemas a partir de algumas observações no campo da ecologia de comunidades e de populações (Viglio and Ferreira 2013).

Na época, ecólogos que estudavam o desenvolvimento de plantas em associação a outros organismos em áreas florestais, falavam que as plantas passavam por várias sucessões em direção a um estágio de maturidade, até o último, denominado clímax (Cowles 1899; Clements 1916; Tansley 1935). À medida que o processo de sucessão ocorria, eles observaram uma diminuição da variação ambiental e o aumento da complexidade estrutural e funcional da floresta. Já no âmbito da ecologia de populações havia o fortalecimento no desenvolvimento de modelos de crescimento populacional que descreviam um suposto equilíbrio entre taxa intrínseca de crescimento populacional e capacidade suporte, à medida que a densidade populacional se aproxima do limite máximo de utilização dos recursos disponíveis em determinado ambiente (Malthus 1798; Verhulst 1838). Para a literatura clássica, os dois casos relatados remetem a uma sequência de acontecimentos que resultaria em equilíbrio ou estabilidade.

Baseado nas propriedades estruturais e funcionais das comunidades e aspectos da história de vida dos organismos, Odum (1969) definiu 24 atributos para classificar o estágio de maturidade dos ecossistemas e formulou um modelo preditivo do comportamento ecossistêmico em função da proximidade do clímax. Apesar de ter sido precursor, os atributos propostos pelo autor, continuam tendo uma elevada aceitação e embasando a maioria dos estudos sobre ecossistemas (Corman *et. al.* 2019). No entanto, poucos desses estudos de fato, testaram as hipóteses levantadas por Odum (1969). Neste sentido, um estudo de meta-análise, reuniu 3.169 manuscritos que faziam menção ao modelo clássico de desenvolvimento dos ecossistemas, proposto por Odum (1969), sendo que desses, menos da metade, de fato, testaram as hipóteses preconizadas pelo modelo. Entre os que testaram essas hipóteses, foram encontradas algumas divergências, sobretudo, quanto a tendência de determinados ecossistemas fugirem ao padrão de maturidade esperado. Especialmente as hipóteses de: (1) Similaridade entre produção e consumo à medida que o ecossistema se aproxima da maturidade, (2) Incremento de tamanho dos organismos com o passar do tempo e (3) Mudança de um ciclo de vida simples e curto para um longo e complexo.

A visão de ecossistema de Odum (1969), baseada no conceito de sucessão de Clements (1936), pressupõe um processo unidirecional de maior controle de homeostase, à medida que Produção (P) e Consumo (C) se equiparam. Nessa circunstância, a proximidade do clímax tende a estabilizar a biomassa, resultando na estagnação quase completa da produção líquida do sistema. No entanto, para a ecologia moderna, P e C não se equiparam com a proximidade do clímax, mas, ao invés disso, o sistema continua a acumular carbono, mantendo elevada a produção no sistema e em níveis superiores ao consumo (Schulze *et al.* 2000; Zhou *et al.* 2006; Luyssaert *et al.* 2008; Luyssaert *et al.* 2011; Stephenson *et al.* 2014; Hermosillo-Núñez, Ortiz and Rodríguez-Zaragoza 2019). Assim, é possível que o clímax (ou maturidade) possa ocorrer em algumas situações, como por exemplo, o equilíbrio do número de espécies, mas não em termos energéticos, pois os sistemas tenderiam a manter elevada a produção líquida (PPL) (Viglio and Ferreira 2013). O modelo atual também prevê a resposta do ecossistema à ocorrência de distúrbios ambientais ou de natureza antrópica, que passam a ser incorporados como propriedade intrínseca dos sistemas ecológicos. Nessa perspectiva a ocorrência de distúrbios não só se torna previsível ao sistema, como pode ser utilizado por ele como fator de variação entre diferentes estados de equilíbrio (Connell and Sousa 1983; Petraitis and Dudgeon 2016; Michaels, Eppinga and Bever 2020).

Apesar da nova concepção, algumas das previsões de Odum (1969) continuam sendo fortemente utilizadas e avaliadas de forma independente para predizer o grau de maturidade dos ecossistemas, em relação ao que seria considerado estável, negligenciando as propriedades emergentes ecossistêmicas que, frequentemente, agregam complexidade funcional (Corman *et al.* 2019). Isso explica, em partes, a lacuna que ainda persiste no campo da ecologia de ecossistemas sobre o conceito de estabilidade. Segundo Grimm and Wissel (1997), para este termo, há pelo menos 163 definições na literatura. Algumas delas coincidem com outros conceitos, por exemplo: "permanecer essencialmente inalterado" (constância), "retornar ao estado de referência após um distúrbio temporário" (resiliência) ou ainda "insistência ao longo do tempo de um sistema ecológico" (persistência).

Para a física, estabilidade é uma propriedade de sistemas com dinâmica simples, descritos por poucos graus de liberdade. Na natureza, porém, os sistemas apresentam dinâmica altamente complexa, envolvendo uma grande diversidade de variáveis para descrevê-los e n graus de liberdade (Grimm *et al.* 1992). Assim, o conceito de estabilidade, inevitavelmente, remete os sistemas ecológicos a um sistema simples, à medida que é inferida uma determinada variável de estado, de referência, um tipo particular de perturbação e assim sucessivamente (Grimm and Wissel 1997).

Adicionalmente, existe outra problemática relacionada a um dos pilares da própria estabilidade ecossistêmica, o conceito de resiliência. Inicialmente, Holling (1973), definiu a resiliência como sendo a quantidade de perturbação que um sistema poderia absorver sem alterar sua organização estrutural e funcional. Mais tarde, essa definição passaria a ser mais conveniente ao conceito de resistência (Gunderson 2000). Outros autores passaram a considerar a resiliência como sendo o tempo de retorno de um ecossistema para um estado estável após uma perturbação (Holling 1973; Beddington *et al.* 1976; Harrison 1979; Webster *et al.* 1979; DeAngelis 1980; Pimm 1991). Mais uma vez, implícito nesta definição está à hipótese de que o sistema tende a persistir numa condição de equilíbrio único ou global. Dessa forma, a medida da resiliência mensura o desvio que o sistema sofreu do ponto de equilíbrio e a velocidade com que ele retorna a esse ponto inicial (Ludwig, Walker and Holling 1996; Qin *et al.* 2021; Wollstein *et al.* 2022)

Atualmente, uma nova definição reconhece a presença de múltiplos estados estáveis ou domínios de estabilidade. Nela, a resiliência é medida pela magnitude do distúrbio que pode ser absorvido por um determinado sistema, que o possibilite regenerar-se, sem precisar transitar entre diferentes domínios de estabilidade (Folke *et al.* 2004; Briske *et al.* 2020; Arumugam, Lutscher and Guichard 2021). Portanto, a resiliência passa a ser uma propriedade que intermedia a transição entre diferentes estados alternativos.

Estados alternativos de equilíbrio têm sido reportados para diversos ecossistemas, incluindo florestas, paisagens semiáridas, lagos, estuários e recifes de corais (Capon *et al.* 2015; Petraitis and Dudgeon 2016; Arumugam, Lutscher and Guichard 2021; Moi *et al.* 2021). Nestes sistemas, a resiliência é mantida por processos de reestruturação em diferentes níveis ecológicos, fontes de renovação e diversidade funcional. Na prática, manter uma capacidade de renovação em um ambiente dinâmico, fornece uma variedade de opções ecológicas que protege o sistema contra a destruição (Gunderson 2000).

Outro paradigma incoerente é a concepção de que os ecossistemas seriam unidades autorreguladas e independentes. Neste sentido, a literatura vem reportando o estabelecimento de importantes subsídios interecossistêmicos, que promovem estruturação e funcionamento dos componentes envolvidos, subsidiando a resiliência. (Varpe, Fiksen and Slotte 2005; Mumby and Hastings 2008; Olds, Pitt and Maxwell 2012). Com base nisso, Loreau, Mouquet and Holt (2003), propuseram o conceito de meta-ecossistemas, definido como um conjunto de sistemas conectados por fluxos de matéria, energia e organismos, que excede aos limites espaciais ecossistêmicos e promove uma espécie de protocooperação entre seus componentes ecossistêmicos, cujos benefícios são ainda pouco conhecidos na literatura (Loreau, Mouquet and Holt 2003; Massol *et al.* 2011; Gounand *et al.* 2014; 2018)

Dessa forma, torna-se crucial a inclusão dos novos conceitos, a avaliação conjunta dos atributos ou indicadores ecossistêmicos e a inclusão de análises temporais e espaciais, dado a dinâmica ecossistêmica que envolve uma série de descritores e promove mudanças estruturais e funcionais ao longo do espaço-tempo.

2.2 A conectividade na Concepção de Metaecossistema

Ecossistemas são sistemas abertos e por isto sujeitos a padrões e processos que operam em múltiplas escalas. Neste sentido, o conceito de metaecossistema (Loreau, Mouquet and Holt 2003) surge para buscar novos insights sobre a dinâmica de fluxos espaciais entre ecossistemas locais que interferem no funcionamento dos sistemas em níveis regional e global (Gounand *et al.* 2018). A teoria de metaecossistema é uma extensão natural dos conceitos de metapopulação e metacomunidade (Hanski and Gilpin 1991). Os três modelos preconizam um estado de equilíbrio entre entradas e saídas. Na teoria metapopulacional a persistência regional das populações é dependente das dinâmicas de colonização e extinção entre manchas de habitat disponíveis (Levins 1969). Por outro lado, na teoria de metacomunidade, extinções e colonizações locais passam a ser influenciadas por interações interespecíficas, como predação e competição (Hanski and Gilpin 1991; Wilson 1992; Holt 1993; Hubbell 2001; Mouquet and Loreau 2002). Na perspectiva da metacomunidade é possível descrever não somente o conjunto de manchas de habitat ocupado por cada espécie, mas também produzir probabilidades de co-ocorrência interespecífica. A análise conjunta das distribuições das espécies permite identificar o quanto a presença de uma espécie irá influenciar a ocorrência das demais (e.g. agindo como facilitador, competidor ou predador (Hanski and Gilpin 1991).

O conceito de metacomunidade, no entanto, tem foco nos componentes bióticos dos ecossistemas e desconsidera as propriedades da comunidade que são afetadas por restrições e feedbacks abióticos (Mouquet and Loreau 2002; Haegeman and Loreau 2014).

Neste sentido, a ecologia de paisagem pode suprir essa lacuna, pois permite a integração desses processos dentro da heterogeneidade ambiental produzida pelas atividades antrópicas, que fragmentam os ecossistemas em mosaicos de manchas (Turner, Gardner and O'neill 2001; Gounand *et al.* 2018). O foco principal é a avaliação da fragilidade ou vulnerabilidade ambiental decorrente da fragmentação, que normalmente é mensurada a partir de métricas e índices que avaliam a qualidade desses ambientes (e.g. índice de área central; índice de circularidade; distância do vizinho mais próximo; proximidade à curso d'água; grau de erodibilidade do solo) (Etto *et al.*, 2013; Silva *et al.*, 2019). Apesar da importância desse tipo de avaliação, havia a necessidade usual de avaliar a paisagem, sob a premissa de ocorrência de fluxos inter-ecossistêmicos e como isso poderia contribuir para a manutenção, recuperação e evolução conjunta desses ecossistemas (Gounand *et al.* 2018).

A definição original de um metaecossistema como um conjunto de ecossistemas conectados por fluxos espaciais de energia, materiais e organismos através das fronteiras do ecossistema é suficientemente geral para aplicar-se a diferentes escalas (Loreau, Mouquet and Holt 2003). Essa flexibilidade torna o conceito relevante para abordar questões sobre dinâmica espacial entre quaisquer entidades ecológicas coerentes, ligadas por fluxos bióticos ou abióticos, com a escala variando de acordo com o organismo ou processo de interesse (Gounand *et al.* 2018; Woodson *et al.* 2018). O conceito de metaecossistema, portanto, tem o potencial de integrar ecologia da comunidade e da paisagem e fornecer novos insights fundamentais sobre a dinâmica e o funcionamento dos ecossistemas de escala local à global, além de aumentar a previsibilidade sobre os processos ecossistêmicos resultantes de alterações antrópicas e naturais.

No campo do metaecossistema os subsídios (fluxos espaciais de energia, materiais e organismos) são normalmente transportados por agentes físicos, como ventos, correntes oceânicas, cursos fluviais ou ainda agentes biológicos, como organismos migratórios (Varpe, Fiksen and Slotte 2005). Isso significa que cada ecossistema passa a ser dependente, em partes, de um tipo predominante de subsídio que pode promover efeitos distintos sobre componentes específicos da estrutura trófica do sistema receptor (Gounand *et al.* 2014).

Exemplos de aplicações desse conceito podem ser vistos desde a década de 60. No trabalho de Weir (1969), por exemplo, é reportado um transporte de grandes quantidades de biomassa e nutrientes realizados por pássaros, entre diferentes ecossistemas terrestres, durante eventos migratórios. McNaughton (1985) descreve uma situação semelhante, porém, envolvendo grandes herbívoros. Outros estudos enfatizam a contribuição de ecossistemas florestais para a manutenção da produtividade secundária em sistemas lóticos e lênticos (Nakano and Murakami 2001; Sabo and Power 2002; Thorp and Delong 2002; Junk and Wantzen 2004; Thorp, Thoms and Delong 2006; Yue *et al.* 2016; Harvey *et al.* 2017; Gounand *et al.* 2018).

O conceito de metaecossistema também tem sido associado a sistemas costeiros. Apesar de mangues, estuários e regiões marinhas diferirem em características físicas, produtiva e estrutura trófica (Loreau, Mouquet and Holt 2003), são ecossistemas conectados por processos espaciais. Dentre estes: sedimentação de detritos, afloramento de nutrientes, movimentos de fitoplâncton, zooplâncton e peixes (Boero *et al.* 1996; Schindler and Scheuerell 2002; Spiecker, Gouhier and Guichard 2016). Estes últimos representam um importante elo entre estuários e ecossistemas marítimos, através de larvas, acúmulo de biomassa e deslocamento de adultos (Yhfiez-Arancibia 1994), exportando nutrientes e energia. Varpe, Fiksen and Slotte (2005) por exemplo, avaliaram o transporte de energia realizado pelo arenque *Clupea harengus* entre ecossistemas costeiros e oceânicos na Costa da Noruega durante eventos migratórios. Os autores constataram que a biomassa transportada para a costa e deixada como produção reprodutiva, na ordem de 1,3 x10^6 ton. representou um dos maiores fluxos de energia já registrados no mundo, ocasionado por uma única população. Neste caso, há dois efeitos importantes a serem considerados: (1) a adição de consumidores a estrutura trófica do sistema receptor e o consequente incremento da pressão de consumo sobre as presas locais existentes; (2) a entrada de matéria orgânica sob a forma de recurso para predadores locais e cadeia detritívora presentes, resultando em diferentes efeitos top-down ou botton-up, pouco reportados até o presente.

2.3 Sazonalidade e a Conectividade de Ecossistemas Costeiros Tropicais

Ecossistemas costeiros diferem substancialmente em habitat físico, produtividade biológica e estrutura trófica (Schindler and Scheuerell 2002; Gounand *et al.* 2018; da Silva, Dolbeth and Fabré 2021). Entretanto, frequentemente são acoplados por fluxos espaciais com potencial para desestabilizar estrutural e funcionalmente suas tramas tróficas (Boero *et al.* 1996). Assim, sistemas costeiros adjacentes supostamente seriam beneficiados pela entrada de aporte externo, podendo, inclusive manter parte de sua produtividade, aumentar a resiliência e, em algumas situações, atingir rapidamente estágios de sucessão ecológica mais elevados (Holling 1973; Webster *et al.* 1975; May 1977; Scheffer 1998; Loreau, Mouquet and Holt 2003).

Frequentemente a ocorrência de fluxos entre ecossistemas costeiros, como estuário e região nerítica, aqui definida como faixa de mar que recobre toda a extensão da plataforma continental (Hedgpeth 1957), incluindo os recifes costeiros, é impulsionada por mudanças nos parâmetros físico-químicos ambientais decorrentes da variação sazonal (Longhurst and Pauly, 1987; Blaber *et al.*, 1997; Barletta-Bergan *et al.*, 2002a, b; Barletta *et al.*, 2003; Lima *et al.*, 2014). Em regiões subtropicais e temperadas, variações de temperatura e incidência luminosa costumam ser marcantes (Odum and Odum 1955; Moberg and Folke 1999; Brander, Van Beukering and Cesar 2007; Weijerman *et al.* 2015). Nos trópicos, fotoperíodo e temperatura são constantes ao longo do ano, e prevalece a variação previsível da precipitação (McConnell and Lowe-McConnell 1987).

Um caso predominante nos trópicos é a incidência de processos de estuarização (Longhurst and Pauly 1987; Blaber *et al.*, 1997; Barletta-Bergan *et al.*, 2002a, b; Barletta *et al.*, 2003; Krumme, Herbeck and Wang 2012; Lima *et al.*, 2014; Passos *et al.* 2016), que consiste de uma expansão sazonal das condições estuarinas na região nerítica (Passos *et al.* 2016). Isso ocorre em períodos com maiores incidências de chuva, quando aumentam vazão e descarga de sedimento dos rios. Em algumas regiões as mudanças são tão marcantes que impossibilitam a distinção dos limites físico-químicos entre estuário e zona nerítica (Longhurst and Pauly 1987). Esse processo é semelhante ao 'estuário offshore' descrito por McHugh (1967) e coerente com processos observados nas plataformas internas da Guiana (Lowe-McConnell 1962), de Nova Jersey (Milstein 1981), do Golfo do México (Chittenden e McEachran 1976; Yán˜ez-Arancibia *et al.* 1985) e de Carpentenia (Ranier 1984; Blaber, Brewer and Salini 1989).

Apesar de marcantes, os efeitos da variação sazonal sobre a dinâmica trófica dos ecossistemas costeiros tropicais ainda são pouco conhecidos. Neste sentido, García-Seoane *et al.* (2019) analisaram variações espaço-temporais na composição da ictiofauna presente na zona nerítica do Atlântico Norte. Para esses autores grandes vazões de água doce, associadas a sistemas de ressurgência, promovem uma forte estratificação da coluna de água, contribuindo para o aumento da produção primária, incremento do pastejo zooplanctônico e agregação de peixes pelágicos oceanodromus. Para regiões neríticas tropicais do Atlântico Sul foi observado que o regime hidrológico tem forte influência sobre a produção de clorofila-a, principalmente em regiões neríticas de até 40 m de profundidade (Lima *et al.* 2014). Segundo esses autores no período chuvoso, aumenta a disponibilidade de nutrientes transportados pelos rios, resultando em maior atividade fitoplanctônica. De modo similar, De Barros *et al.* (2022), investigando a reprodução e o recrutamento de camarões peneídeos tropicais, também encontrou correlação positiva entre o recrutamento de *Xiphopenaeus kroyeri* e *Penaeus schmitti* e o aumento da produção primária que ocorre nas estações chuvosas. Além de produtores e consumidores primários, a ocorrência da estuarização parece afetar a diversidade funcional ictiofaunística tropical. Neste sentido, Passos *et al.* (2016), evidenciaram uma forte correlação linear entre turbidez, salinidade e diversidade funcional das assembleias de peixes costeiros, limitando a similaridade funcional na estação seca e permitindo que peixes adaptados aos estuários, com um conjunto diferente de características funcionais, possam ocupar águas rasas da plataforma continental durante a estação chuvosa. Já Da Silva, Dolbeth e Fabré (2021) analisaram diferentes dimensões da diversidade de peixes, no espaço e no tempo, em mosaicos de habitats costeiros e constataram um aumento na diversidade filogenética na zona nerítica, com a chegada da estuarização.

Esse conjunto de resultados indica que, de fato, a variação sazonal tende a promover fortes mudanças na dinâmica dos ecossistemas costeiros tropicais e seus componentes tróficos. Contudo, a fragmentação dos resultados dificulta a identificação de possíveis padrões e processos ecossistêmicos, sendo necessária uma abordagem mais holística que nos permita avaliar que efeitos a sazonalidade promove sobre cada componente trófico de ecossistemas conectados no espaço-tempo, bem como, esses efeitos podem contribuir para a manutenção e/ou amadurecimento conjunto desses sistemas.

2.4 Modelagem Ecotrófica Aplicada a Estudos Que Envolvem Conectividade

A utilização de modelos matemáticos consiste de uma ferramenta valiosa da ciência moderna para a elucidação de estudos ecossistêmicos (Frigg and Hartmann 2006). Os modelos são criados para organizar a compreensão dos sistemas, avaliar os dados observados, auxiliar na compreensão das relações entre os componentes, definir os problemas e fazer previsões (Trolle *et al.* 2012; Evans *et al.* 2013; Montero, Christensen and Hernández 2021).

Na prática, a modelagem pode ser utilizada para responder questões ecológicas importantes, dentre elas, o efeito de estressores ou mudanças climáticas sobre a produtividade ecossistêmica (Scheffer *et al.*1993; Sinnickson, Chagaris and Allen 2021), a ocorrência de variações entre estados alternativos de equilíbrio (van den Koppel *et al.* 1997; Rietkerk *et al.* 1997; Rahmstorf 1997), maturidade ecossistêmica (Lira *et al.* 2018) ou, ainda, inferir sobre a existência de meta-ecossistemas (Macedo *et al.* 2021).

Felizmente, a modelagem vem ganhando cada vez mais espaço no âmbito da literatura de ecossistemas, através da criação de modelos cada vez mais robustos, formulados a partir de pacotes computacionais altamente complexos (e.g. Ecopath com Ecosim EwE). Alguns pacotes são disponibilizados gratuitamente e os modelos gerados a partir deles, podem ser acessados através de redes globais de cooperação focadas na pesquisa, desenvolvimento e sustentabilidade, como é o caso do repositório EcoBase, que atualmente conta com 205 modelos EwE disponíveis para download, incluindo oito modelos criados na costa brasileira, além de 471 modelos EwE com metadados (EcoBase 2022)

O software EwE foi inicialmente desenvolvido por Polovina (1984), para analisar recifes de corais do Havaí, utilizando parâmetros de biomassa, produção e consumo de grupos de espécies, para inferir sobre o estado de desenvolvimento do ecossistema. Posteriormente, foi desenvolvido por Christensen e Pauly (1992) e passou a ser amplamente utilizado para avaliar a estrutura trófica e o fluxo de energia dos ecossistemas aquáticos, sobretudo, inerente a exploração pesqueira (Colléter *et al.* 2015). A modelagem realizada por meio deste software presume um ecossistema em equilíbrio, isto é, a média anual da biomassa para cada grupo de espécies se mantém constante ao longo dos anos (Polovina 1984).

O desenvolvimento do software Ecopath ganhou impulso quando Carl Walters, do UBC Fisheries Center, Vancouver, se juntou ao projeto em 1995 e desenvolveu o modelo de simulação temporal dinâmico, Ecosim (Walters, Christensen and Pauly 1997). Posteriormente o mesmo autor agregou um modelo de simulação espacial dinâmico, Ecospace (Walters, Christensen and Pauly 1999)

O surgimento do Ecosim possibilitou simular questões temporais, tais como: o comportamento do sistema frente à diminuição ou intensificação da pesca ao longo do tempo. A ferramenta permitiu ainda, simular o comportamento do ecossistema em caso de variação nas capturas (Christensen 2009). O Ecospace, por sua vez, introduziu ao pacote a possibilidade de modelar diferentes regiões ou sistemas, simultaneamente, considerando possíveis interações. Por último, um novo módulo foi acrescentado à base Ecopath, o Ecotrace. Este permite modelar os mecanismos de transferência e o efeito cumulativo de poluentes através das redes alimentares (Christensen 2009, Colléter *et al.* 2015).

Dado a variedade de recursos disponíveis em um único pacote, Fretzer (2016), classificou o pacote Ecopath e seus módulos, como a ferramenta de número um para o gerenciamento ambiental. Segundo o autor, o pacote pode fornecer os resultados necessários para atender a diversos setores ambientais com dinamicidade. Além disso, proporciona uma avaliação integrada de diversos parâmetros, fornecendo conclusões claras e objetivas que subsidiam a tomada de decisão.

Apesar da variedade de recursos disponíveis em um único pacote, a maioria dos usuários não explora o software por completo, limitando-se aos módulos de base, Ecopath com Ecosim, o que pode estar atrelado à finalidade da criação dos modelos (Christensen 2009), bem como as dificuldades para obtenção de dados, visto que a exploração de todos os módulos do software requer uma grande diversidade de variáveis e na maioria das vezes há pouco tempo hábil para obtenção das mesmas. Um levantamento realizado por Morissete (2007) mostra que a maioria dos modelos (42%) construídos a partir do ecopath, descrevem a estrutura ecossistêmica e suas redes tróficas, 30% destinam-se ao manejo pesqueiro, 11% são criados para incrementar a ecologia teórica, 9% tem abordado questões políticas e cerca de 6% contemplam áreas protegidas. Para se ter uma idéia, até o presente momento, o módulo Ecotrace, por exemplo, foi explorado apenas por Coombs (2004), Booth and Zeller (2005), Christensen and Booth (2006) e Sandberg, Kumblad and Kautsky (2007).

No Brasil, a maioria dos estudos com modelos Ecopath foi realizada na zona costeira e região sul do país (Rocha *et al.*, 1998; Gasalla e Rossi-Wongtschowski, 2004; Velasco e Castello, 2005; Rocha *et al.*, 2007; Nascimento *et al.*, 2011; Araújo *et al.*, 2017; Bornatowski *et al.*, 2017). Dois modelos em águas continentais da região Norte (Wolff *et al.*, 2000; Capitani *et al.* 2021a), e quatro estudos, sendo três não publicados, desenvolvidos no Nordeste do Brasil (Xavier 2013; Ferreira 2018; Lira *et al.* 2018; Capitani *et al.* 2021b).

Esses estudos têm contribuído fortemente para uma melhor avaliação estrutural e funcional ecossistêmica, promovendo informações fundamentais para a elaboração de planos de manejo e gerenciamento de recursos. No entanto, é necessário criar novos modelos na perspectiva de meta-ecossistemas, permitindo uma visão conservacionista mais integrada, no sentido de que, a conectividade passe a ser um componente chave para o arranjo e a qualidade dos ecossistemas, bem como para a dispersão das espécies.

2.5 Referências

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3 TROPHIC STRUCTURE OF COASTAL META-ECOSYSTEMS IN A TROPICAL REGION

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Abstract: Coastal and oceanic ecosystems have their own structural and functional dynamics, but they are typically connected by the transfer of nutrients and organisms. These organic matter and energy flows mean these environments function as a meta-ecosystem. In the tropics, the transfers between estuaries and the neritic ecosystems or nearshore can be driven by estuarization events, which are poorly understood. Here, we analyze the effects of seasonal estuarization on the trophic structure of estuarine and neritic ecosystems connected by biological and physical flows in space and time. Specifically, we evaluated trophic connectivity and the flow of fish species from the South Atlantic, based on the assumption of meta-ecosystem functionality. We used standard sampling gear and fishing effort to evaluate the estuarine and neritic ecosystems during the dry and the rainy seasons of the region. The diet and trophic niche of fish species were estimated for both environments. We also reconstructed the trophic connections between species and food items for each season to evaluate the changes in the food web of each environment. During the dry season, the estuarine and neritic ecosystems are both characterized by a simpler trophic structure in terms of biomass distribution among trophic levels, but in the rainy season, the migration of species associated with estuarine and oceanic ecosystems to the neritic ecosystem changed the trophic structure of this area. The movements of organisms between ecosystems increases the complexity of the trophic structure of neritic ecosystem, allowing the transfers of organic matter and energy, confirming this complex as a meta-ecosystem.

Keywords: coastal waters, ecosystem interactions, estuarine processes, trophic cascade, trophic convergence

3.1 Introduction

Although estuarine and oceanic ecosystems are structurally and functionally distinct, inter-ecosystem movements of nutrients and organisms significantly influence energy flow and the functioning of these environments (Boero *et al.*, 1996; Schindler and Scheuerell, 2002). In this context, these environments can be conceptualized as 'meta-ecosystems' (sensu Loreau *et al.*, 2003), which are defined as a set of ecosystems connected by spatial flows of energy, materials, and organisms across their boundaries. This concept is broad enough to be applied at different scales (Loreau, Mouquet and Holt, 2003; Massol *et al.*, 2011; Gounand *et al.*, 2014), making it ideal for addressing questions about spatial dynamics between ecological entities, linked by biotic or abiotic flows, with the scale varying according to the organism or process of interest (Gounand *et al.*, 2014).

The original meta-ecosystem model proposed by Loreau, Mouquet and Holt (2003) and later refined by Gounand *et al.*, (2014, 2018) is based on the premise that nutrient flows occur between local ecosystems, whether in the form of inorganic elements, debris or living organisms (Polis, 1996). These exchanges will inevitable affect one or more trophic compartments of each ecosystem, which can range from entire trophic levels to functional groups or single species, allowing inferences at the ecosystem level based on some components of local trophic structure (Loreau *et al.* 2003; Marleau *et al.*, 2010, Gounand *et al.*, 2014). The flexibility to analyze the connections between natural ecosystems using a limited number of components is especially valuable for meta-ecosystems with multifaceted connections, such as the estuary-nearshore-ocean complex (Boero *et al.*, 1996; Marleau *et al.*, 2010, Gounand *et al.*, 2014).

Organic matter, resource and energy transfers between estuaries and the neritic ecosystem or nearshore are driven by a wide set of factors, such as river flows, ocean currents, and species movements (Loreau, Mouquet and Holt, 2003; Varpe, Fiksen and Slotte, 2005; Bartley *et al.*, 2019). The latter being one of the most challenging factors to be analyzed since the frequency and intensity of these movements may vary according to environmental conditions and specific intrinsic characteristics (physiological tolerance and life cycle of different species). Furthermore, the nature of this connection between ecosystems has some particularities that make analysis very difficult, with estuaries being typically used as nurseries by juveniles of marine species (da Silva and Fabré, 2019), and only adults of estuarine species migrating to the neritic environment (Passos *et al.*, 2016). This means that distinct components of fish populations are integrated into each ecosystem, with the meta-ecosystem mechanism being driving by the life cycle of species and resource flows (Gounand *et al.*, 2018). Yet, species migrations between these two ecosystems are extremely important, being key elements of trophic connections (da Silva and Fabré, 2019). Specifically, the expressive incoming of species causes rearrangements of food webs that can trigger significant changes in ecosystem functioning (Varpe *et al.*, 2005; Woodson *et al.*, 2018).

Even though these fish migrations are complex, many studies have shown that organisms movements may be driven or even facilitated by distinct changes in environmental conditions (Barletta-Bergan *et al.*, 2002; Blaber *et al.*, 1997; Lima *et al.*, 2014; Longhurst and Pauly, 1987). For instance, in the tropics, while photoperiod and temperature are relatively constant throughout the year, rainfall varies considerably and may trigger migrations, with repercussions on fish assemblages' structure (McConnell, 1962; Passos *et al.*, 2016). Rainfall frequency and volume intensify a process called "estuarization" - the expansion of estuarine condition to the neritic ecosystem (Barletta *et al.*, 2003; Blaber *et al.*, 1997; Krumme *et al.*, 2012; Longhurst and Pauly, 1987).

Depending on river flow and sediment discharge, the connectivity between these two ecosystems may even make it difficult to distinguish them (Longhurst and Pauly, 1987).

Estuarization (similar to the estuary offshore concept of McHugh (1967)), has been documented in many regions around the globe, including the Guiana shelf (McConnell, 1962) and the Gulf of the Mexico (Chittenden, 1976; Yanez-Arancibia, 1985). This process may affect oceanic ecosystems, depending on the extension of the continental shelf. It is estimated that in tropical oceans approximately 11x106 t/year-1 of sediment from freshwater systems is deposited in marine ecosystems, representing more than 83% of all sediments discharged into oceans worldwide (Longhurst and Pauly, 1987). These movements of water bodies, nutrients and sediments have huge impacts on productivity levels by increasing zooplankton activity that, in turn, attracts fish species from adjacent regions (Docmac *et al.*, 2017; García-seoane *et al.*, 2019; Nelson *et al.*, 2019; Polovina *et al.*, 2001).

In theory, changes in environmental conditions and food webs caused by estuarization could affect the control mechanisms (top-down or bottom-up), compromising the sustainability of functional groups (Gounand *et al.*, 2014). However, functional connectivity can also act as a stabilizer, allowing species to migrate between both ecosystems and balancing increases in population density (Spiecker *et al.*, 2016). For instance, in the Southwestern Atlantic, estuarization increases the functional diversity of fish assemblages in the neritic ecosystem (Passos *et al.*, 2016) and also boosts chlorophyll-a production and productivity levels (Neto *et al.*, 2014).

The aim of this work is to document the effects of seasonal estuarization events on the trophic structure of estuarine and tropical neritic ecosystems connected by biological and physical flows in space and time. Specifically, we evaluate trophic connectivity and the flow of fish species from the South Atlantic, based on the assumptions of meta-ecosystem functionality.

3.2 Material and Methods

3.2.1 Study area and sampling design

This study was carried out in the tropical southwestern Atlantic marine ecoregion, with a sampling design that covers a coastline of 192 km long in northeast Brazil (Fig. 1). The region is characterized by a narrow continental shelf (20–50 km) and two well-defined seasons driven by rainfall: a dry season from September to February, with mean pluviometry of 45 mm and a rainy season between March and August at which the mean pluviometry is 1800 mm. Water temperature in the area varies between 25°C and 31°C and salinity from 18 to 34 PSU. The continental slopes of 1:700 and 1:300 are reached at depths of 40 to 80 m (Araújo *et al.*, 2006).

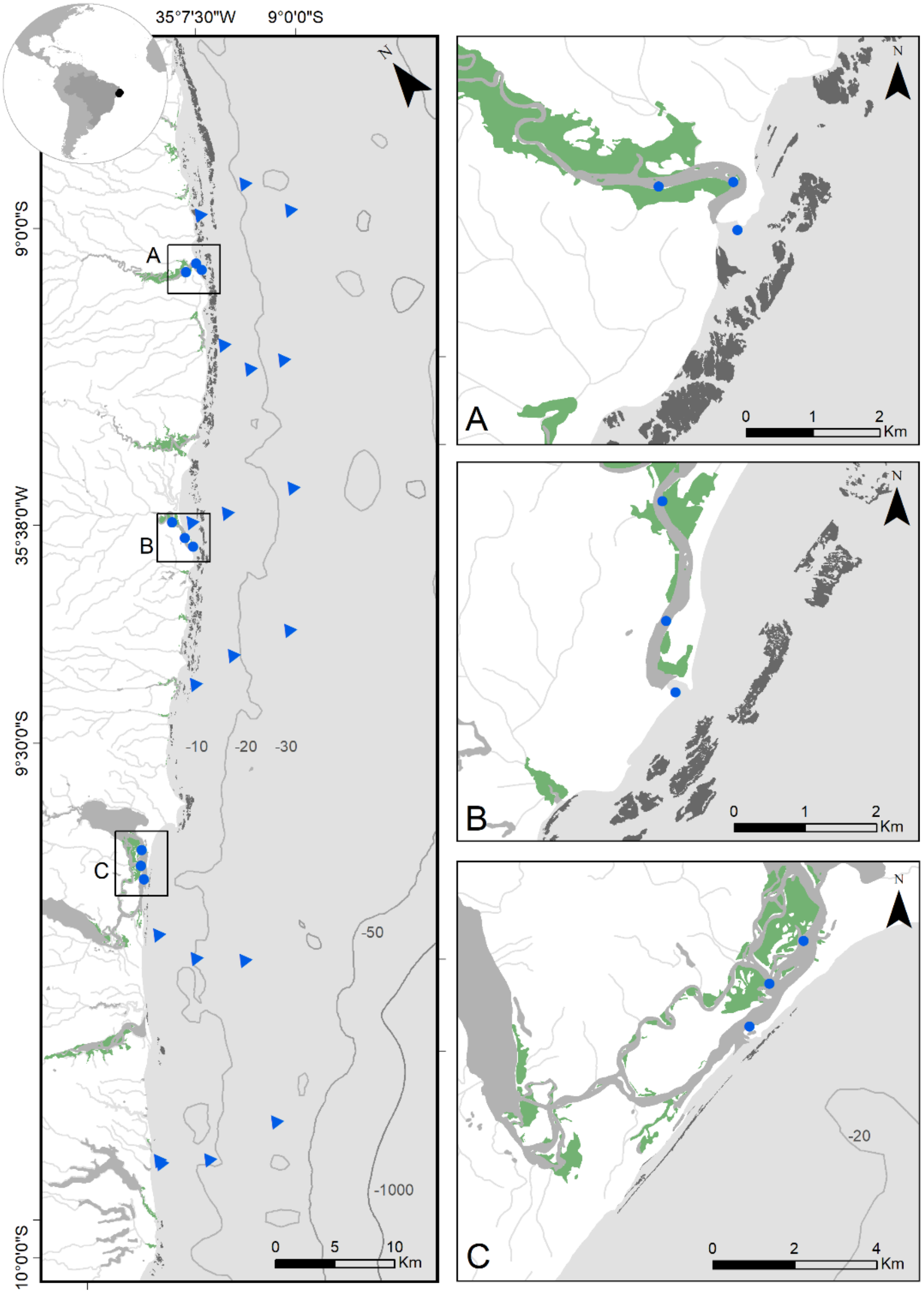

Figure 0-I- Neritic and estuarine areas (Brazilian Northeast). A, B and C are the three studied estuarine areas: the Manguaba river estuary, the Santo Antônio river estuary, and the Mundaú-Manguaba estuarine-lagoon complex, respectively. Isobaths of 10, 20, 30 and 50m are indicated. Triangles: sampling points in the neritic ecosystem; Circles: sampling points in estuarine ecosystems. The green color represents the mangrove forests.

This work considers the neritic ecosystem to be the entire sea length above the continental shelf (Garcia, 2003). However, our samples were restricted to isobaths between 10 and 30m deep. Considering that the continental shelf break occurs between 40 to 80 m isobaths, then our sampling area covers a considerable extent of the neritic ecosystem.

The neritic ecosystem is intensely irrigated by expressive hydrographic basins, whose flows subsidize the transport and accumulation of sediments on the continental shelf. In the study area, 19 rivers flow into the neritic ecosystem (Araújo *et al.*, 2010). This causes sediment deposits that allow the formation of dunes, sandbanks, and mangroves (Araújo *et al.*, 2010). Among the most important freshwater systems in the area we could highlight, from north to south, the Manguaba (787 km²) and Santo Antônio (929 km²) rivers, the Mundaú-Manguaba estuarine-lagoon complex (23,122 km²) and the São Francisco River (639,219 km²) (Santos, 1996). These systems influence the neritic ecosystem through a column of sediments that can extend from 2 to 10 km parallel to the beach line and from 4 to 20 km towards the ocean (Santos, 1996).

3.2.2 Data collection

To analyze and compare the food web structure in estuarine and neritic ecosystems, we used standard sampling equipment and a fishing effort to quantify trophic group's biomass in each ecosystem during the dry and rainy season. In each estuary, six sampling stations were established, resulting in 18 sampling stations that were sampled for a fixed time of five minutes, using 2 m high seine nets of 12 mm mesh size. In the neritic ecosystem, we established six stations in each section of the region, resulting in 18 sampling stations distributed in isobaths of 10, 20, and 30 m deep (Fig. 1). In this system, the fish assemblages were sampled by ten linked nylon gillnets connected by ropes in an arrangement 100 m long and 2.9 m high, with 20 to 80 mm meshes randomly located along the chain.

Sampled fish were stored in ice and taken to the laboratory where individuals were identified at species level following regional taxonomic keys (Figueiredo and Menezes, 1978, 1980; Menezes and Figueiredo, 1980, 1985). Each fish was weighted and had its stomach removed, weighed, and stored in labeled vials with formalin (4%). Gut contents were gravimetrically analyzed with the help of a stereoscopic microscope using a precision scale (0.001 g precision), with each food item being identified to the lowest possible taxonomic level.

3.2.3 Diet analysis

To evaluate the relative importance of food items for each species, we used the gravimetric method, measuring the frequency of occurrence Fi% and total weight Wi% of items, using their wet weight (Hyslop, 1980). We then used this information to calculate the feeding index (Fix; Kawakami and Vazzoler, 1980) which is the product of Fi% and Wi%. Each food item was characterized based on the most representative taxonomic level: (1) macroalgae; (2) sessile invertebrates; (3) Platyhelminthes; (4) Trematoda; (5) Annelida; (6) Sipuncula; (7) Polychaeta; (8) Gastropoda; (9) Bivalvia, (10) Scaphopoda; (11) Cephalopoda; (12) other molluscs; (13) Decapoda; (14) Isopoda; (15) Amphipoda; (16) other crustaceans; (17) Hexapoda; (18) Ophiroidea; (19) Asteroid; (20) other echinoderms; (21) Osteichthyes; (22) scales; (23) fish eggs; (24) detritus and (25) sediments. The Trophic Level values of these categories are based on literature (Table SM 3) and were used to estimate the trophic level of each fish species using the following equation:

$$TL=1+\sum \text{▒} 〖(\text{feeding index} \times \text{TL of prey}〗)$$

where:

feeding index = feeding index based on gut content; TL of prey = based on literature (Table SM3)

Species classification into guilds

Identified species were classified into the trophic guilds defined by Elliott *et al.* (2007) according to their diet: Zooplanktivore (ZP) – feeding predominantly on zooplankton (e.g. hydroids, planktonic crustaceans, fish eggs/larvae); Detritivore (DV) – feeding predominantly on detritus and/or microphytobenthos; Herbivore (HV) – Grazing predominantly on living macroalgal and macrophyte material or phytoplankton; Omnivore (OV) – Feeding predominantly on filamentous algae, macrophytes, periphyton, epifauna and infauna; Piscivore (PV) – Feeding predominantly on finfish but may include large nektonic invertebrates; Zoobenthivore (ZB) – Feeding predominantly on invertebrates associated with the substratum, including animals that live just above the sediment (hyperbenthos), on the sediment (epifauna) or in the sediment (infauna); Opportunist (OP) – Feeding on such a diverse range of food that it cannot be readily assigned to one of the above categories.

We also categorized species based on how they use the estuarine and the neritic ecosystems. To guarantee uniformity, we compiled information about habitat use, migratory movements and dependency on ecosystems for each species to create six meta-ecosystem mobility guilds adapted from existing classification of fish species (Potter *et al.* 2015): Freshwater Migratory (FWM) – freshwater fish that can migrate to estuarine systems or even the neritic ecosystem such as estuarine and freshwater species; Common in Estuaries and Neritic Ecosystems (CEN) – species that are typically found in both ecosystems throughout their life cycle; Marine Migratory (MM) – marine fish that depend on estuaries to complete parts of their life cycle such as marine estuarine-dependent; Marine Estuarine-Opportunist (MEO) – marine species that occasionally enter estuaries, especially as juveniles; Reef Associated (REF) – fish that are strictly associated with reefs and do not depend on estuaries or oceanic ecosystems to complete their life cycle; Epipelagic (EPP) – species that are typical of epipelagic regions or found along the continental slope can migrate to coastal areas.

3.2.4 Data analyzes

The biomass of species found in different seasonal periods (dry and rainy) was estimated for the estuarine and neritic zones separately, considering the different sampling strategies used.

In estuaries, biomass was estimated from the total weight of each species divided by the total area covered by the drag in g/m². The area was estimated by the classical method of the swept area (Sparre and Venema, 1997) and adopting the fraction of the length of the upper hoist (X2 = 0.5), as suggested by (Pauly, 1983). For the neritic, biomass was estimated as the total weight of species divided by the network area (m²). We then estimate the relative biomass by dividing the absolute biomass of each species by the total biomass per season (dry and rainy).

Temporal and spatial changes in the biomass of each trophic level were tested by permutation analysis of variance (PERMANOVA) using the Bray-Curtis similarity measure and considering a 2-way crossed design for ecosystems (estuarine and neritic) and seasons (dry and rainy) (Anderson and Walsh, 2013). Significant results were further investigated by a post-hoc test using the function “pairwise.adonis” in the pairwiseAdonis package (Martinez Arbizu, 2020).

We used the derivative proposed by Loreau, Mouquet and Holt (2003) to describe the instantaneous change in nutrient stocks in compartment i in a ecosystem j. We aim to describe the dynamics of a state variable through time. Compartments may be defined at various levels of resolution, from that of entire trophic levels up to that of functional groups or species. Here we used fish compartments according to their trophic level in the dry and the rainy seasons.

This equation assumes a source-sink dynamic between compartments of different ecosystems, implying a meta-ecosystem connection. In this dynamic, it is assumed that there is mass conservation, which means that part of the biomass that is located within a given compartment of an ecosystem is incorporated into another ecosystem, using the equation:

〖dX〗_ij/dt=∑_k▒F_ikj -∑_k▒F_ijk +G_ij

with F_ijj= 0 for all i and j.

We assumed local mass conservations in the absence of spatial flows and local growth rates were set to 0:

∑_i▒G_ij = 0

where:

F_ikj is the directed spatial flow of nutrients stored in compartment i from ecosystem k to ecosystem j. In this study, it represents the biomass (in absolute units g/m²) of the fish compartment (migrants herbivores, detritivores, benthivores and piscivores), produced in ecosystem k, which must be exported to ecosystem j in a given season.

F_ijk is the directed spatial flow of nutrients stored in compartment i from ecosystem j to ecosystem k. In this study, it represents the biomass (in absolute units g/m²) of the fish compartment (migrants herbivores, detritivores, benthivores and piscivores), produced in ecosystem j, which must be exported to ecosystem k in a given season;

G_ij measures the local growth rate of the state variable. Here we consider the biomass (in absolute units g/m²) that is produced and consumed in the ecosystem itself (non-migrants herbivores, detritivores, benthivores and piscivores).

The trophic structure of each ecosystem and station was approximated using the following variables: the relative biomass of each species (fish biomass/initial biomass of species i), and species' trophic level and guild of meta-ecosystem mobility. Although the total biomass of producers could not be estimated, producers found in the gut content of species were included in the trophic structure to indicate the energy sources for fish species (TL = 1 for producers, sediments and detritus). All possible predator-prey connections were recreated in the software Gephi®, which is typically used to identify interactions between connected entities (Ciribeli and Paiva, 2011).

3.3 Results

A total of 4054 individuals of 125 species, distributed in 42 families and 82 genera were collected during the study period (Tables SM4 and SM5). Sixty-seven of those species were exclusively captured in the estuarine ecosystem, while 40 species were only found in the neritic ecosystem, and 18 were common to both ecosystems. Most species from the estuarine ecosystem were exclusively found during the dry season (53%). In contrast, the highest numbers of individuals registered in the neritic area were captured during the rainy season (79%).

In the estuaries, *Sphoeroides testudineus* represented 90.9% of the total biomass alone during the rainy season, and *Mugil curema* was 73.8% of the total biomass during the dry season. Also, during the dry season, *S. testudineus* represented 12.26% of the total biomass, both species together add up to 86.1% of the total biomass. It is important to note that the rest of the species represented less than 1% of the total biomass (Table SM 4). In the neritic ecosystem, three species represent more than 20% of biomass (*Albula vulpes, Bagre marinus, and Lutjanus synagris*) in the dry season. Otherwise, in the rainy season, biomass was evenly distributed among species (Table SM 5).

Five meta-ecosystemic mobility guilds were identified in the study area, with extensive spatial-temporal variation in their biomass (Fig. 2). In the estuarine ecosystem, marine migratory fish (MM) and species common to both ecosystems (CEM) were the most representative guilds, but their dominance changed between seasons. In the estuaries, During the dry season, MM contributed with 81% of the relative biomass, while CEN only contributed with 14% of biomass. In the rainy season, the contribution of MM and CEN shifted, with 4% and 94% of biomass, respectively (Fig. 2; Table SM 4). In the neritic ecosystem, marine estuarine-opportunist (MEO) species were the most representative in terms of biomass, contributing with 83% and 45% of the total biomass during the dry and rainy season, respectively. The second most important guild in the neritic ecosystem was the epipelagic (EPP) guild, which contributed with 10% of the total biomass in the dry season, and 27% in the rainy season (Fig. 2; Table SM 5).

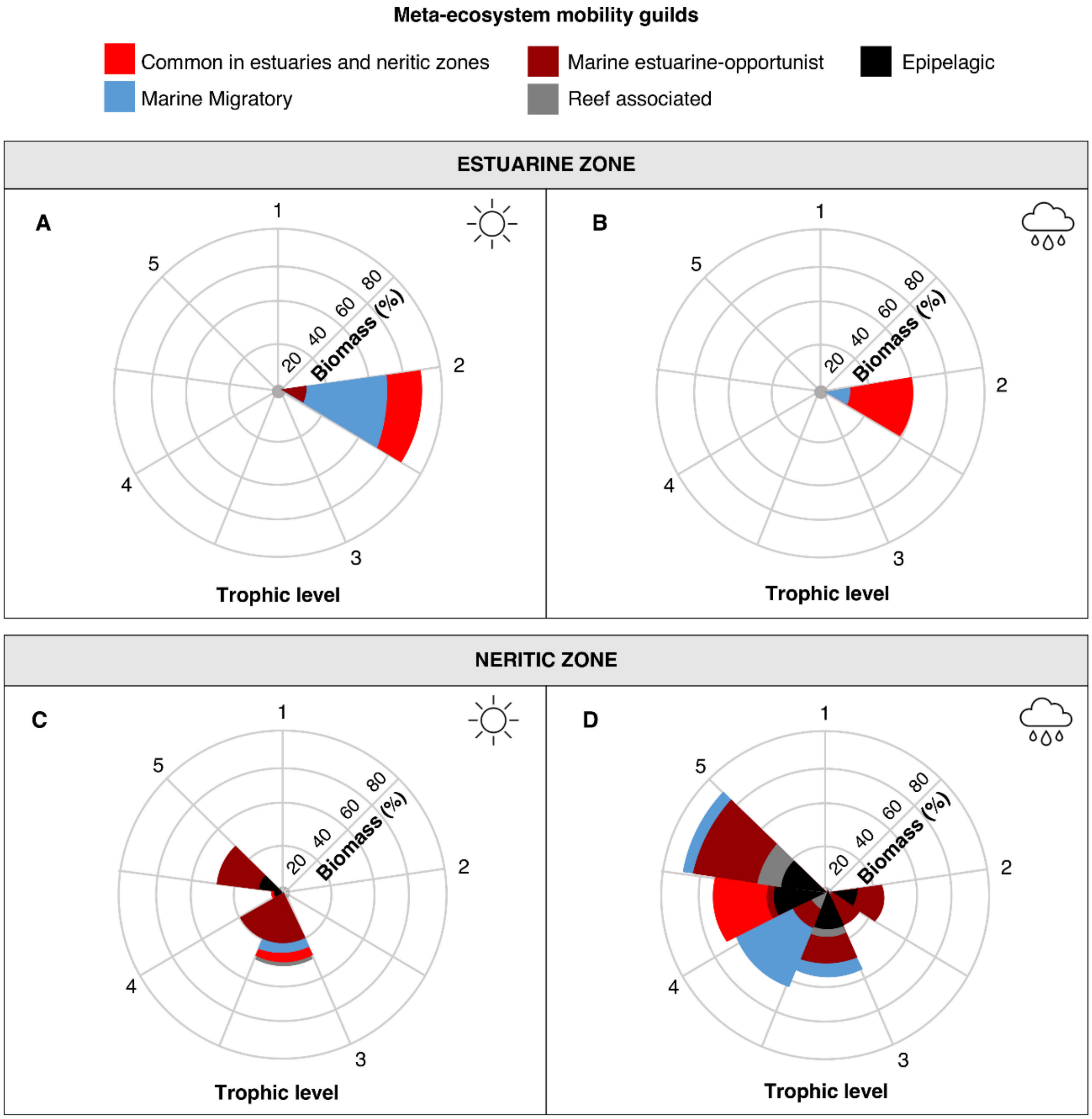

Figure 0-II- Seasonal variability of the relative biomass of meta-ecosystem mobility guilds per trophic level in the estuarine zone (A and B) and the neritic zone (C and D) of the tropical southwestern Atlantic.

Seven trophic guilds were identified based on species diet: zoo-planktivorous, detritivores, herbivorous, omnivores, piscivorous, zoo-benthivores and opportunists. In the estuaries, the detritivores were dominant in the dry season (82% of the total biomass) and zoo-benthivores in the rainy season (92% of the total biomass), reflecting the dominance of lower trophic levels species on this ecosystem (TL < 3) during both seasons ($p = 0.001$, Table 1). In the neritic ecosystem, the piscivore guild was the most representative during both seasons, contributing with 66% and 57% of the total biomass during the dry and the rainy seasons, respectively. (Fig. 3 and Table SM 7). Trophic level values of fish species in this ecosystem were typically greater than 3, especially during the rainy season with addition of carnivorous coastal and epipelagic species with TL higher than 4 ($p = 0.006$, Table 1 and $p = 0.003$, Table 2).

Table 1- PERMANOVA using Bray-Curtis similarity matrix for relative biomass of trophic guilds from fish species regarding ecosystems (estuary and neritic) and seasons (dry and rainy), in the tropical southwestern Atlantic. DF = Degree Freedom, F value and p values (in bold: $p < 0.05$).

Variation Source	**DF**	**F**	**p**
Ecosystems	**1**	**3.8136**	**0.001***
Season	**1**	**6.6646**	**0.001***
Interaction	**1**	**-11.548**	**0.001***
Residual	**38**		

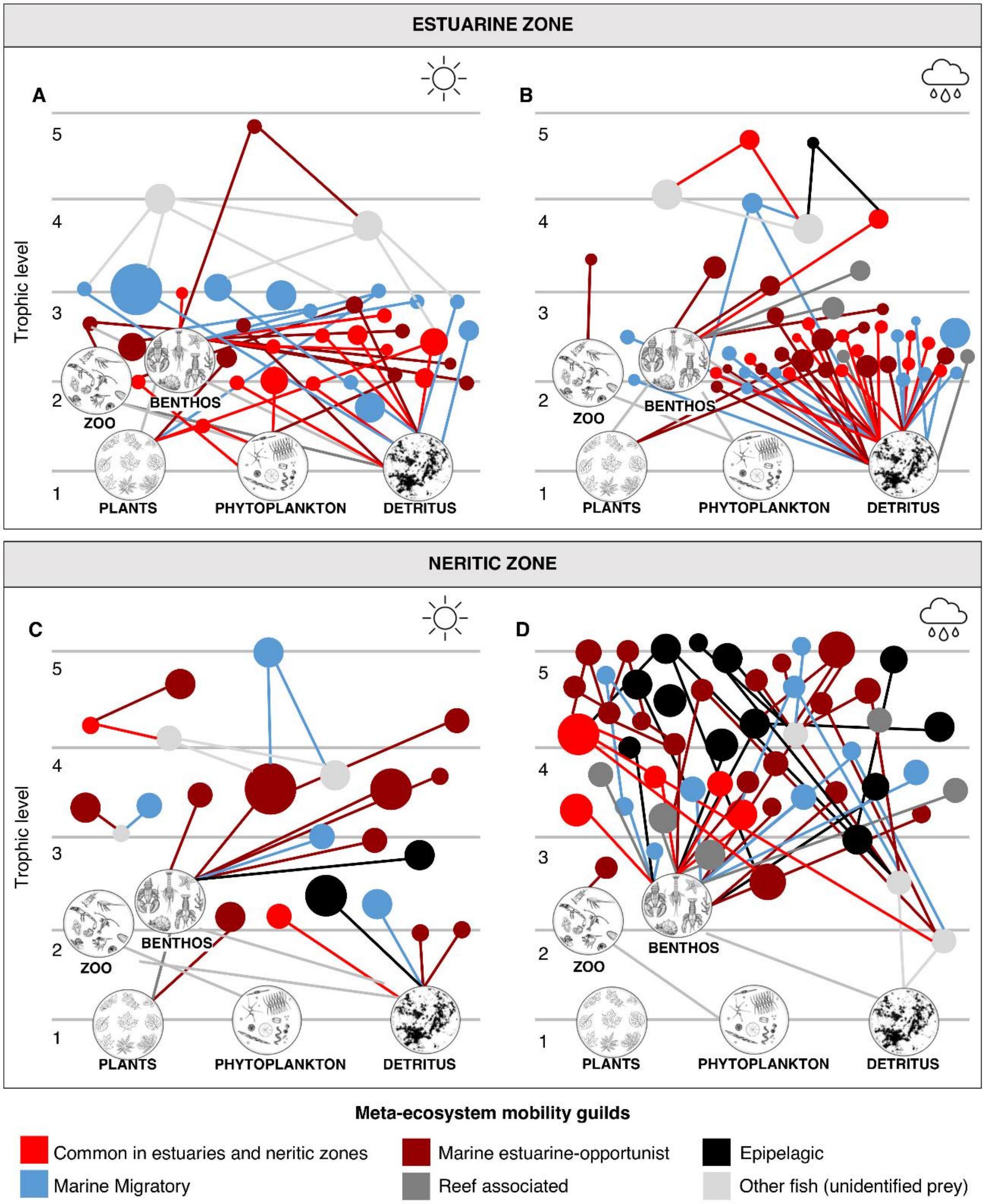

Figure 0-III- Seasonal variation in the trophic structure of the estuarine (A - dry season, B - rainy season) and neritic (C - dry season, D - rainy season) ecosystems in the tropical southwestern Atlantic based on the ichthyofauna diet and the temporal variation of the meta-ecosystem mobility guilds. Each circle represents one fish species, with its respective meta-ecosystem mobility guild (color), and its relative biomass (diameter of the circle) for each ecosystem and season.

Table 2 -

Table 2- P-values of the post-hoc PERMANOVA test using the Bray-Curtis similarity matrix for the relative biomass of trophic guilds from fish species across ecosystems (estuary and neritic) and seasons (dry and rainy). Asterisked values are significant (p<0.05).

Variation Source		**Estuarine zone**		**Neritic zone**	
		Dry	**Rainy**	**Dry**	**Rainy**
Estuarine zone	**Dry**	–			
	Rainy	0.866	–		
Neritic zone	**Dry**	0.204	0.327	–	
	Rainy	**0.001***	**0.003***	0.473	–

Our meta-ecosystem model showed the dynamics of biomass between the neritic and estuarine ecosystems in the dry and rainy seasons. The highest contributions of species in guilds associated with the estuarine and oceanic areas to the neritic ecosystem occurred during the rainy season, with the addition of MM, MEO and EPP species to the neritic trophic structure ($dXij/dt = +0.0055g/m^2$) (Fig. 4). On the other hand, the estuarine ecosystem showed an instant change in fish biomass due to reduced trophic levels during this season ($dXij/dt = -0.00010g/m^2$). In the dry season, an inversion occurs when several species return to their ecosystems of origin (neritic: $dXij/dt = -0.0053g/m^2$; estuary: $dXij/dt = +0.00012g/m^2$). The post-hoc tests by PERMANOVA and Friedman showed that the variation in biomass between ecosystems and seasons is related to the variation in trophic levels ($p = 0.001$, Table 1; $p = 0.001$ and $p = 0.003$, Table 2; $p = 0.003$, Table 3). This was also evident in the reconstruction of the trophic webs of these ecosystems (Fig. 3). The trophic structure of the neritic ecosystem showed a strong seasonal change in the diversity of trophic connections, with an increase of interactions during the rainy season, especially for species with trophic levels greater than 3 (Fig. 3). Specifically, we found that during the rainy season the number of carnivores and piscivorous increases in this ecosystem, boosting the consumption of benthic organisms.

Table 3- Friedman test to relative biomass of epipelagic fish from neritic ecosystem regarding different seasons, in the tropical southwestern Atlantic. DF=Degree Freedom, F value and p values (in bold: $p < 0.05$).

Effect	**DF**	**F**	**p**
Intercept	**1**	**5.31**	**0.032***
Habitat vs Seasonal Period	**1**	**5.18**	**0.003***
Error	**20**		

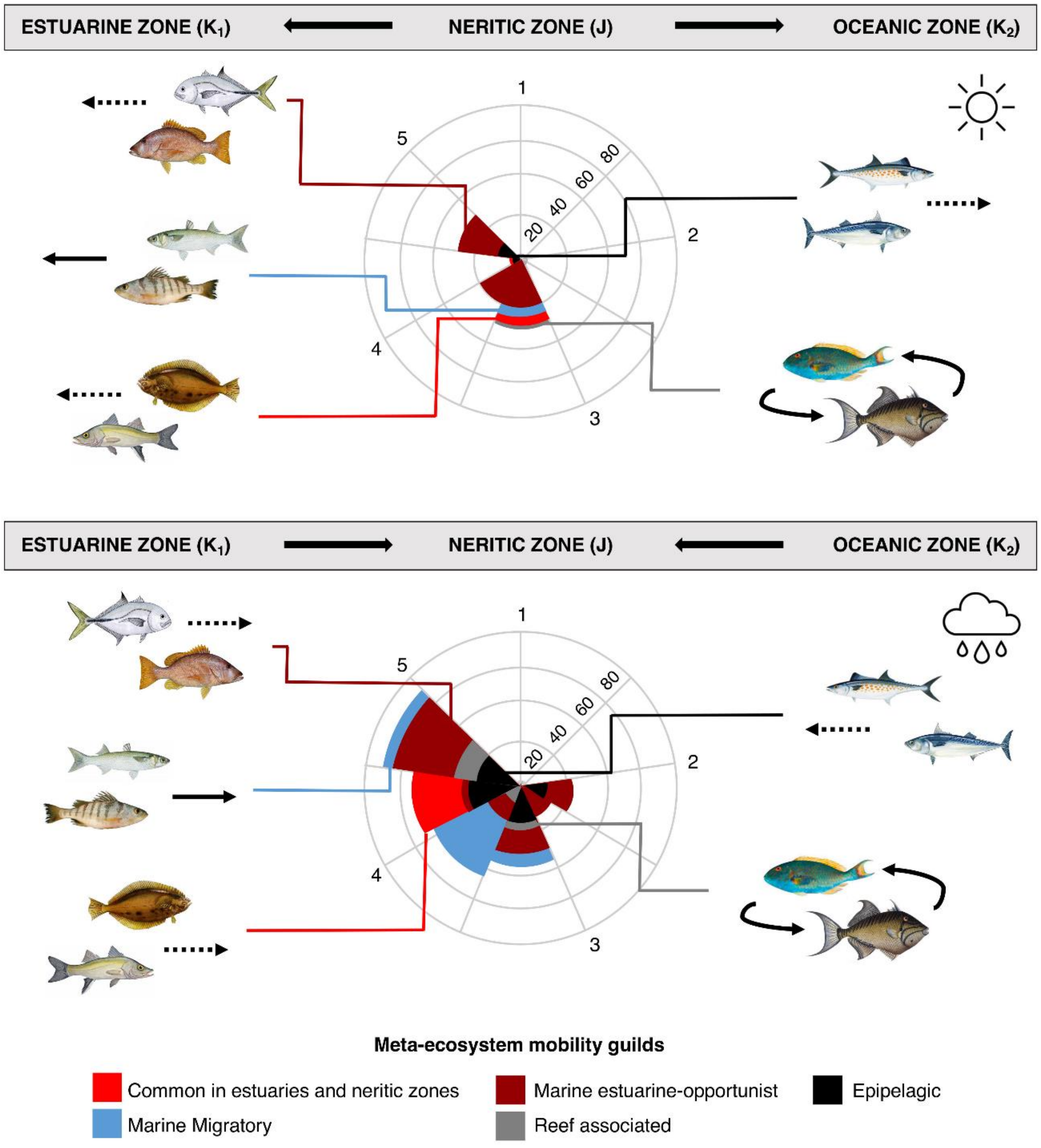

Figure 0-IV- Spatial and temporal variation of the relative biomass of fish species (20-80) classified into of meta-ecosystem mobility guilds in relation to their trophic level (1-5) in the southwest tropical Atlantic. The model represents the movement of fish (emigrants and immigrants) in the estuary-neritic-oceanic meta-ecosystem complex during the dry and rainy seasons. Continuous arrow indicates mandatory movement and dotted arrow represents occasional movement. K and J refer to the meta-ecosystem equation described in the material and methods section.

3.4 Discussion

Our results clearly show how rainfall regimes drive the distribution of estuarine and epipelagic groups in tropical neritic ecosystems. During the dry season, the estuarine and neritic ecosystems are both characterized by a simpler trophic structure in terms of biomass distribution among trophic levels. In the rainy season, the high migration of species associated to the estuarine and epipelagic zones alters the trophic structure of the neritic ecosystem (estuarization), increasing its complexity and predatory biomass. In contrast, there is a reduction in the biomass of carnivorous and piscivorous species in the estuaries, indicating that there is a dynamic source-sink between the ecosystems involved, with the estuaries acting as a source during the rainy season and sink during the drought. The reverse occurs in the neritic ecosystem.

In the neritic ecosystem, there are changes in the composition of guilds between seasons, with the input of estuarine species (i.e. Bagre bagre (Linnaers, 1766) and Opisthonema oglinum (Lesueur, 1818)) and top predators as epipelagic fish, Sphyrna lewini (Griffith and Smith, 1834) and Scomberomorus cavalla (Cuvier, 1829), during the rainy season. This pattern may be related to estuarization of the continental shelf which allows estuarine species to undertake migrations to the neritic ecosystem (Passos *et al.*, 2016), increases productivity (Neto *et al.*, 2014), and attracts epipelagic species from deeper regions. It is important to note that the narrow continental shelf in this region plays a significant role in the migration of both groups, especially for epipelagic species (Barletta-Bergan *et al.*, 2002; Barletta *et al.*, 2003; Lima *et al.*, 2014). These results indicate that the seasonal process of estuarization increases the movement of estuarine (da Silva, Dolbeth and Fabré 2021) and epipelagic species to the neritic ecosystem, enriching the trophic structure of this ecosystem and creating a trophic meta-ecosystem convergence.

One of the main features of a meta-ecosystem is that there are significant fluxes of resources and energy between distinct systems (Loreau, Mouquet and Holt, 2003) with the potential to affect productivity levels of both ecosystems. We show that trophic convergence acts mainly in the neritic ecosystem, increasing the number of trophic connections among the highest trophic levels (TL>3). This process facilitates energy transfers between both ecosystems supporting their food web structure. The high complexity of trophic structures may be an indicator of ecosystem maturity, which is associated with a great diversity of species, low niche specialization and resilience to extreme disturbances (Odum, 1968).

Our estuary-neritic-ocean complex may be classified as a meta-ecosystem based on resource flow, among adjacent ecosystems with distinct features (Gounand *et al.* 2018). The movement of fish species can be triggered by different factors, but in our model, migrations appear to be linked to two may factors: life-cycle requirements (Sciades herzbergii, Caranx spp., Lutjanidae) and foraging (Scomberomorus cavalla, Scomberomorus brasiliensis, Sphyrna lewinni). Between estuary and neritic ecosystem, there is a prevalence of life-cycle migrations, as many marine species (Table SM 4) use estuaries as nursery areas (da Silva *et al*., 2018; Nagelkerken *et al*., 2015). Several fish species leave the estuaries and return to the neritic ecosystem when they are larger and older. These flows are often as temporally specific pulses and can be of a magnitude that constitutes a shift in the recipient community structure compared to otherwise prevailing local. Between the neritic ecosystem and the oceanic region, migrations are mainly related to the increasing productivity in the neritic area by the estuarization of the continental shelf, which triggers epipelagic species to undertake foraging migrations. To Gounand *et al.* (2018) for both types of movement, the asymmetry in animal activity constitutes an important net flow of resource from one ecosystem to another in addition to the consumption pressure organisms exert where they are.

The addition of top predators to the neritic ecosystem could cause top-down pressures in the region, although the simultaneous addition of estuarine and benthivore species will have a stabilizing effect. To test this hypothesis is necessary to understand the spatial and temporal dynamics of all components of the trophic structure (Pace *et al.*, 1999), and our meta-ecosystem model showed that the inclusion of estuarine and epipelagic species had a positive effect in the neritic ecosystem by increasing the total biomass of the neritic ecosystem.

Organic matter transfers between local ecosystems are an additional sum of flows that probably contributes to total system throughput (Ulanowicz, 1980). In this case, part of an ecosystem's energy will subsidize the increase in the maturity of another ecosystem because this, the meta-ecosystem persists. The seasonality of this subsidy allows the components of the trophic network to have enough energy to complete their life cycle, even in the season with lowest inputs. The emigration of species makes it possible to establish new energy connections when they are incorporated into other food webs (Varpe *et al.*, 2005).

Our results indicate that fish species flow between local ecosystems and among different seasons is important for the integrity of connected ecosystems. Further studies with the standardization of capture strategies would be necessary to provide new insights into the observed dynamics. Our study highlights the importance of estuaries and seasonality for the maintenance of fishing productivity and by extension, suggests that this important meta-ecosystem may be particularly vulnerable to the impact of climate anomalies (e.g. droughts).

3.5 Acknowledges

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3.7 Supplementary Material

Supplementary Tabel 1 - Temporal-Spatial variation or relative biomass of fish species classified in meta-ecosystem mobility guilds captured in the estuarine ecosystem. TL = Trophic Level values; TG= Trophic guilds (zoo-planktivorous (ZP), detritivores (DV), herbivorous (HV), omnivores (OV), piscivorous (PV), zoobentivores (ZB) and opportunists (OP) in Northeast Brazilian coast between 2017 July and 2018 June.

META-ECOSYSTEM MOBILTY GUILDS	**SPECIES**	**RELATIVE BIOMASS %**		**TL**	**TG**
		Dry	**Rainy**		
	Genyatremus luteus	0.00	0.00	3.5	ZB
	Achirus declivis	0.00	0.00	4.1	PV
	Achirus lineatus	0.07	0.29	3.5	DV
Common in Estuarine and Neritic Systems (CEN)	*Aconthostracian polygonius*	0.00	0.00	3.4	ZB
	Archosargus probatocephalus	0.00	0.00	3.5	ZB
	Archosargus rhomboidalis	0.00	0.02	2.0	OV
	Bairdiella ronchus	0.05	0.10	2.0	DV
	Bathygobius soporator	0.17	0.46	2.6	DV
	Bothus robinsi	0.00	0.00	3.7	ZB
	Calamus pennatula	0.03	0.00	2.0	DV
	Cantherhines pullus	0.00	0.00	2.6	OV
	Cathorops spixii	0.38	0.88	2.0	HV
	Centropomus parallelus	0.42	0.04	4.0	OP
	Cephalopholis fulva	0.00	0.00	4.1	PV
Common in Estuarine and Neritic Ecosystems (CEN)	*Chilomycterus spinosus spinosus*	0.06	0.00	2.0	HV
	Diapterus auratus	0.04	0.32	2.0	DV
	Eugerres brasilianus	0.15	0.00	2.0	HV
	Genyatremus luteus	0.00	0.00	3.5	ZB
	Gobionellus oceanicus	0.00	0.14	2.0	DV
	Lagodon rhomboides	0.06	0.00	4.4	PV

META-ECOSYSTEM MOBILTY GUILDS	SPECIES	RELATIVE BIOMASS %		TL	TG
		Dry	Rainy		
Common in Estuarine and Neritic Systems (CEN)	*Odontesthes bonariensis*	0.02	0.00	2.0	DV
	Ophioscion punctatissimus	0.01	0.08	2.0	DV
	Pseudupeneus maculatus	0.00	0.00	2.0	DV
	Sciades herzbergii	0.35	1.04	2.0	DV
	Sphoeroides greeleyi	0.45	0.03	2.6	ZB
	Sphoeroides testudineus	12.26	90.90	2.6	ZB
	Strongylura timicu	0.12	0.00	4.5	PV
	Syacium papillosum	0.00	0.00	3.0	ZB
Total CEN		**14.66%**	**94.30%**		
Epipelagic (EPP)	*Aluterus monoceros*	0.00	0.00	3.0	ZB
	Anchoviella lepidentostole	0.01	0.00	3.1	ZB
	Atherinella brasiliensis	0.72	0.66	2.0	OP
	Caranx bartholomaei	0.00	0.00	4.5	PV
	Opisthonema oglinum	0.00	0.00	2.1	DV
	Sardinella brasiliensis	0.00	0.00	2.0	DV
	Scomberomorus brasiliensis	0.00	0.00	5.0	PV
	Sphyraena barracuda	0.00	0.00	4.4	PV
Total EPP		**0.73%**	**0.66%**		
Marine Estuarine-Opportunist (MEO)	*Acanthurus coeruleos*	0.00	0.09	2.0	DV
	Albula nemoptera	0.00	0.00	3.2	ZB
	Albula vulpes	0.42	0.00	2.0	ZB
	Anchoa lyolepis	0.00	0.00	3.4	ZB
	Bagre marinus	0.00	0.00	4.8	PV
	Caranx crysos	0.01	0.00	5.0	PV
	Caranx hippos	0.00	0.00	4.9	PV
	Caranx latus	0.13	0.00	2.0	DV
	Chirocentrodon bleekerianus	0.00	0.00	3.3	OP
	Chloroscombrus chrysurus	0.00	0.00	2.9	DV

META-ECOSYSTEM MOBILTY GUILDS	SPECIES	RELATIVE BIOMASS %		TL	TG
		Dry	Rainy		
Marine Estuarine-Opportunist (MEO)	*Citharichthys arenaceus*	0.08	0.00	3.5	ZB
	Citharichthys spilopterus	0.04	0.00	2.5	DV
	Harengula clupeola	0.41	0.05	2.0	DV
	Larimus breviceps	0.01	0.17	2.0	DV
	Lutjanus apodus	0.12	0.00	3.2	ZB
	Lutjanus griseus	0.00	0.11	2.0	OP
	Lutjanus jocu	0.99	0.00	2.0	DV
	Menticirrhus americanus	0.00	0.00	2.0	DV
	Menticirrhus littoralis	0.20	0.00	2.0	HV
	Oligoplites palometa	0.00	0.18	3.9	OP
	Oligoplites saliens	0.00	0.02	2.0	DV
	Paralonchurus brasiliensis	0.01	0.00	2.0	HV
	Polydactylus virginicus	0.03	0.11	2.0	HV
	Pomadasys corvinaeformis	0.00	0.07	2.0	DV
	Pseudobatos percellens	0.00	0.00	2.0	DV
	Selene vomer	0.01	0.00	3.6	ZV
	Sphyraena guachancho	0.00	0.00	4.2	PV
Marine Estuarine-Opportunist (MEO)	*Symphurus plagusia*	0.00	0.01	2.0	DV
	Trachinotus goodei	0.12	0.00	2.0	DV
Total MEO		**2.60%**	**0.82%**		
Marine Migratory (MM)	*Bagre bagre*	0.00	0.00	3.5	ZB
	Centropomus pectinatus	0.04	0.00	4.0	OP
	Centropomus undecimalis	1.56	1.06	2.0	HV
	Cetengraulis edentulus	0.08	0.18	2.0	DV
	Chaetodipterus faber	0.03	0.07	3.5	ZB
	Conodon nobilis	0.10	0.00	2.0	HV
	Cynoscion acoupa	0.00	0.05	2.0	DV
	Diapterus rhombeus	0.11	0.00	2.0	DV

META-ECOSYSTEM MOBILTY GUILDS	**SPECIES**	**RELATIVE BIOMASS %**		**TL**	**TG**
		Dry	**Rainy**		
Marine Migratory (MM)	*Eucinostomus argenteus*	1.35	0.00	2.0	HV
	Eucinostomus gula	2.47	0.56	3.0	ZB
	Eucinostomus melanopterus	0.12	0.19	2.0	DV
	Lycengraulis grossidens	0.64	0.00	2.0	HV
	Mugil curema	73.80	0.64	2.0	DV
	Mugil curvidens	0.10	0.00	2.0	DV
	Mugil liza	0.00	0.42	2.0	DV
	Mugil rubrioculus	0.21	0.01	2.0	DV
	Stellifer brasiliensis	0.01	0.10	2.0	DV
	Stellifer rastrifer	0.00	0.09	2.0	DV
	Strongylura marina	0.48	0.38	4.2	PV
	Symphurus tessellatus	0.00	0.01	2.0	DV
	Symphurus jenynsi	0.00	0.03	2.0	DV
	Trinectes microphthalmus	0.00	0.01	2.0	DV
	Trinectes paulistanus	0.00	0.39	2.0	DV
Total MM		**81.11%**	**4.18%**		
Reef Associated Fish (RAF)	*Balistes capriscus*	0.00	0.00	3.5	ZB
	Balistes vetula	0.00	0.00	3.8	ZB
	Bothus ocellatus	0.00	0.00	3.8	ZB
	Citharichthys macrops	0.07	0.00	2.0	DV
	Dactylopterus volitans	0.00	0.00	3.0	ZB
	Halichoeris poeyi	0.07	0.00	3.7	ZB
Reef Associated Fish (RAF)	*Hemiramphus brasiliensis*	0.02	0.00	2.0	HV
	Hippocampus erectus	0.02	0.00	3.5	ZB
	HIppocampus reid	0.05	0.00	3.5	ZB
	Hyporhamphus unifasciatus	0.25	0.00	2.0	HV
	Prionotus punctatus	0.00	0.00	3.0	ZB
	Sparisoma axillare	0.07	0.00	2.0	HV

META-ECOSYSTEM MOBILTY GUILDS	**SPECIES**	**RELATIVE BIOMASS %**		**TL**	**TG**
		Dry	**Rainy**		
Reef Associated Fish (RAF)	*Sparisoma chrysopterus*	0.15	0.00	2.0	HV
	Sparisoma rubripinnes	0.19	0.00	2.0	HV
	Synodus intermedius	0.00	0.00	3.0	ZB
	Trachinotus falcatus	0.01	0.04	2.0	DV
	Ulaema lefroyi	0.01	0.00	3.5	ZB
Total RAF		**0.90%**	**0.04%**		
GRAND TOTAL		**100.00%**	**100.00%**		

Supplementary Tabel 2 - Temporal-Spatial variation or relative biomass of fish species classified in meta-ecosystem mobility guilds captured in the neritic ecosystem. TL = Trophic Level values; TG= Trophic guilds (zoo-planktivorous (ZP), detritivores (DV), herbivorous (HV), omnivores (OV), piscivorous (PV), zoobentivores (ZB) and opportunists (OP) in Northeast Brazilian coast between 2017 July and 2018 June.

META-ECOSYSTEM MOBILTY GUILDS	**SPECIES**	**RELATIVE BIOMASS %**		**TL**	**TG**
		Dry	**Rainy**		
Common in Estuarine and Neritic Ecosystems (CEN)	*Genyatremus luteus*	0.00	0.00	3.5	ZB
	Achirus declivis	0.18	0.00	4.1	PV
	Aconthostracian polygonius	1.36	0.00	3.4	ZB
	Archosargus probatocephalus	0.00	0.01	3.5	ZB
	Archosargus rhomboidalis	0.00	0.00	2.0	OV
	Bothus robinsi	0.17	0.00	3.7	ZB
	Cantherhines pullus	0.00	0.00	2.6	OV
	Cathorops spixii	0.00	11.90	4.1	HV
	Centropomus parallelus	0.00	0.00	4.0	OP
	Cephalopholis fulva	0.94	0.00	4.1	PV
	Sphoeroides testudineus	0.00	0.01	3.4	ZB
Total CEN		**2.64%**	**11.92%**		
Epipelagic (EPP)	*Aluterus monoceros*	0.00	4.57	3.0	ZB
	Anchoviella lepidentostole	0.00	0.07	3.1	ZB
	Atherinella brasiliensis	0.00	2.11	2.0	OP
	Auxis thazard	2.45	6.78	4.4	PV
	Caranx bartholomaei	0.00	0.30	4.5	PV
	Opisthonema oglinum	0.00	4.78	4.2	OP
	Scomberomorus brasiliensis	8.18	4.83	5.0	PV
	Scomberomorus cavalla	0.00	2.95	5.0	PV
	Selar crumenophthalmus	0.00	0.07	3.8	ZB
	Sphyrna lewinni	0.00	0.24	5.0	PV

META-ECOSYSTEM MOBILTY GUILDS	SPECIES	RELATIVE BIOMASS %		TL	TG
		Dry	Rainy		
	Symphurus trewavasae	0.00	0.01	4.0	OP
	Trachinocephalus myops	0.00	0.15	4.4	PV
	Upeneus parvus	0.00	0.03	4.0	OP
Total EPP		**10.62%**	**26.88%**		
Marine Estuarine-Opportunist (MEO)	*Acanthurus coeruleos*	0.00	0.00	2.0	DV
	Albula nemoptera	2.14	0.42	3.2	ZB
	Albula vulpes	23.87	3.52	3.2	ZB
	Anchoa lyolepis	0.00	0.00	3.4	ZP
	Bagre marinus	25.51	8.15	4.8	PV
	Caranx crysos	0.00	6.82	5.0	PV
	Caranx hippos	0.00	0.54	4.9	PV
	Caranx latus	0.00	0.85	3.1	DV
	Chirocentrodon bleekerianus	0.00	0.01	3.3	OP
	Citharichthys arenaceus	0.00	0.00	3.5	ZB
	Cynoscion virescens	0.00	5.26	5.0	ZB
	Lagocephalus laevigatus	0.00	0.00	4.1	PV
	Larimus breviceps	0.00	2.97	3.3	ZB
	Lutjanus griseus	0.00	0.03	3.5	OP
	Lutjanus synagris	28.99	0.73	4.2	PV
	Menticirrhus americanus	0.00	0.72	5.0	DV
	Menticirrhus littoralis	0.00	0.57	3.9	HV
	Oligoplites palometa	0.00	0.00	3.9	OP
Marine Estuarine-Opportunist (MEO)	*Oligoplites saurus*	0.00	0.68	3.6	ZB
	Peprilus paru	0.00	0.02	4.5	PV
	Pseudobatos percellens	0.00	0.35	3.6	DV
	Rhizoprionodon lalandii	3.05	5.74	4.0	ZB
	Rhizoprionodon porosus	0.00	0.18	4.9	PV
	Selene setapinnis	0.00	0.12	4.7	PV

META-ECOSYSTEM MOBILTY GUILDS	SPECIES	RELATIVE BIOMASS %		TL	TG
		Dry	Rainy		
	Sphyraena guachancho	0.00	0.86	5.0	PV
	Syacium micrurum	0.00	6.44	3.7	HV
Total MEO		**83.55%**	**44.97%**		
Marine Migratory (MM)	*Bagre bagre*	2.62	0.91	3.5	ZP
	Centropomus pectinatus	0.00	0.00	4.0	OP
	Cetengraulis edentulus	0.00	0.13	5.0	DV
	Chaetodipterus faber	0.00	0.40	3.5	ZP
	Conodon nobilis	0.00	1.04	3.8	HV
	Cynoscion jamaicensis	0.00	0.36	5.0	PV
	Eucinostomus gula	0.56	0.00	3.0	ZB
	Lycengraulis grossidens	0.00	0.05	4.7	HV
	Micropogonias furnieri	0.00	9.29	3.6	ZB
	Stellifer brasiliensis	0.00	0.21	3.0	DV
	Symphurus tessellatus	0.00	0.01	3.7	DV
	Umbrina coroides	0.00	0.87	3.0	ZB
Total MM		**3.18%**	**13.27%**		
Reef Associated Fish (RAF)	*Balistes capriscus*	0.00	0.22	3.5	BV
	Balistes vetula	0.00	0.64	3.8	ZB
	Bothus ocellatus	0.00	0.12	3.8	ZB
Reef Associated Fish (RAF)	*Fistularia tabacaria*	0.00	1.74	5.0	PV
	Priacanthus cruentatus	0.00	0.05	3.9	ZB
	Prionotus punctatus	0.00	0.19	3.0	ZB
Total RAF		**0.00%**	**2.96%**		
GRAND TOTAL		**100.00%**	**100.00%**		

Supplementary Tabel 3 - Trophic level of prey categories that make up the predator diet based on the literature. The TL values described for prey here were used to estimate the predators' TL.

TAXONOMIC GROUP	TROPHIC LEVEL (TL)	REFERENCE
Epiphyton	1,00	Lira *et al.* (2018)
Microphytobenthos	1,00	Lira *et al.* (2018)
Other Phytoplankton	1,00	Pauly *et al.* (2000)
Benthic algae, peripheryton and terrestrial plants	1,00	Pauly *et al.* (2000)
Zooplankton	2,10	Angelini *et al.* (2018)
Sponges, tunicates and ascidians	2,00	Pauly *et al.* (2000)
Jellyfish and Hidroides	3,00	Pauly *et al.* (2000)
Other Cnidaria	2,50	Pauly *et al.* (2000)
Polychaeta	2,19	Lira *et al.* (2018)
Bivalve	2,00	Lira *et al.* (2018)
Gastropod	2,53	Angelini *et al.* (2018)
Other benthic invertebrates	2,50	Pauly *et al.* (2000)
Squid and sepia	3,50	Pauly *et al.* (2000)
Benthic copepods	2,00	Pauly *et al.* (2000)
Insects	2,20	Pauly *et al.* (2000)
Shrimp	2,32	Lira *et al.* (2018)

Crabs	2,93	Angelini *et al.* (2018)
Crayfish	3,20	Pauly *et al.* (2000)
Urchins	2,00	Pauly *et al.* (2000)
Starfish and ophiuroids	3,10	Pauly *et al.* (2000)
Sardine	2,56	Lira *et al.* (2018)
Mullet	2,02	Lira *et al.* (2018)
Flatfish	2,99	Lira *et al.* (2018)
Puffer	2,78	Lira *et al.* (2018)
Eucinostomus spp.	2,95	Lira *et al.* (2018)
Other Catfish	2,90	Lira *et al.* (2018)
Detritus, sediment, scales and eggs	1,00	Pauly *et al.* (2000)

Supplementary Tabel 4 - Spatio-temporal variation in the relative biomass of the different categories of trophic guilds identified (zooplanktivorous (ZP), detritivores (DV), herbivorous (HV), omnivores (OV), piscivorous (PV), zoobentivores (ZB) and opportunists (OP) in Northeast Brazilian coast between 2017 July and 2018 June.

	ESTUARY ZONE		**NERITIC ZONE**	
TROPHIC GUILD	**DRY**	**RAINY**	**DRY**	**RAINY**
ZB	13,09	92,30	33,76	32,44
DV	82,43	4,16	0,00	0,42
HV	3,09	2,15	0,00	2,15
OP	1,18	0,99	0,00	7,90
OV	0,00	0,02	0,00	0,03
PV	0,20	0,38	66,24	57,06
ZP	0,01	0,00	0,00	0,00
GRAND TOTAL	**100%**	**100%**	**100%**	**100%**

4 INFLUENCE OF TROPHIC CONNECTIVITY ON THE INDICATORS OF MATURITY IN TROPICAL COASTAL ECOSYSTEMS

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Abstract: Coastal marine ecosystems have structural and functional features usually connected by the seasonal transfer of nutrients and organisms. These organic matter and energy fluxes mean that these environments can utilize inter-ecosystem subsidies to increase resilience and, consequently, increase maturity. However, the nature of this connection and the mechanisms that enhance maturity are still poorly understood. Furthermore, the effects of seasonality on these processes have been little reported. Here we assess the effect of connectivity, marked by seasonality, on the characteristics and indicators of maturity in tropical coastal ecosystems. For that, we modeled the estuarine and neritic dynamics in the Tropical Southwest Atlantic, during the dry and rainy seasons, using the Ecopath software. Our results show inter-ecosystem movements of nutrients and organisms that produce structural and functional benefits to those involved. The joint analysis of the ecological indicators of productivity, ascendency, overhead and energy flow, shows that the dry season is the most stressful period for both ecosystems; however, estuary and neritic ecosystems benefit from the exchange of components that reduce predatory pressure on specific groups, reducing competition and maintaining the energy flow necessary for the functioning of trophic webs. When the frequency and volume of rainfall intensify, the physicochemical conditions of the two ecosystems become similar (estuarization). This process strengthens the connectivity between them and the exchange of subsidies that improve the trophic quality of the two ecosystems, contributing to the increase of maturity.

Keywords: meta-ecosystems; trophic connection; ecosystem development; estuarine fish; EwE

4.1 Introduction

One of the classic paradigms of traditional ecology is the assumption that ecosystems are self-regulating units, following a linear trajectory that leads towards a state of stability, called climax (Clements 1936; Elton 1927; Tansley 1935; Lindeman 1942; Odum 1969). However, in this proposal each ecosystem is seen as an independent unit, which seeks to achieve individual stability. Disturbances, for instance, are not considered intrinsic properties of the system and always promote ecological imbalance (Viglio and Ferreira 2013).

The ecosystem view of Odum (1969), based on the ecological succession concept (Clements 1936), assumes a unidirectional process of homeostasis control, as production and consumption become equal. In this circumstance, the proximity of the climax state tends to stabilize the biomass, resulting in a complete stagnation of the system's net production. However, there is evidence that even when an ecosystem reaches its climax, the biomass does not stabilize. It instead continues to accumulate carbon indefinitely, keeping the system's net production high (Schulze *et al.* 2000; Zhou *et al.* 2006; Luyssaert *et al.* 2008; Luyssaert *et al.* 2011; Stephenson *et al.* 2014).

Another essential attribute advocated by Odum (1969) is the increase in the predictability of flows between ecosystem compartments as their development increases. This concept was summarized in a metric called ascendency (Ulanowicz 1986). For Odum (1969), in the absence of major external disturbances, systems would have a natural propensity to increase in ascendency. However, Christensen (1995) observed that ascendency was inversely correlated with a maturity ranking for 41 models of aquatic ecosystems. Furthermore, these cases' maturity was related to overhead, a metric that measures the unpredictability of the occurrence of flows or entropy increment. This means that the development of ecosystems would tend to increase in complexity and unpredictability.

Although controversial, some of Odum (1969) predictions are still heavily used to forecast the degree of ecosystem maturity, disregarding the emergent properties (Corman *et al.* 2018). Thus, it is essential to reassess the internal ecosystem processes that lead to maturity, considering external factors that can affect these processes and their metrics (Marleau, Guichard and Loreau 2014).

Marine ecosystems are highly interconnected, influencing each other. Estuaries and oceans, for example, are linked by multifaceted connections in neritic regions, especially in areas where the continental shelf is shallow and narrow, as seen in some tropical coastal ecosystems. (Passos *et al.* 2016; Neto *et al.* 2015; Ferreira *et al.* 2015; Ferreira *et al.* al. 2019; da Silva and Fabré 2019; da Silva, Dolbeth and Fabré 2021). In these regions, the short distance between these systems, associated with seasonal processes such as currents and river flows, enable the movement of species and the transfer of organic matter and energy that subsidize the maturity process of these ecosystems (Loreau, Mouquet and Holt 2003; Varpe, Fiksen, and Slotte 2005; Bartley *et al.* 2019).

However, understanding how connectivity promotes maturity to tropical coastal ecosystems is a difficult challenge, due to the high dynamism of the organic matter, nutrients, and energy flows between different ecosystems, that may occur in a short period and under extreme conditions (Able 2005; Society 2012; Nagelkerken 2014; Sheaves 2014). In this sense, a convenient approach is using eco-trophic modeling as a tool to overcome these issues. These models are created to organize the understanding of systems, assess observed data, help understand the relationships between components, to define problems and make predictions (Fragoso Jr., Ferreira and Marques 2009; Trolle *et al.* 2012; Angelini *et al.* 2018).

Ecosystems' modeling can be used to answer important ecological questions, including the effect of seasonal variation or climate change on ecosystem maturity, as well as the occurrence of variations between alternative equilibrium states (May 1977; Knowlton 1992; Lira *et al.* 2018; Macedo *et al.* 2021). Ecopath with Ecosim (EwE) modelling approach, for example, allows us to understand the structural and functional organization of one or more ecosystems, through the flows of organic matter and energy between their trophic components (Heymans *et al.* 2014; 2016). Based on the dynamics of these flows, it is also possible to estimate a series of indicators of ecosystem status, which, added to the seasonality factor, can infer about the ecosystem's maturity (Gubiani *et al.* 2011, Capitani *et al.* 2021a).

The set of indicators generated from the EwE allows the assessment of the organization, complexity, productivity, and ecosystem efficiency (Ulanowicz 1986). This provides valuable insights into the state of ecosystems. Still, when seasonality is not considered a significant factor, it becomes inappropriate for attesting maturity because it induces the researcher to an inert view, when, in fact, maturity is determined by a set of highly dynamic processes (Gardner and Ashby 1970; Ulanowicz 1986; Heymans 2014; Coll and Steenbeek, 2017). Until now, ecosystem maturity indicators have been generated from ecopath tool, but without the inclusion of the seasonal factor (Wolff, Hartmann and Koch 1996; Wolff, Koch and Isaac 2000; Colléter *et al.* 2012; Villanueva 2015; Abdul and Adekoya 2016; Simon and Raffaelli 2016; Lira *et al.* 2018). For the first time, the assembly of trophic models, with the help of the EwE, allowed us to investigate how seasonal variation affects the performance of ecological indicators of two adjacent coastal ecosystems and connected by physical and biological flows.

In this paper, our objective was to evaluate the effect of trophic connectivity, driven by seasonality, on tropical coastal ecosystems' properties and maturity indicators. We investigate how seasonal variation affects productivity, ascendency, overhead, and energy flow of tropical coastal ecosystems under inter-ecosystem connectivity. We hope that the creation of dynamic models can provide new insights into ecosystem maturity and its components and be used as a simulation and predictability tool in the face of local and global environmental disturbances.

4.2 Material and Methods

4.2.1 Study area and sampling design

The present study took place in the marine ecoregion of the southwest tropical Atlantic, on a 52 km long stretch of coast in northeastern Brazil, in the marine protected area Costa dos Corais (Figure 1). This region has a narrow continental shelf (38 km) (Carneiro 2017), characterized by an extensive coral barrier, which occupies about 73% of the area. The choice of the area to compose the models was due to the short extension of the platform, combined with the incidence of expressive rivers that subsidize the transport and accumulation of sediments on the continental shelf (Araújo *et al.* 2006). Among the most important freshwater systems, from north to south, are the Manguaba watershed, with a drainage area of 787.2 km², and the Santo Antônio watershed, with a drainage area of 929.9 km² (Semarh 2014).

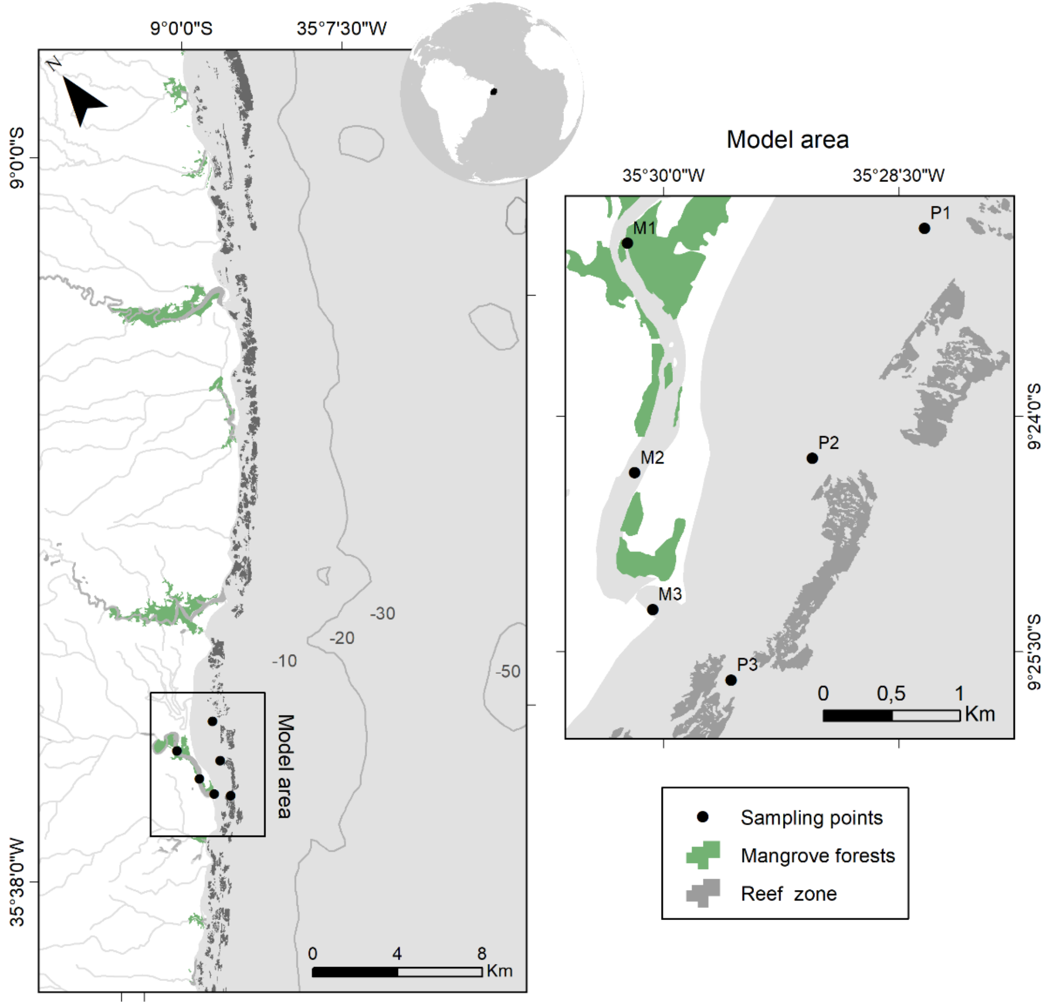


Figure 1- Delimitation of the sampling area in the Southwest Tropical Atlantic. The solid line represents the area of the models. M1, M2 and M3 are sampling points in the estuary. P1, P2 and P3 are sampling points on Neritic. 10, 20, 30 and 50m are isobaths.

There are two climatic seasons in the region defined by the rainfall regime: a dry season, from September to February, with an average annual rainfall of 45 mm, and a rainy season, from March to August, with an average annual rainfall of 2000 mm. The water temperature in the area varies between 25°C and 31°C during the rainy and dry seasons, respectively (Barros 2012). The mean salinity of the sea surface ranges from 18 to 35 between the wet and dry seasons, respectively. The greatest variations are observed between isobaths from zero to 10 meters (Woa 2021).

The neritic ecosystem is represented by the entire continental shelf (Garcia and Serge 2003), but our samples were obtained up to the 10m isobath. In this study, neritic and estuary were considered ecologically distinct ecosystems due to the physical-chemical and biotic components spatial variations and the ecological function that each one plays for the fish species (Passos *et al.* 2016; Neto *et al.* 2015; Ferreira *et al.* 2015; Ferreira *et al.* 2019; da Silva and Fabré 2019).

4.2.2 Mass balancing model

To analyze connectivity and seasonality effects on resource flow and trophic interactions, we use the Ecopath with Ecosim software (EwE 6.6.5; available at www.ecopath.org). We developed four Ecopath models: dry estuary, wet estuary, dry neritic, and wet neritic. An Ecopath model is based on linear equations involving production and consumption. These equations quantify the trophic flow between species and functional groups based on the premise that there is a mass balance in ecosystems. To express this balance, the model considers that: all biomass produced by species i (or a model compartment) minus biomass consumed by all predators minus biomass removed by other activities (capture, fishing, diseases, migration, etc.) is equal to zero (Polovina 1984; Christensen and Pauly 1992; Villy Christensen and Walters 2004).

B_i × 〖P/B〗_i × 〖EE〗_i −∑_(j=1)^n▒〖(Bj〗 × 〖Q/B〗_i × 〖DC〗_ji) – 〖EX〗_i = 0

where:

B_i represents the prey biomass (i); P/B_i is the biomass production of the compartment (i); 〖EE〗_i is the ecotrophic efficiency of (i) – which ranges from 0 to 1; Bj corresponds to the predator's biomass (j); Q/Bj is the predator's biomass consumption (j); 〖DC〗 ji is the prey biomass (i) found in the predator's diet (j); 〖EX〗_i represents the biomass captured by fishing and/or that migrates to other environments (Patrício and Marques 2006).

Ecopath can estimate one of four required parameter values (B, B/B, Q/B or EE) for each group. In this study, we let Ecopath estimate EE. Biomass was expressed in ton.km^{-2} and P/B and Q/B expressed in ton.km^{-2}.year^{-1} (Christensen and Pauly 1992).

4.2.3 Model components

The models were standardized and they have 14 trophic groups: two primary producer groups, one zooplankton compartment, two macro invertebrate groups, nine fish groups and one detritus group. The ichthyofauna was selected due to the importance of its biomass, relevance in fishing landings and representation in different mobility guilds. Species were grouped according to the trophic guilds described by Elliott *et al.* (2007), based on analysis of stomach contents.

4.2.4 Fish

Fish were captured in four sampling surveys, two during the dry season and two during the rainy season, between April 2019 and March 2020, with the help of local fishermen (Federal Scientific License for Fish Sampling 1,837,810). We defined six sampling stations, three in the estuarine region and three in the neritic region (Figure 1). At each station, we operate a trawl with 7 m long, 1.8 m of master rope length and 10 mm of mesh size, with the assistance of a motorized vessel, with an average trawl speed of 1.8 km/h, for a fixed time of 15 minutes. All captures were carried out during the quadrature tides and always against the current. We also record the initial and final geographic units of each trawl to assist in estimating the swept area.

The total coverage area by trawls in the estuarine and neritic ecosystems, in each season, was estimated at 2.63 km^2 and 3.48 km^2, respectively, using the swept area method (Sparre and Venema 1997) and adopting the effective upper haul length fraction in hauls ($X2 = 0.5$), as suggested by Pauly (1983). Fish biomass was estimated in two seasonal periods (dry and rainy), from the sum of the individual catch weights of each species divided by the total trawl coverage area per ecosystem, expressed in $t \cdot km^{-2}$.

In the estuarine ecosystem, samples were taken between the isobaths of two to five meters and in the neritic ecosystem, the samples were taken from the 10m isobath. At each sampling station, individuals were separated according to their morphotypes, cryo-anesthetized and taken to the Laboratory of Fish, Fisheries, and Ecology (LaEPP) at the Federal University of Alagoas (UFAL), where they were identified at species level with regional taxonomic keys (Menezes *et al.* 2003; Figueiredo and Menezes 2015; Nóbrega, Lessa and Santana 2009; Garcia Júnior *et al.* 2010) and later submitted to stomach content analysis (Freitas *et al.* 2011; Liao, Pierce and Larscheid 2011).

To minimize the sampling bias inherent to the capture method's selectivity, we used the catchability model proposed by Lauretta *et al.* (2013). The model considers the hydrodynamic shape of fish, based on the catchability coefficient q of each species.

$$p = q \times E \times A^{(-1)}$$

$$N = C \times p^{(-1)}$$

Where p is the average proportion of the population captured. This proportion can be obtained from the relationship between: q, that is the catchability coefficient; E, that is the fishing effort (total sampled area – km^2) and A, that is the model area in Km^2. C is the capture per unit area ($t \cdot km^{-2}$) and N is the final biomass corrected from the catchability model ($t \cdot km^{-2}$).

The biomass production rate (P/B), expressed in $ton.km^{-2}.year^{-1}$, was quantified from the natural mortality (M), using the empirical regression of Pauly (1980):

$$M = K^{(0,65)} \times [L_\infty]^{(-0,279)} \times T^{(0,463)}$$

Where M represents natural mortality (year^{-1}) or BP; K and $L\infty$ are the parameters of the von Bertalanffy equation (K = growth constant, expressed in year^{-1} and $L\infty$ = asymptotic length in cm); T corresponds to the ecosystem water temperature (°C). The parameters K and $L\infty$ were obtained from the literature, considering nearby locations. T was measured in situ and the mean temperature of the dry (31.0°C) and rainy (29.9°C) periods was considered.

The biomass consumption rate (Q/B) was estimated from the empirical regression of Palomares and Pauly (1998):

$$\log Q/B = 7{,}964 – 0{,}204 \times \log W\infty – 1{,}965 \times T' + 0{,}083 \times Ar + 0{,}532 \times H + 0{,}398 \times D$$

Where Q/B represents the annual consumption/biomass ratio; $W\infty$ is the asymptotic weight (estimated by the equation W∞ = a × 〚L∞ 〛^(b)); T' is the mean water temperature in Kelvin [1000 / (temperature in °C + 273.15)]; Ar corresponds to the caudal fin shape index [$Ar = h^2 / s$ (h – fin height in mm and s – fin surface in mm^2); H and D represent food type index, where: H = 1 for herbivores; D = 1 for detritivores and iliophages; H = D = 0 for carnivores and other food categories (Christensen and Pauly 1992).

4.2.5 Diet composition

The fish diet composition matrix was built from the analysis of stomach contents, using the Food Importance Index (IAi) as the basis. When the information was not available and for the other groups that constituted the model, the information was based on the literature (Table Supplementary 1).

4.2.6 Other compartments

In addition to the ichthyofauna, the groups that integrated the models were: macroalgae, phytoplankton, zooplankton, suspensivore and carnivores macroinvertebrates (Frame Supplementary 1). Phytoplankton biomass was estimated from field collections, simultaneously with fish sampling. The biomasses of macroalgae, zooplankton, filtering macroinvertebrates and carnivores were estimated by models based on the EE fixation.

Phytoplankton were collected with a 20µm net, measuring 1.00 m in length and 0.30 m in diameter at the mouth, with a collecting cup attached to the terminal portion of the net. The collected material was fixed with 4% neutral formalin and stored in glass flasks according to the methodology described by Caspers (1965) Their density was estimated (ind./m²) according to the method of Utermöhl (2017) and converted into biomass ($t \cdot km - ^2$), according to Cushing *et al.* (1958). P/B was estimated from the expression:

$$P/B = 20.19 \times TL{-}3.26 \times \exp(0.041 \times T)$$

Where TL is the trophic level of phytoplankton and T represents the mean annual seawater temperature (°C).

The micro invertebrate fauna was collected from sediment samples from the sampling stations, with the help of a dredger, measuring 25 cm in length and 15 cm of mouth opening, following standardized methodology (Gomes et al 2002; Netto and Gallucci 2003; Rosa- Filho *et al.* 2006). At each station, three samples of sediment were collected, later placed in labeled plastic bags and cryo-anesthetized. In the laboratory, the organisms were sorted and weighed. P/B was estimated from the multiparameter model of Brey (2012) and Q/B, estimated from the breathing equation proposed by Humphreys (1979).

4.2.7 Fishing landings

Additionally, we estimate the seasonal capture of the main types of fisheries operating in the model area from the Relative Catch-Per-Unit-Effort (CPUEr), considering different effort measures (Sparre and Venema 1997) and incorporate the results into the Mixed Impact Matrices (MTIs) (Frame 1). The Trophic Impact Matrix - MTI (Ulanowicz and Puccia 1990) allows analyze the direct and indirect impacts of a single functional group on the others, including fisheries. These groups are called impacting groups and variations in their biomass can promote: Positive Impact (if it causes an increase in the biomass of other groups called impacted) or Negative Impact (if it causes a reduction in the biomass of the impacted groups). This analysis allows the identification of groups of system keys quantified by the keystone index (KS3), developed by Valls *et al.* (2015). Keystone species is that which has a disproportionately large effect on its natural environment relative to its abundance (Paine 1969).

Frame 1- Effort Units used for CPUEr calculation (Sparre and Venema 1997).

Fishing gears	Unit of Effort
line and longline	Number of fishermen x day
gill net	Number of nets launched x days
Trawnet	Number of trawlers x day
shellfish fishing	Number of fishermen x hour
siege net	Net length x siege time

4.2.8 Validation, sensitivity and balancing of models

The models were considered ecologically and thermodynamically balanced when six fundamental criteria were met (Heymans *et al.* 2016): (1) EE <1 for all functional groups; (2) P / Q values (rate of production / consumption or efficiency feed conversion ratio – GE) with values between 0.1 and 0.35, except for some fast growing groups (Guénette 2015); (3) R / A (Respiration / assimilation of food) <1; (4) R / B (Respiration / Biomass) with values between 1 and 10 for fish and higher values for small organisms; (5) NE (Net feed conversion efficiency) > GE and; (6) P / R (Production / Respiration) <1 (Heymans *et al.* 2016) (Table Supplementary 2). Once these criteria were achieved, the reliability of the models was analyzed using the PREBAL, routine procedure recommended by Heymans *et al.* (2016) and based on general ecological principles. The PREBAL seeks to identify problems or attest to the reality of the models (Link 2010). Includes the relationship between the input parameters of each compartment (B, P/Q, P/B, and Q/B) and its trophic level through linear regression and F significance tests.

Finally, we calculated the pedigree index to quantify the degree of uncertainty related to each input value in the models (B, P/B, Q/B, diet and capture) (Christensen, Walters and Pauly 2005), ranging from 0 (low precision information) to 1 (data and parameters entirely based on local data) (Table Supplementary 3).

4.2.9 Comparisons between models

We performed a permutation of variance analysis (PERMANOVA) using the Bray-Curtis similarity measure, assuming the null hypothesis of spatial-temporal similarity between fish compartment biomass in the four investigated models (Anderson and Walsh, 2013). For that, we used the significance level of 0.05. Subsequently, we applied a percentage of similarity test (SIMPER) to identify the compartments that most contributed to total dissimilarities.

We estimated all ecosystem attributes available in the ecopath data package to investigate the possible stages of development of the four models in the study area and finally selected four of these indicators to compare our results with those of estuarine and neritic models from tropical, subtropical and temperate regions, available in the literature and in the EcoBase repository. Specifically, we selected 21 models: 12 estuarine (four per geographic area) and 9 neritic (three per geographic area) (Frame 2).

The selected indicators are related to: (1) Food web organization (A/C - Ascendency/Capacity), (2) Ecosystem reserve capacity (O/C - Overhead/Capacity), (3) Flows (TST - Total System Throughput) and (4) Productivity (TPP/TR - Primary Production/Total Respiration). We use these indicators to investigate whether the ecosystem indicators generated from our models for the dry and rainy seasons resemble models for other geographic zones. The four selected indices are known for their high robustness. According to Heymans *et al.* (2014), these indicators do not show collinearity and, therefore, are not influenced by the size of the trophic chains, being among the most suitable for evaluating the characteristics of ecosystems. the results was plotted using boxplots.

Frame 2- Models used for analysis of ecosystem development compared to our models.

Ecosystem Type	Climate Region	Source
Estuaries	Tropical	Lira *et al.* 2018
	Tropical	Ferreira *et al.* 2018
	Tropical	Xavier *et al.* 2013
	Tropical	Wolff *et al.* 2000
	Subtropical	Lercari *et al.* 2015
	Subtropical	Duan *et al.* 2009
	Subtropical	Lin et. *al*. 2016
	Subtropical	Han *et al.* 2007
	Temperate	Mutsert *et al.* 2012
	Temperate	Selleslagh *et al.* 2012
	Temperate	Rybarczyk *et al.* 2003
	Temperate	Lobry *et al.* 2008
Shelves and Seas	Tropical	Hermosillo-Núñez *et al.* 2019
	Tropical	Hermosillo-Núñez *et al.* 2019
	Tropical	Xavier *et al.* 2013
	Subtropical	Canziani *et al.* 2007
	Subtropical	Taylor *et al.* 2008
	Subtropical	Cox *et al.*1998
	Temperate	Torres *et al.* 2013
	Temperate	Essekhyr *et al.* 2019
	Temperate	Couce-Montero *et al.* 2015

4.3 Results

4.3.1 Model balancing

Four representative models of seasonal variation (dry and rainy seasons) in the estuary and neritic systems were built, and their balance was achieved by adapting the diet of some groups of fish that initially presented Ecotrophic Efficiency greater than one (EE > 1). EE value close to 0 means that the group is not consumed by another group in the system. If the EE value is close to 1 then the group is highly consumed by predators (another group) or caught by fishing activities (Ullah *et al.* 2012). We followed the assumptions based on the relationships between: Production / Consumption (P/Q), Respiration / Assimilation (R/A) and Respiration / Biomass (R/B) to assess the degree of reliability of the model, reaching acceptable ranges (Table 1).

Furthermore, the relationships between B, P/B and Q/B, evaluated using the PREBAL routine was significantly, and inversely, correlated to trophic levels (TL) (Figure Supplementary 1 and 2). The pedigree index, which assess model robustness, were within the expected range (between 0.164 and 0.675), according to Morissette, Hammill and Savenkoff (2006), with 0.302 and 0.317 for the neritic ecosystem and estuary models, respectively, regardless of the seasonal period.

4.3.2 Basic estimates

The models evaluated showed significant spatial and temporal variations on the fish biomass distribution by compartments ($p < 0.05$) (Table Supplementary 4 A and B). Furthermore, a significant difference was found between the rainy neritic ecosystem model and the two estuarine models. The macro-benthivores carnivores, epipelagic, and estuarine piscivorous are responsible for the differences found (Table Supplementary 4 C).

The four models showed an asynchronous pattern in biomass distribution by compartments, both considering the same environment between different seasons and for both environments in the same season, except for phytoplankton, which showed a synchronous spatio-temporal pattern (Table 1).

Table 1- Basic estimates and outputs estimated by EwE in bold, for the functional groups presented in the four estuarine and neritic models, in the dry and rainy seasons of the Southwest Tropical Atlantic. TL = Trophic Level, B (〖t.Km〗 ^(-2)) = Biomass, P/ B (〖year〗 ^(-1)) = Production per Biomass Unit, Q / B (〖ano〗 ^(-1)) = Consumption Rate per Biomass Unit, EE = Ecotrophic Efficiency, OI = Omnivory Index. Values in bold were estimated by Ecopath.

	Compartments	TL	B	P / B	Q / B	EE	OI
Estuary Dry	Phytoplankton	**1.00**	1.28	173.59		**0.55**	
	Macroalgae	**1.00**	35.10	6.25		**0.10**	
	Zooplankton	**2.11**	1.84	25.11	75.33	**0.96**	**0.11**
	Suspensivore Macrobenthos	**2.12**	**2.43**	15.66	110.45	0.70	**0.12**
	Carnivores Macrobenthos	**2.55**	**4.26**	2.47	8.11	0.70	**0.31**
	Epipelagic Suspens Macrobent Fish	**3.13**	**0.83**	0.70	2.86	0.95	**0.02**
	Epipelagic Pisc Fish	**4.03**	0.10	0.70	3.66	**0.39**	**0.45**
	Estuarine Associated Suspens Macrobent Fish	**3.14**	0.14	1.30	6.49	**0.61**	**0.11**
	Estuarine Associated Carniv Macrobent Fish	**3.31**	0.39	0.84	4.96	**0.63**	**0.25**
	Estuarine Associated Detrit Fish	**2.07**	3.49	1.39	29.90	**0.21**	**0.08**
	Estuarine Associated Pisc Fish	**3.73**	0.86	0.83	4.35	**0.40**	**0.30**
	Estuarine Associated Zoo Fish	**3.11**	0.18	0.86	5.24	**0.49**	**0.10**
	Reef Associated Carniv Macrobent Fish	**3.32**	**1.81**	0.42	2.80	0.95	**0.20**
	Reef Associated Pisc Fish	**4.16**	0.03	1.50	5.38	**0.49**	**0.35**
	Detritus	**1.00**				**0.79**	**0.31**
Estuary Rainy	Phytoplankton	**1.00**	5.20	764.00		**0.03**	
	Macroalgae	**1.00**	35.10	6.25		**0.10**	
	Zooplankton	**2.11**	1.85	25.11	75.33	**0.82**	**0.11**
	Suspensivore Macrobenthos	**2.12**	**1.98**	15.65	110.45	0.50	**0.12**
	Carnivore Macrobenthos	**2.55**	**1.33**	4.93	16.21	0.50	**0.31**
	Epipelagic Suspens Macrobent Fish	**3.13**	0.30	0.70	2.86	**1.00**	**0.02**
	Epipelagic Pisc Fish	**4.00**	0.01	0.70	3.66	**0.79**	**0.41**
	Estuarine Associated Suspens Macrobent Fish	**3.14**	0.25	1.30	5.52	**0.81**	**0.11**
	Estuarine Associated Carniv Macrobent Fish	**3.31**	0.28	0.84	4.27	**0.60**	**0.25**
	Estuarine Associated Detrit Fish	**2.07**	1.77	1.39	29.90	**0.42**	**0.08**
	Estuarine Associated Pisc Fish	**3.55**	0.94	0.83	3.43	**0.24**	**0.21**
	Estuarine Associated Zoo Fish	**3.11**	0.05	0.86	5.37	**0.76**	**0.10**
	Reef Associated Carniv Macrobent Fish	**3.32**	0.16	0.42	2.80	**0.53**	**0.20**
	Reef Associated Pisc Fish	**4.13**	0.01	1.50	5.38	**0.20**	**0.31**
	Detritus	**1.00**				**0.06**	**0.04**

Compartments		TL	B	P / B	Q / B	EE	OI
Neritic Dry	Phytoplankton	**1.00**	1.29	173.59		**0.79**	
	Macroalgae	**1.00**	55.39	6.25		**0.10**	
	Zooplankton	**2.11**	1.23	40.00	160.00	**0.98**	**0.11**
	Suspensivore Macrobenthos	**2.06**	**4.32**	15.66	110.45	0.50	**0.06**
	Carnivore Macrobenthos	**2.45**	**7.49**	2.47	8.11	0.50	**0.27**
	Epipelagic Suspens Macrobent Fish	**3.09**	0.46	0.89	4.20	**0.83**	**0.01**
	Epipelagic Pisc Fish	**3.60**	1.10	0.80	5.47	**0.61**	**0.21**
	Estuarine Associated Suspens Macrobent Fish	**3.06**	0.40	1.20	5.65	**0.86**	**0.10**
	Estuarine Associated Carniv Macrobent Fish	**3.24**	0.50	1.20	5.42	**0.57**	**0.22**
	Estuarine Associated Detrit Fish	**2.09**	0.20	1.21	29.90	**0.10**	**0.09**
	Estuarine Associated Pisc Fish	**3.47**	1.67	0.78	3.40	**0.98**	**0.18**
	Estuarine Associated Zoo Fish	**3.11**	0.65	0.91	7.45	**0.67**	**0.10**
	Reef Associated Carniv Macrobent Fish	**3.24**	0.12	0.59	2.80	**0.60**	**0.18**
	Reef Associated Pisc Fish	**3.87**	0.10	0.60	5.38	**0.34**	**0.22**
	Detritus	**1.00**				**0.78**	**0.33**
Neritic Rainy	Phytoplankton	**1.00**	2.22	326.36		**0.07**	
	Macroalgae	**1.00**	55.39	6.25		**0.10**	
	Zooplankton	**2.11**	0.89	40.00	80.00	**0.97**	**0.11**
	Suspensivore Macrobenthos	**2.08**	**2.42**	15.66	110.45	0.50	**0.08**
	Carnivore Macrobenthos	**2.38**	**2.52**	2.47	8.11	0.70	**0.26**
	Epipelagic Suspens Macrobent Fish	**3.10**	2.70	0.89	2.86	**1.00**	**0.02**
	Epipelagic Pisc Fish	**3.67**	1.50	0.80	3.37	**0.65**	**0.20**
	Estuarine Associated Suspens Macrobent Fish	**3.07**	0.28	1.20	6.64	**0.99**	**0.09**
	Estuarine Associated Carniv Macrobent Fish	**3.18**	0.28	1.20	4.86	**0.68**	**0.20**
	Estuarine Associated Detrit Fish	**2.09**	0.83	1.21	14.95	**0.11**	**0.09**
	Estuarine Associated Pisc Fish	**3.89**	0.22	0.78	4.33	**0.92**	**0.30**
	Estuarine Associated Zoo Fish	**3.11**	1.20	0.91	7.88	**0.65**	**0.10**
	Reef Associated Carniv Macrobent Fish	**3.19**	0.40	0.59	2.80	**0.87**	**0.15**
	Reef Associated Pisc Fish	**4.14**	0.17	0.60	5.38	**0.77**	**0.15**
	Detritus	**1.00**				**0.26**	**0.12**

The models showed intense predations (EE > 0.9) in the neritic ecosystem, mainly in the dry season, specifically for the zooplankton and piscivorous estuarine fish compartments. In the rainy season, EE was higher than 0.9 only for the macro-benthivore fish compartment (Table 1). In all cases, the increase in predation coincided with the increase in the biomass of its main natural predators.

In all evaluated models, The System Omnivory Index (SOI) was less than 0.2, mainly in the neritic and during the rainy season (SOI est.dry = 0.16 > SOI est.rainy = 0.15; SOI ner.dry = 0.13 > SOI ner.rainy = 0.11; Tables 1 and 2). SOI is based on the variance of the TL of prey consumed by predators, ranging between 0 (full specialist consumers) and 1 (dominance of groups with high food plasticity; Christensen *et al.* 2008).

4.3.3 Trophic structure and flow analysis

The four models evaluated presented trophic structures with the potential to efficiently sustain the energy flow of at least five trophic levels (Figure 2). In all models, carnivorous and suspensivore macrobenthos represented a representative portion of the total biomass, especially during the dry season, representing 12.6% of the total estuarine biomass and 15.7% of the total biomass in the neritic ecosystem. This reflects the importance of lower trophic level compartments (LT < 3) in the structure of trophic webs. During the rainy season, these groups suffered a decrease of 50% in biomass in both ecosystems. Most of the total biomass was concentrated around trophic level two in the estuarine ecosystem. In the neritic ecosystem, this only occurred in the dry season, with the rainy period being marked by the concentration of biomass at levels three and four. The increase in trophic level values coincided with the increase in the biomass of piscivorous fish (especially reef and epipelagic species; Table 1).

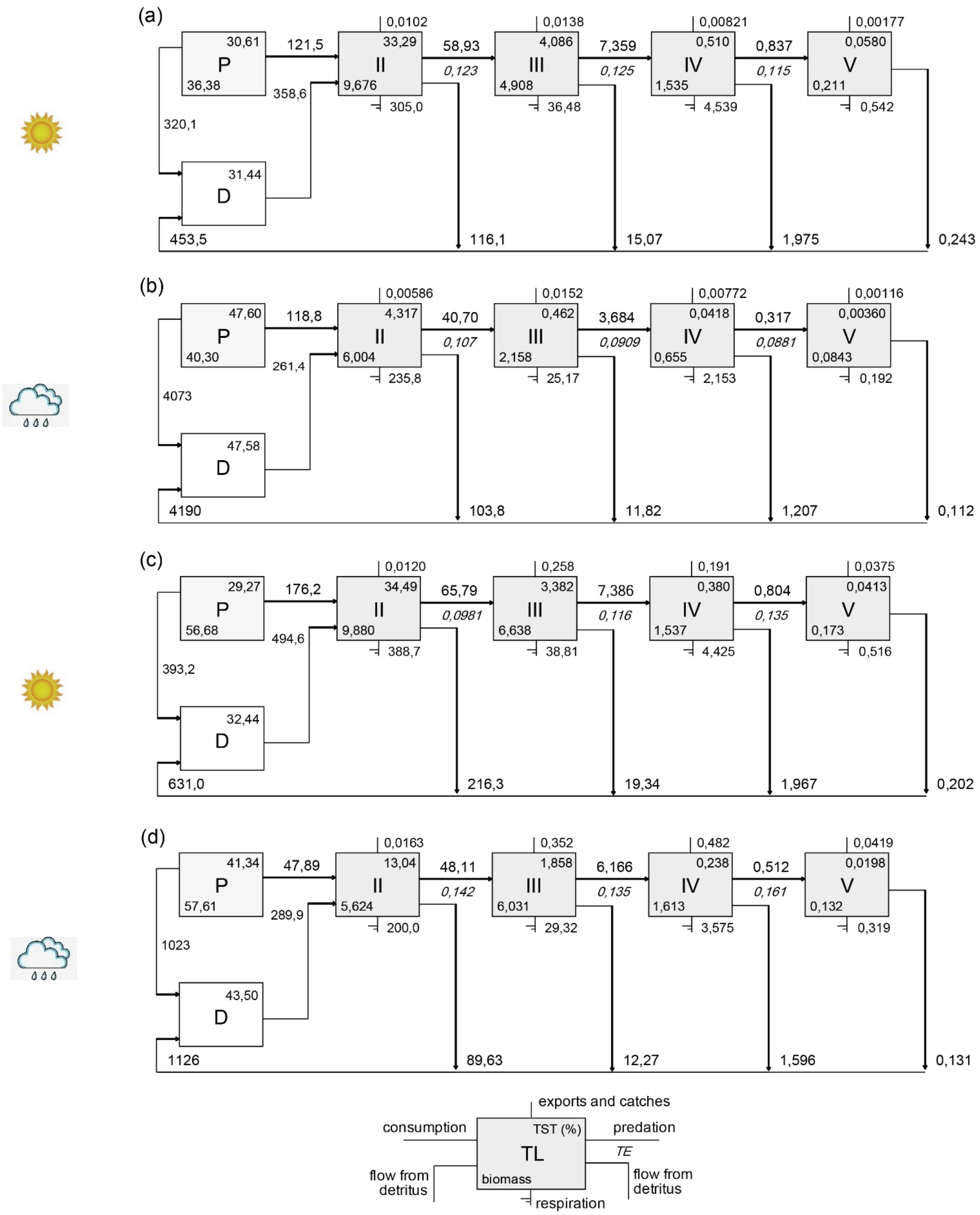

(a)
30,61
P
36,38
121,5
358,6
320,1
0,0102
33,29
II
9,676
305,0
58,93
0,123
0,0138
4,086
III
4,908
36,48
7,359
0,125
0,00821
0,510
IV
1,535
4,539
0,837
0,115
0,00177
0,0580
V
0,211
0,542
31,44
D
453,5
116,1
15,07
1,975
0,243
(b)
47,60
P
40,30
118,8
261,4
4073
0,00586
4,317
II
6,004
235,8
40,70
0,107
0,0152
0,462
III
2,158
25,17
3,684
0,0909
0,00772
0,0418
IV
0,655
2,153
0,317
0,0881
0,00116
0,00360
V
0,0843
0,192
47,58
D
4190
103,8
11,82
1,207
0,112
(c)
29,27
P
56,68
176,2
494,6
393,2
0,0120
34,49
II
9,880
388,7
65,79
0,0981
0,258
3,382
III
6,638
38,81
7,386
0,116
0,191
0,380
IV
1,537
4,425
0,804
0,135
0,0375
0,0413
V
0,173
0,516
32,44
D
631,0
216,3
19,34
1,967
0,202
(d)
41,34
P
57,61
47,89
289,9
1023
0,0163
13,04
II
5,624
200,0
48,11
0,142
0,352
1,858
III
6,031
29,32
6,166
0,135
0,482
0,238
IV
1,613
3,575
0,512
0,161
0,0419
0,0198
V
0,132
0,319
43,50
D
1126
89,63
12,27
1,596
0,131
exports and catches
consumption
TST (%)
predation
TL
TE
flow from detritus
biomass
flow from detritus
respiration

Figure 2- Lindeman Spine for estuary (A and B) and neritic (C and D), in the dry and rainy seasons of the Southwest Tropical Atlantic. P and D represent Primary Production and Detritivores, respectively. The values in the boxes indicate the biomass, import and Total system throughput (TST) for each trophic level TL (II, III, IV and V). The values above and below the arrows show the energy transfer efficiency (TE) at each trophic level (TL).

Regarding the nature of the predominant flow, the four models indicated that the greatest contribution to the second trophic level comes from the detritivore chain. In the estuary, this contribution is almost three times higher during the dry season (358.6 t.Km-2 * semester-1) than to herbivory (ratio Detritivory/Herbivory D/H = 2.95). In the rainy season this value decrease (261.4 t.Km-2 * semester-1; D/H = 2.20). Likewise, in the neritic ecosystem, the highest energy flow from the two producer's compartments also occurs in the dry season; however, the D/H ratio shows that the contribution of detritivory is greater during the rainy season (Figure 2).

The energy transfer efficiency (TE) for consecutive trophic levels followed the same trend, being higher in the estuary during the dry season (TE = 12%) and in the neritic ecosystem during the rainy season (TE = 14%). The two ecosystems released greater energy on respiration during the dry season (Table 2).

4.3.4 Trophic impact matrices (MTI) and key species

Considering the variations between impacted and impacting groups in the four models analyzed, we observed that the most expressive changes occurred between different seasons within the same ecosystem (Table Supplementary 5 A and B). In a more refined analysis, we show that increases in detritus biomass and macrobenthos positively impacts most functional groups in the four models, except for primary producers, which can be negatively impacted by excess detritus, especially during the rainy season. (Figure Supplementary 3-6).

Specifically, in estuarine models, the piscivorous fish compartment associated with the estuary are potential generators of negative impacts on many compartments in the two seasonal periods (Figure Supplementary 3 and 4). In the neritic ecosystem models, this group also promotes negative impacts. However, the intensity of these impacts tends to be greater if it occurs during the dry season. On the other hand, these impacts could be reduced by increasing the biomass of epipelagic piscivores and decreasing the predator´s pressure (Figure Supplementary 5). In the estuary (rainy season), there is a decrease in piscivores but an increase of epipelagic piscivores. It causes impacts to other epipelagic species, while indirectly benefiting their prey (Figure Supplementary 6). Regarding capture strategies, a possible increase in fishing effort tends to have a marked impact in neritic ecosystem models. In this sense, only fisheries involving gillnets and longline/line tend to impact some compartments.

The carnivorous fish compartments: reef, estuarine, epipelagic, and suspensivore macrobenthos are key-species with high values of KS3 in the four models. However, the phytoplankton compartment also presented a high KS3 value, only in the dry season models (Tab Supplementary 6). All groups with high KS3 values showed reduced relative biomass and high impact on the trophic chains analyzed. In addition to them, the carnivorous and suspensivore macrobenthos compartments also followed the same trend. Therefore, according MTIs and based on key species indices, the piscivorous fish compartment associated with the estuary should be considered the compartment that causes the most relative total impact in the evaluated models. On the other hand, as a key producer, the phytoplankton compartment is an important indirect source of energy transfer to the highest trophic levels, especially in the dry season models.

4.3.5 Statistics and ecological indicators

In the present study, we identified three groups of ecological and flow indicators that responded differently to seasonal variation in the two ecosystems evaluated: indicators directly proportional to the increase in rainfall (Total System Transfer Rate - TST and its components, Sum of Total Production - TP, Total Net Primary Production - TNPP, Total Primary Production / Total Respiration - TPP/TR, Total Primary Production / Total Biomass - TPP/TB and Ascendency), indicators inversely proportional to the increase in rainfall (Total Biomass / Total Transfer - TB /TST, Total Biomass - TB, Omnivory Index - SOI, Overhead and Finn Cycling Index - FCI) and indicators that diverged between ecosystems, according to seasonal variation (Connection Index - CI, Number of Paths - PATH and Major Trophic Group - HIGTL) (Table 2).

Table 2- Ecosystem attributes, ecological indicators and estimated flows for the four trophic models of the Southwest Tropical Atlantic.

Ecosystem Attributes	Code	Relationship with Rainfall	Unit	Ecosystem			
				Estuary		Neritic	
				Season			
				Dry	Rainy	Dry	Rainy
Sum of all Consumption	TC	+	t·km^{-2}·sem^{-1}	561.35	439.01	764.83	399.84
Sum of all Exports	TE	+	t·km^{-2}·sem^{-1}	94.92	3928.89	136.88	837.43
Sum of all Respiratory Flows	TR	+	t·km^{-2}·sem^{-1}	346.64	263.28	432.53	233.28
Sum of all Flows Into Detritus	TD	+	t·km^{-2}·sem^{-1}	453.51	4190.31	631.01	1126.44
Total System Throughput	**TST**	+	**t·km^{-2}·sem^{-1}**	**1456.42**	**8821.49**	**1965.25**	**2596.99**
Sum of all Production	TP	+	_	544.00	4280.10	709.35	1157.30
Gross Efficiency (catch/net p.p.)	GEFF	0	_	0.00	0.00	0.00	0.00
Calculated Total Net Primary Production	TNPP	+	t·km^{-2}·sem^{-1}	441.56	4192.18	569.42	1070.71
Total Primary Production/Total Respiration	TPP/TR	+	_	1.27	15.92	1.32	4.59
Total Primary Production/Total Biomass	TPP/TB	+	_	8.38	85.20	7.60	15.08
Total Biomass/Total Throughput	TB/TST	-	/sem	0.04	0.01	0.04	0.03
Total Biomass (excluding detritus)	TB	-	t·km^{-2}	52.72	49.20	74.91	71.01
Net System Production	NSP	+	t·km^{-2}·sem^{-1}	94.92	3928.89	136.88	837.43
Total Catch	TCATCH	0	t·km^{-2}·sem^{-1}	0.03	0.03	0.50	0.89
Connectance Index	CI	0	_	0.26	0.26	0.24	0.26
System Omnivory Index	SOI	-	_	0.16	0.15	0.13	0.11
Lindeman Spine - PP to TL II	PPTLII	-	_	121.50	118.80	176.20	47.89
Lindeman Spine - detritu to TL II	DTTLII	-	_	358.60	261.40	494.60	289.90
H/D Herbivore/Detritivore Ratio				**0.34**	**0.45**	**0.36**	**0.17**
Transfer Efficiency Total	TT	0	%	0.12	0.10	0.12	0.15
Flux Originated in Detritus	_	-	%	0.59	0.51	0.60	0.56
Number of Paths	PATH	0	_	345.00	345.00	378.00	485.00
Primary Production Required	PPR	0	_	10.65	12.31	279.20	180.00
Ascendency	ASC	+	%	31.90	61.72	36.14	42.44
Overhead	OVER	-	%	68.10	38.28	63.86	57.56
Capacity (flowbits)	CAPC	+		5699.00	16073.00	6984.00	7522.00
Finn's Cycling Index	FCI	-	% of TST	11.04	1.06	14.36	4.32
Finn's Mean Path Length	PL	-	_	3.30	2.10	3.45	2.43
Mean Trophic Level of the Catch	_	+	_	3.08	3.18	3.55	3.64
Higher Group TL	HIGTL	0	_	4.03	4.00	3.87	4.14
Model Pedigree	_		_	0.32	0.32	0.30	0.30
Average Model Fit	_		_	1.10	1.10	1.16	1.16

4.3.6 Directly proportional indicators to increased rainfall

During the dry season, 62% from the Total Transfer Rate of the Estuarine System (TSTe) was destined for consumption and breathing and 38% for export and the detritivores' chain. However, in the rainy season, TSTe suffered an increase of approximately 500% and changes in the direction of flows, with a minor portion (8%) destined for consumption and breathing and the majority (92%) to export and detritivorous chain. Following the same trend as the estuary, the Total Transfer Rate of the neritic ecosystem (TSTzp) in the rainy season increased by approximately 32% compared to the dry season and showed changes in the direction of flows, with a smaller part (24.38%) destined for consumption and breathing and most (75.62%) for exports and the detritivorous chain (Table 2).

The main productivity indicators of the two ecosystems (TP, TNPP, TPP/TR and TPP/TB) and ascendency also reached higher values during the rainy season. In the estuary, the increments were 687% (TP), 849% (TNPP), 1,150% (TPP/TR) and 917% (TPP/TB), with TPP > TR and TPP > TB.

In the neritic ecosystem, these increases were 63% (TP), 88% (TNPP), 249% (TPP/TR) and 98% (TPP/TB), similarly, being TPP > TR and TPP > TB. Regarding ascendency, in the estuarine ecosystem this indicator ranged from 31.9% (dry) to 61.72% (rain), while in the neritic ecosystem the variation was from 36.14% (dry) to 42.44% (rain).

4.3.7 Inversely proportional indicators to increased rainfall

Indicators such as: Total Biomass / Total Transfer (TB/TST), Total Biomass (TB), Omnivory Index (SOI), Overhead and Finn Cycling Index (FCI), were negatively affected with the increase in rainfall in both ecosystems, reducing their values during this season. In the estuary, we observed a reduction of -85% (TB/TST), -7% (TB) and -8% (SOI), with TB < TST. We also identified a reduction in the overhead of the estuarine system in the season with the highest rainfall (O dry = 68.1%; O rainy = 38.2%), in addition to a reduction in the Finn Cycling Index (FCI dry = 11.4%; FCI rainy = 1.06%) (Table 2).

Following the same trend, in the neritic ecosystem these reductions were -28% (TB/TST), -5% (TB) and -16% (SOI), with TB < TST. We also identified a reduction in the overload of the estuarine system (overhead) in the season with the highest rainfall (O dry = 42.44%; O rainy = 36.14%), in addition to a reduction in the Finn Cycling Index (FCI dry = 42.44%; FCI rainy = 36.14%).

4.3.7 Divergent indicators among ecosystems, according to seasonal variation

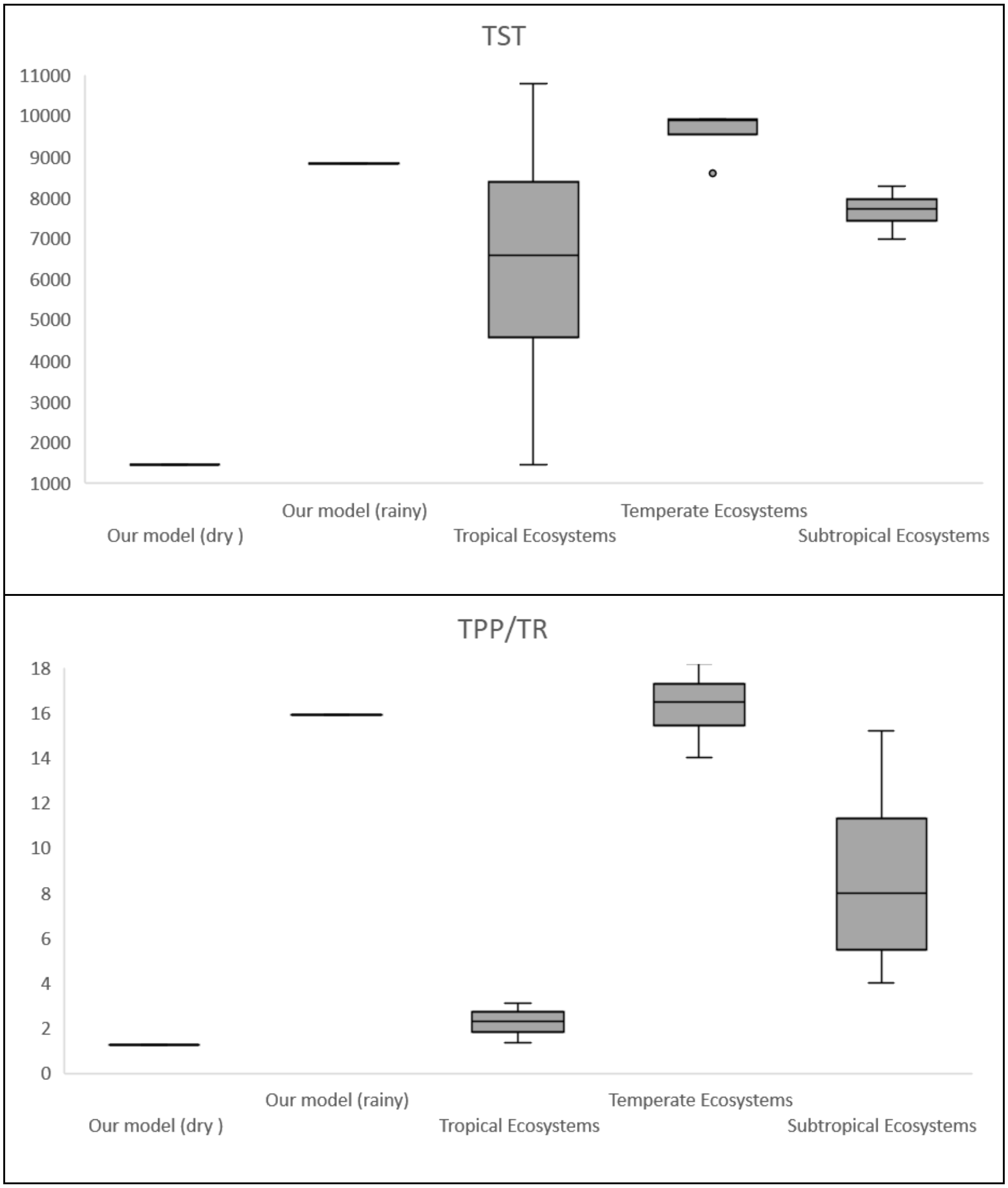
Only three indicators behaved differently between the estuary and the neritic ecosystem according to seasonal changes: Connectivity Index (CI), Number of Paths (PATH) and Major Trophic Group (HIGTL).

In the estuary, CI and PATH were not sensitive to seasonal variation, but in the neritic ecosystem they increased during the rainy season.

HIGTL was inversely proportional between the estuary and the neritic ecosystem during the dry (HIGTL est. = 4.03; HIGTL ner. = 3.87) and rainy seasons (HIGTL est. = 4.0; HIGTL ner. = 4.14), with greater effect on the neritic ecosystem (Table 2).

4.3.8 Comparisons among models

The four ecosystem attributes (TST, TPP/TR, A/C, and O/C) selected to compare our ecosystem models with those of other tropical, subtropical and temperate regions indicated greater similarity between our rainy season estuarine models and subtropical and temperate climate models. In contrast, our dry season estuarine models were more similar to other tropical models. In the case of marine models, only the TST and TPP/TR productivity indicators of our model of the rainy season approached the average predicted for models of subtropical regions. On the other hand, our dry season marine models were similar to other tropical models, following the same trend (Figures 3 and 4).


TST
11000
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
Our model (rainy)
Temperate Ecosystems
Our model (dry)
Tropical Ecosystems
Subtropical Ecosystems
TPP/TR
18
16
14
12
10
8
6
4
2
0
Our model (rainy)
Temperate Ecosystems
Our model (dry)
Tropical Ecosystems
Subtropical Ecosystems

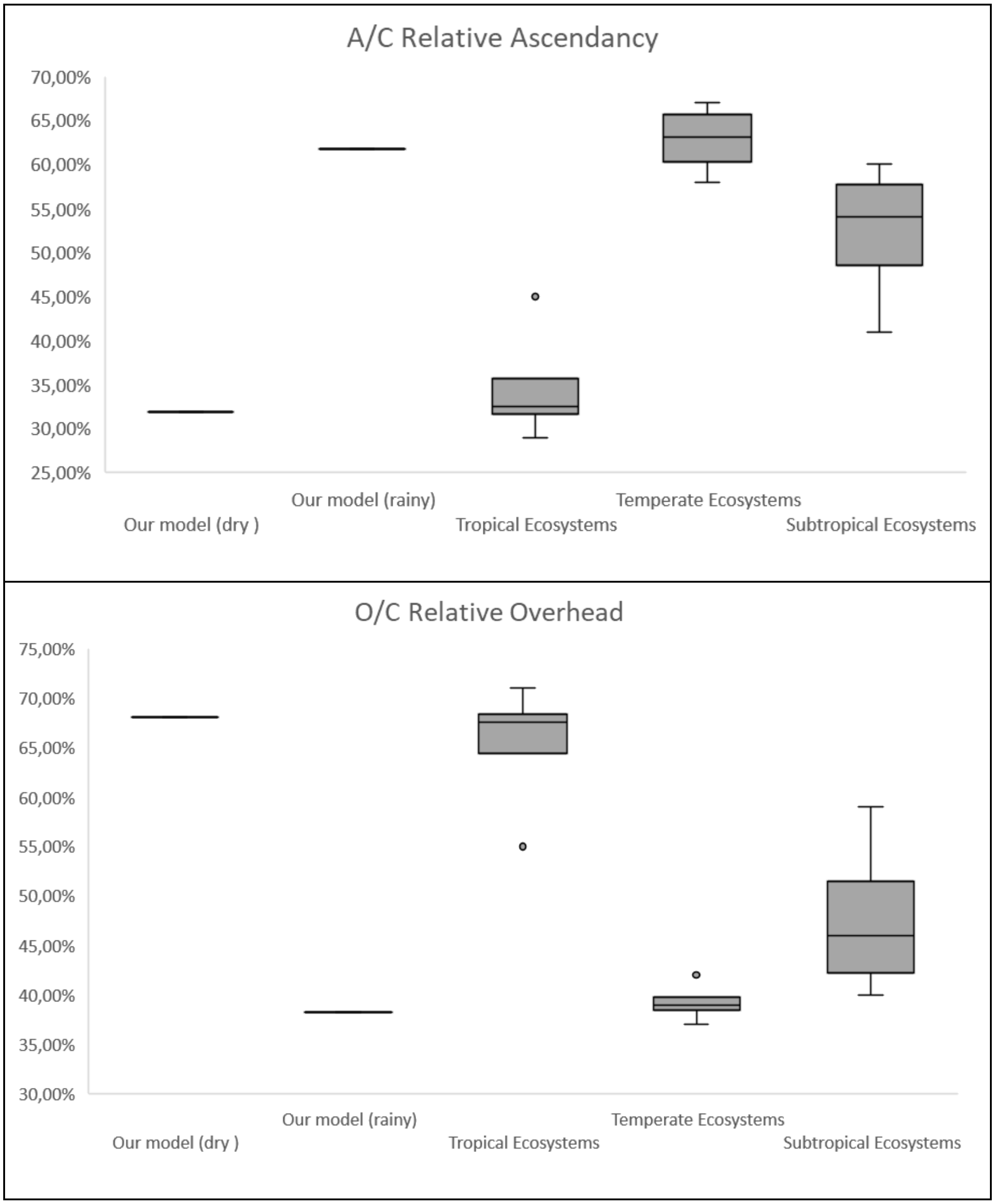
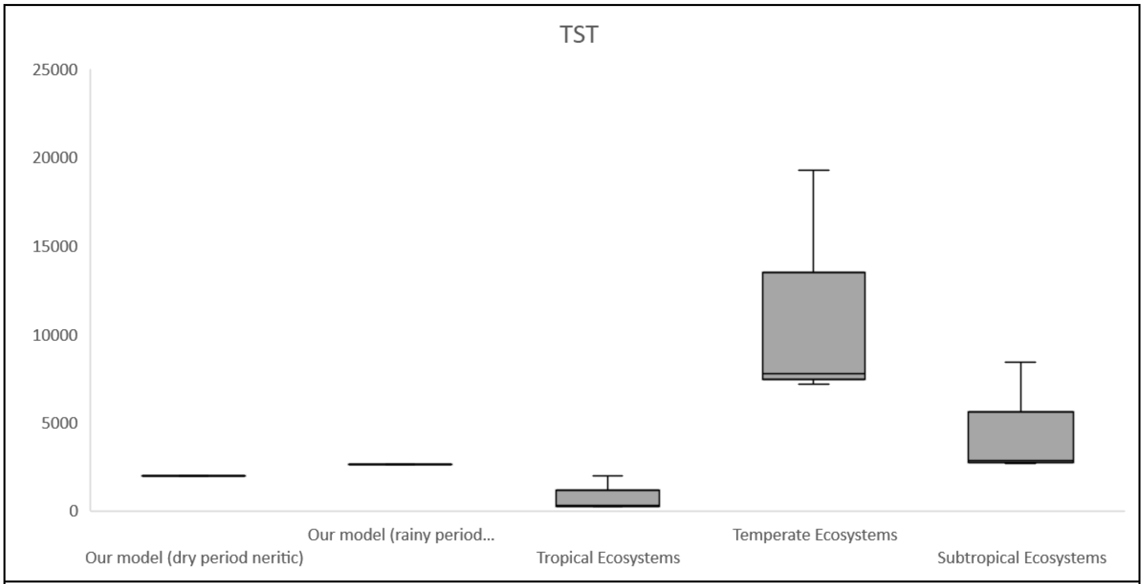


Figure 3- Boxplot of ecosystem indicators from 12 estuarine Ecopath models divided by climatic zone (Temperate; Subtropical; and Tropical) compared with our dry and rainy seasons estuarine models. The horizontal line and box represent the median, value, and interquartile range, respectively. The vertical line is the upper limit (25% of the data). TST - Total System Throughput; TPP/TR - Primary Production/Total Respiration; A/C - Ascendency/Capacity and O/C - Overhead/Capacity.


TST
25000
20000
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5000
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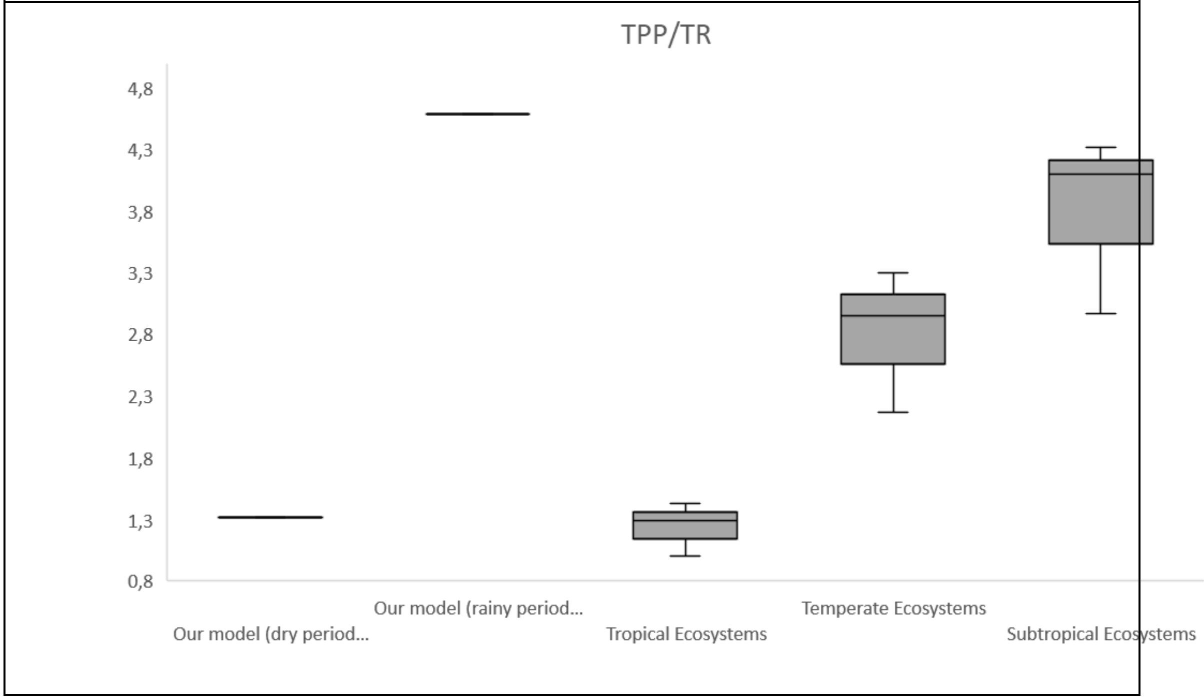
Our model (dry period neritic)
Our model (rainy period...
Tropical Ecosystems
Temperate Ecosystems
Subtropical Ecosystems


TPP/TR
4,8
4,3
3,8
3,3
2,8
2,3
1,8
1,3
0,8
Our model (dry period...
Our model (rainy period...
Tropical Ecosystems
Temperate Ecosystems
Subtropical Ecosystems

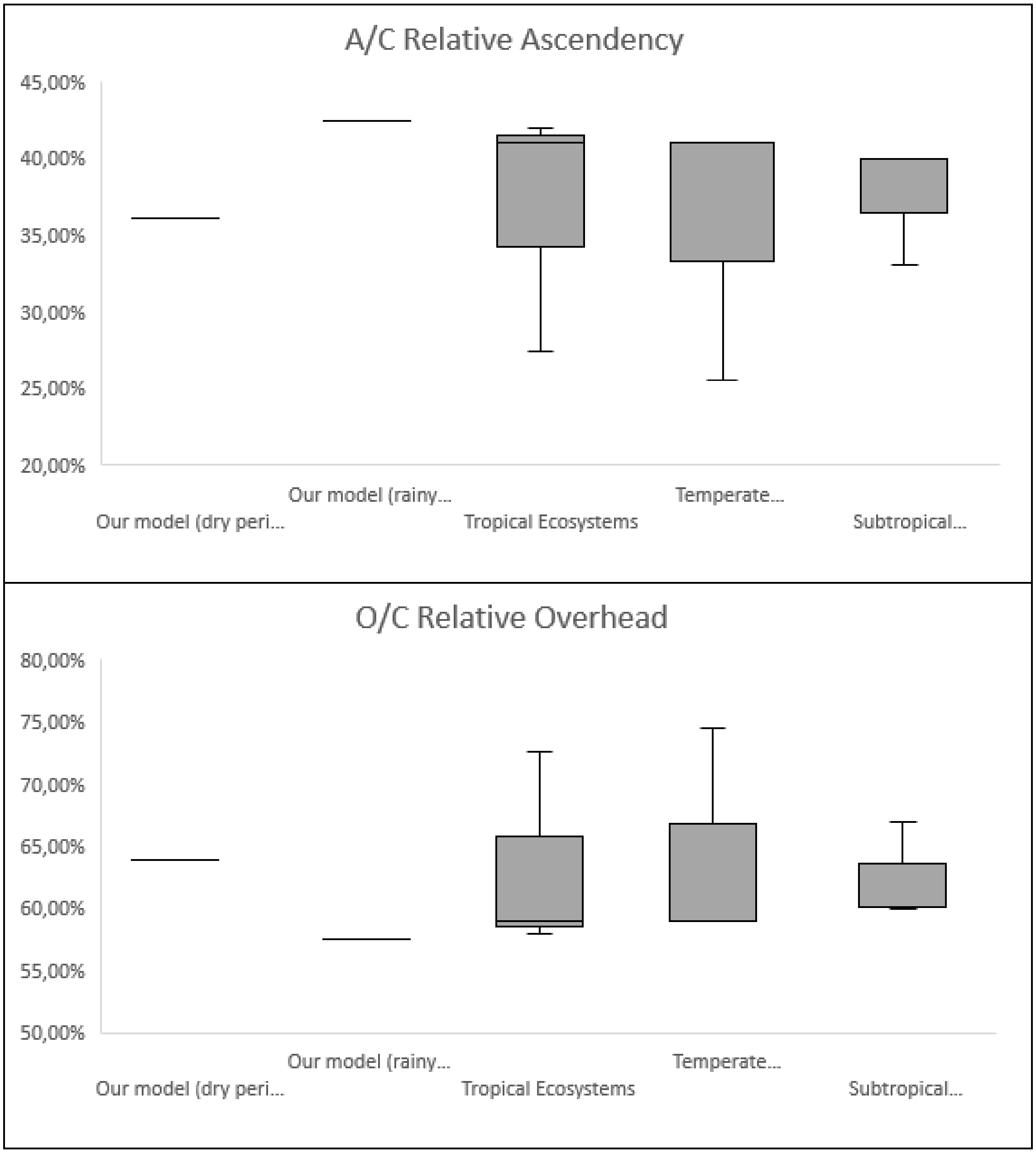


Figure 4- Boxplot of ecosystem indicators from 09 marine Ecopath models divided by climatic zone (Temperate; Subtropical; and Tropical) compared with our dry and rainy seasons neritic models. The horizontal line and box represent the median, value, and interquartile range, respectively. The vertical line is the upper limit (25% of the data). TST - Total System Throughput; TPP/TR - Primary Production/Total Respiration; A/C - Ascendency/Capacity and O/C - Overhead/Capacity.

4.4 Discussion

Our results provide evidence for the occurrence of inter-ecosystem movements of nutrients and organisms that bring structural and functional benefits to the estuarine and neritic zones. The dry season is a stressful period for the two ecosystems, as shown by the decreases in the performance of key ecological indicators: productivity, ascendency and energy flow. However, both, the estuary and neritic zone, benefit through the exchange of components that relieves the pressures of predation on specific groups, reducing competition and maintain the energy flow that is necessary for the functioning of their trophic webs. When the frequency and volume of rainfall intensify, the physical-chemical conditions of the two ecosystems become similar. These favors increased connectivity and the exchange nutrients and organisms, which improves the trophic quality of the two ecosystems, as evidenced by the high performance of key ecological indicators.

In our studies, the first indicative of trophic connectivity is the asynchronous activity in the seasonal variation of fish guilds biomass between the estuary and the neritic ecosystem, as predicted by Macedo *et al.* (2021) for tropical coastal ecosystems. During the dry season, the biomass of detritivores, epipelagic, and piscivorous reef groups increases in the estuary, decreasing in the neritic ecosystem. On the other hand, in the estuary, the biomass of benthivores and piscivorous estuarine fish reduces, while the neritic ecosystem has an increase in these same groups. An inverse dynamic occurs during the rainy season (Figure 5). Temporal changes in the ichthyofauna richness, abundance, and biomass between the estuary and the coast were also investigated by Ferreira *et al.* (2019) in a tropical region. These authors describe patterns similar to those found herein, such as the increase in biomass of detritivores, and estuarine piscivorous in the estuarine ecosystem, during the dry and rainy seasons, respectively. In most cases, biomass variations coincided with variations in species richness and guilds abundance. This demonstrates the functionality of using the biomass variation to infer patterns of ichthyofaunistic mobility.

In the present study, in addition to the ichthyofauna, we incorporated other components into the trophic structures of the estuarine and neritic ecosystems, such as primary producers, zooplankton, and macrobenthos. Our results indicated that the ichthyofauna mobility is strongly associated with variations in the biomass of these structuring compartments, which are more sensitive to environmental fluctuations and determine the intensity of energy flows that will be available to top predators. Therefore, these components become indicators of ecosystem conditions (Vanin *et al.* 1997). In tropical coastal ecosystems, the volume of rainfall and, consequently, the intensity of river nutrients discharge over marine regions determine phytoplankton productivity (Connell; Sousa 1983; Neto *et al.* 2014; Passos *et al.* 2016). Thus, estuarine and neritic ecosystems undergo reductions in the biomass and phytoplankton productivity during the dry season. This can be evidenced by the decrease in the leading primary productivity indicators (TPP/TR and TPP/TB), along with the D/H ratio, in the two ecosystems, during this season.

However, the estuarine and the neritic ecosystems respond differently to this process. In the estuary, the availability of continental inputs increases, probably resulting from the decomposition of organic matter in the mangrove (Navarrete and Olive-Rivera 2002; Bernini and Rezende 2010; Castelblanco-Martínez *et al.* 2012). This important autochthonous source makes it possible to increase the transfer efficiency through the detritivore chain and ensures the flow of local energy, as demonstrated by Claudino *et al.* (2015). In the neritic ecosystem, we evidenced an increase in the predation rate. This may favor the cycling of nutrients by the detritivore chain, which continues to produce energy in the dry season. In addition, the high productivity of reef regions in the same period helps maintain the pasture chain's contribution, as demonstrated by Neto *et al.* (2014). Thus, in the dry season, estuarine and neritic ecosystems maintain their production rates similar to respiration rates (Estuary PPT/RT = 1.27; Neritic TPP/TR= 1.32) (Table 2). These results are close to patterns observed in other tropical coastal systems considered mature, due to the similarity between production and consumption rates (Wolff, Hartmann and Koch 1996; Wolff, Koch and Isaac 2000; Colléter *et al.* 2012; Xavier 2013; Villanueva 2015; Abdul and Adekoya 2016; Simon and Raffaelli 2016; Lira *et al.* 2018). However, seasonal processes were not included in the sample design of these studies, making it difficult to assess the ecosystem indicators analyzed.

The increase in predation, while productivity decreases, does not represent a favorable situation within the ecosystem. On the contrary, it configures a highly stressful situation. Mainly in the marine environment, resulting in forage migrations, mainly of predators, to adjacent systems. This would explain the increase in epipelagic predators and piscivorous reefs in an estuarine environment. At the same time, detritivores marine fish also migrate to estuarine regions, driven by the high availability of mangrove detritus. Particularly, the arrival of epipelagic and reef predators in the estuary tends to drive the departure of estuarine piscivorous predators. This could be evidenced by the biomass increase of this group in the neritic ecosystem at the dry season. The analysis of the diet of these three groups of predators (epipelagic, reef and estuarine) indicated high food overlap and predisposition of estuarine piscivores become prey to reef and epipelagic predators. Thus, it is expected that the most susceptible group will move to another adjacent ecosystem, reducing competition for the same limiting resources (Hutchinson 2015; Chesson 1991; Chesson 2000). The signal that these groups compete for the same resources was evident in the trophic impact matrix of the neritic ecosystem, where increased fishing effort with gillnets directed to epipelagic and reef piscivorous fish compartments, favors the increase in estuarine piscivorous biomass. A strong indicator of interspecific competition is functional redundancy, especially at higher trophic levels. For instance, da Silva, Dolbeth and Fabré (2021) evaluated the effects of spatial and temporal changes on the functional diversity of fish species in the region and indicated that high functional redundancy between the habitats forms a coastal mosaic, evidencing that competition rates tend to be higher in these systems. In this sense, increases in the estuarine macrobenthivores biomass, during the dry season, especially in the neritic ecosystem, enhance the dominance of groups with high food plasticity, as evidenced in this study by the increase in the Systems Omnivory Index (SI) (Christensen *et al.* 2008). More broadly, this is expected to reduce competition between predators and predation pressure on other structuring groups.

The joint analysis of the main ecological indicators (TST and its components: TP, TNPP, TPP/TR, TPP/TB, in addition to Transfer efficiency total (TE) and relative Ascendency (A/C)) allows us to affirm that the arrival of rainfall improves environmental conditions. The frequency and volume of rainfall cause a process called estuarization (Longhurst and Pauly 1987), which is the expansion of the estuarine physicochemical condition within the neritic ecosystem (Longhurst and Pauly 1987; Blaber *et al.* 1997; Barletta *et al.* 2003; Krumme, Herbeck and Wang 2012; Passos *et al.* 2016). Depending on river flow and sediment discharge, it becomes difficult to establish boundaries between the two ecosystems, which increases connectivity (Longhurst and Pauly 1987). The ecological indicators showed that the period in which the estuarization occurs favors the increase of productivity in both ecosystems (TST and its components), with positive reflexes on the general transfer efficiency of these systems. In the estuary, the increase discharge of rivers, predisposes to the leaching, increasing availability of nutrients in the neritic ecosystem. The leaching of this organic matter results in a decrease in estuarine detritivory, but predisposes to an increase in marine detritivory. In addition, the flow of detritus between the two environments promotes an increase in photosynthetic activity, which becomes more active, mainly in the energy distribution of the estuarine trophic structure, compensating for the reduction in the contribution of the detritivore chain (Fig 5). Particularly, the rate of variation of the phytoplankton contribution in the ecosystems investigated here is compatible with the chlorophyll a rates temporal variation (Neto *et al.* 2015). This temporal variation may also explain differences in the relative primary producer’s contribution, observed in models from other tropical regions that did not distinguish between seasonal periods (Lira *et al.* 2018; Ferreira *et al.* 2019).

A comparative analysis between our models and models from other climatic regions, shows that the moment when estuarization occurs can be so favorable to the increase in productivity within tropical coastal ecosystems that it allows them to close performance to other coastal ecosystems highly productive and subject to more severe seasonal variations. In addition to the increase in productivity, we evidence an improvement in the Total Transfer Efficiency of the systems, which exceeds the average rate estimated for tropical and subtropical regions (average TE = 8.6%), and approaches the average rate of regions with temperate climates (TE average > 10%) (Eddy *et al.* 2021). Transfer efficiency is a critical factor shaping marine ecosystems, as subtle changes in transfer efficiency can cause profound changes in the entire trophic structure, including the abundance of top predators (Docmac *et al.* 2017; García-seoane *et al.* 2019; Nelson *et al.* 2019; Polovina *et al.* 2001). This was evident to us with the increase in the biomass of estuarine (detritivorous and zooplanktivorous) and marine (epipelagic and reef predators) fish in the neritic ecosystem, at the same time that we recorded an increase in productivity in this system.

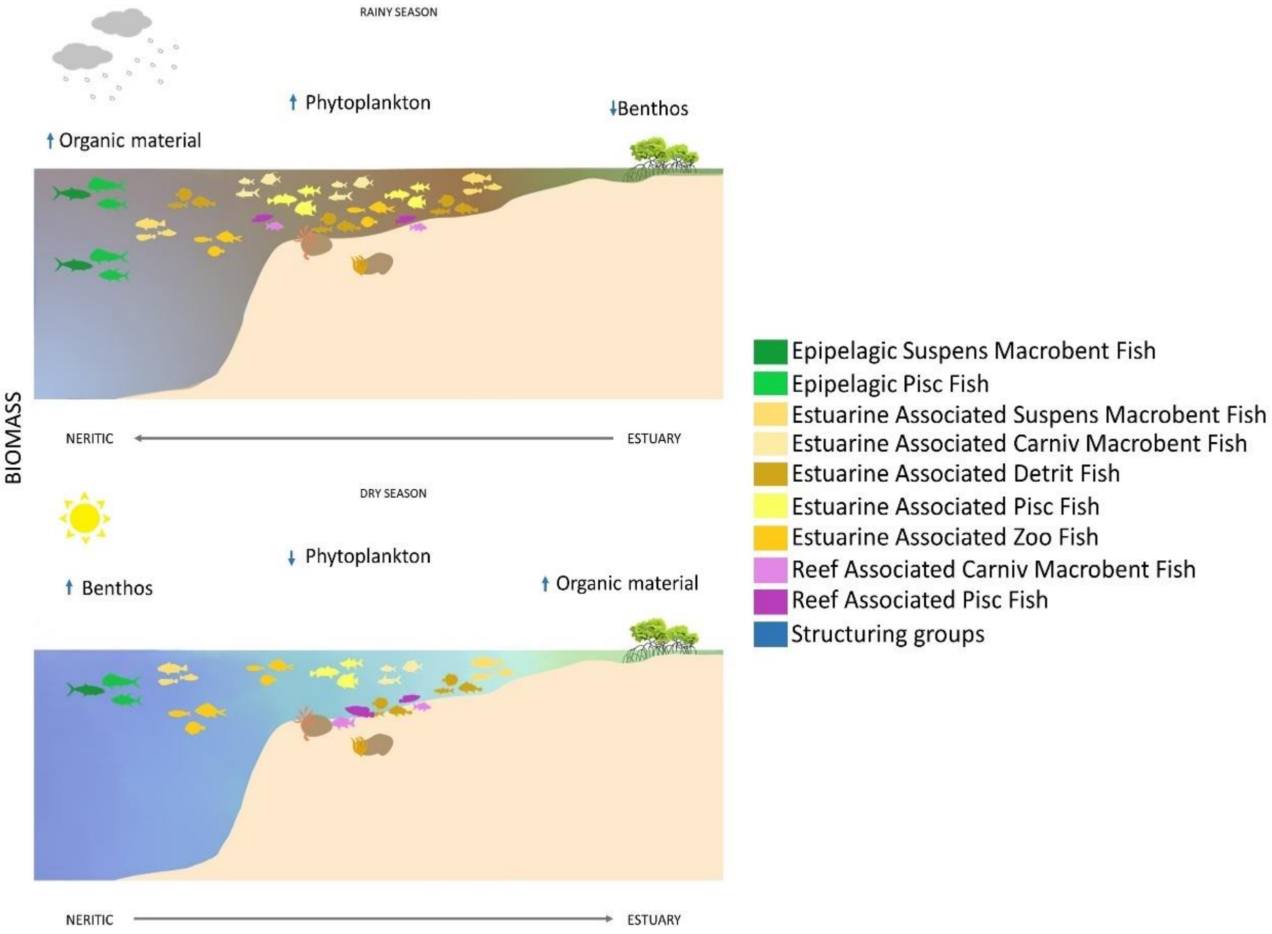


Figure 5- Dynamics of seasonal mobility, based on variations in the biomass of trophic components, between estuarine and neritic ecosystems, during the dry and rainy seasons (estuarization). Horizontal arrows indicate the predominant direction of fish flows between systems (neritic and estuary). The vertical arrows indicate variations in the biomass of the structuring components (phytoplankton, benthos) and organic material.

Our results support the trophic convergence of metaecosystem hypothesis (Macedo *et al.* 2021), which consists of the displacement of estuarine and epipelagic species towards the neritic ecosystem, during the rainy season, enriching the trophic structure of this ecosystem and causing an increase in carnivory. This justifies a better performance of the indices: CI and A/C within the neritic ecosystem in the rainy season at study area. These indices are associated with greater integration and greater predictability of flows in the ecosystem, respectively (Gardner and Ashby 1970; Ulanowicz 1986; Heymans 2014). In particular, ascendency is an indicator that measures the predictability of flows between system components, known as a measure of the degree of system information (Ulanowicz 1986). The more predictable the flows, the greater the ascendency. A less diversified trophic structure implies lower connection and, consequently, greater predictability about the occurrence of flows between its components. As a result, there is an increase in ascendency. In our studies, the increase in carnivory during the rainy season minimized the variety of trophic connections, increasing the level of information in the system and, consequently, the ascendency. This metric would be associated with an increase in ecosystem maturity (Odum 1969). On the other hand, the arrival of the rainy season coincided with the decrease in system overhead, a metric that measures the degree of disorder in the systems, and which would also be correlated with the increase in maturity (Christensen 1995). This for us is strong evidence that the isolated assessment of these indicators alone does not make sense. Only when they are evaluated together and under the influence of seasonal variations, it becomes possible to infer the true state of ecosystem development.

During the environmental changes, some ecological indicators are expected to fluctuate. In this sense, the modeler will need to be aware of these changes and the dynamics of the ecosystem, otherwise he will be misinterpreting its true state of development. When it comes to closely linked ecosystems such as estuary and neritic, seasonal changes become a key factor for the exchange of flows that will promote increased productivity, the accumulation of more biomass and the formation of reserve energy in both systems. These subsidies will allow them to persist in periods of lower connectivity and diminishing inputs. This efficient joint strategy of perpetuation is what promotes resistance and resilience to these ecosystems, which together can reach different states of equilibrium, translated into maturity to withstand new environmental changes.

4.5 Acknowledgment

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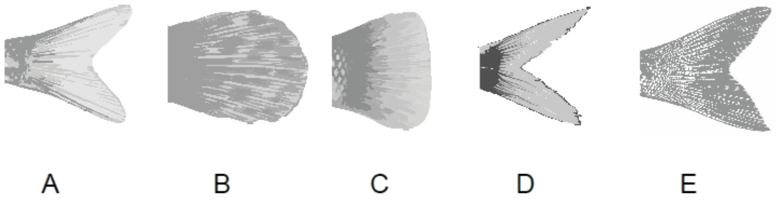
4.7 Supplementary Material

Fram. Supl. 1 - Biomass (t.km-2) of fish before and after the application of the catchability model (Lauretta *et al.*, 2013). qL is the selected catchability coefficient for each species based in morphology of the caudal fin. p is the mean proportion of the population captured by the fishing gear p = (qL*E)/A, where E is effort (total area dragged), A is habitat area.

Ecosystem	**Period**	**Group Names**	**B (t.km-2) Before**	***qL***	***p***	**B (t.km-2) After**	**Caudal fin form**	**Similar group in catchability model**
Estuary	**Dry**	Epipelagic Suspens Macrobent Fish	0.000010	0.688	0.0302	0.00033	D	*Eucinostomus harengulus*
		Epipelagic Pisc Fish	0.000030	0.688	0.0344	0.00087	D	*Lagodon rhomboids*
		Estuarine Associated Suspens Macrobent Fish	0.000422	0.688	0.0302	0.01400	D	*Diapterus rhombeus, Sciades herzbergii and Eucinostomus harengulus*
		Estuarine Associated Carniv Macrobent Fish	0.001169	0.688	0.0302	0.03875	D	*Eucinostomus harengulus*
		Estuarine Associated Detrit Fish	0.200564	0.784	0.0344	5.83624	C	*Fundulus* spp
		Estuarine Associated Pisc Fish	0.000375	0.010	0.0004	0.85629	A	*Centropomus undecimalis*
		Estuarine Associated Zoo Fish	0.000546	0.688	0.0302	0.01809	D	*Eucinostomus harengulus*
		Reef Associated Carniv Macrobent Fish	0.000010	0.582	0.0255	0.00039	E	*Lagodon rhomboides*
		Reef Associated Pisc Fish	0.000034	0.540	0.0237	0.00143	B	*Trinectes maculatus*
Estuary	**Rainy**	Epipelagic Suspens Macrobent Fish	0.00001	0.688	0.0302	0.00033	D	*Eucinostomus harengulus*
		Epipelagic Pisc Fish	0.00003	0.688	0.0344	0.00087	D	*Lagodon rhomboids*
		Estuarine Associated Suspens Macrobent Fish	0.00755	0.688	0.0302	0.25019	D	*Diapterus rhombeus, Sciades herzbergii and Eucinostomus harengulus*
		Estuarine Associated Carniv Macrobent Fish	0.00831	0.688	0.0302	0.27541	D	*Eucinostomus harengulus*
		Estuarine Associated Detrit Fish	0.06071	0.784	0.0344	1.76673	C	*Fundulus* spp
		Estuarine Associated Pisc Fish	0.00041	0.010	0.0004	0.93945	A	*Centropomus undecimalis*
		Estuarine Associated Zoo Fish	0.00043	0.688	0.0302	0.01425	D	*Eucinostomus harengulus*
		Reef Associated Carniv Macrobent Fish	0.00001	0.582	0.0255	0.00039	E	*Lagodon rhomboides*
		Reef Associated Pisc Fish	0.00009	0.540	0.0237	0.00371	B	*Trinectes maculatus*
Neritic	**Dry**	Epipelagic Suspens Macrobent Fish	0.00001	0.688	0.002394	0.004177	D	*Eucinostomus harengulus*
		Epipelagic Pisc Fish	0.00013	0.688	0.002728	0.047648	D	*Lagodon rhomboids*

Ecosystem	Period	Group Names	B (t.km-2) Before	*qL*	*p*	B (t.km-2) After	Caudal fin form	Similar group in catchability model
		Estuarine Associated Suspens Macrobent Fish	0.00046	0.688	0.002394	0.190762	D	*Diapterus rhombeus, Sciades herzbergii and Eucinostomus harengulus*
		Estuarine Associated Carniv Macrobent Fish	0.00033	0.688	0.002394	0.137117	D	*Eucinostomus harengulus*
		Estuarine Associated Detrit Fish	0.00013	0.784	0.002728	0.047648	C	*Fundulus spp*
		Estuarine Associated Pisc Fish	0.00012	0.010	3.48E-05	3.448276	A	*Centropomus undecimalis*
		Estuarine Associated Zoo Fish	0.00003	0.688	0.002394	0.011118	D	*Eucinostomus harengulus*
		Reef Associated Carniv Macrobent Fish	0.00001	0.582	0.002025	0.004937	E	*Lagodon rhomboides*
		Reef Associated Pisc Fish	0.00001	0.540	0.001879	0.005321	B	*Trinectes maculatus*
Neritic	**Rainy**	Epipelagic Suspens Macrobent Fish	0.25010	0.688	0.053205	4.700694	D	*Eucinostomus harengulus*
		Epipelagic Pisc Fish	0.56541	0.688	0.060629	9.32575	D	*Lagodon rhomboids*
		Estuarine Associated Suspens Macrobent Fish	0.00040	0.688	0.002394	0.166985	D	*Diapterus rhombeus, Sciades herzbergii and Eucinostomus harengulus*
		Estuarine Associated Carniv Macrobent Fish	0.00067	0.688	0.002394	0.280454	D	*Eucinostomus harengulus*
		Estuarine Associated Detrit Fish	0.05017	0.784	0.060629	0.827441	C	*Fundulus spp*
		Estuarine Associated Pisc Fish	0.00015	0.010	3.48E-05	4.394546	A	*Centropomus undecimalis*
		Estuarine Associated Zoo Fish	0.00006	0.688	0.002394	0.02631	D	*Eucinostomus harengulus*
		Reef Associated Carniv Macrobent Fish	0.00001	0.582	0.002025	0.004937	E	*Lagodon rhomboides*
		Reef Associated Pisc Fish	0.00001	0.540	0.001879	0.005321	B	*Trinectes maculatus*



Morphology of the caudal fin

Fram. Supl. 2 - Components list of each compartment described in the estuarine and neritic trophic models, in the dry and rainy seasons of the Southwest Tropical Atlantic.

Group Names	**Representative Species**	**Predominant Prey in Diet Composition ***	**Habitat Use Guild adapted from (Potter *et al.* 2015)**	**Literature used in identification**
Phytoplankton	*Chaetoceros lorenzianus; Cylindrospermopsis raciborskii; Guinardia flácida; Protoperidinium sp.1; Protoperidinium sp.2; Thalassiosira leptopus*	–	–	(Caspers 1965) (Müller-Melchers and Ferrando 1956)
Macroalgae	*Hypnea sp; Caulerpa sp; Cryptonemia sp; Dictyota sp ; Dictyopteris delicatula; Galaxaura marginata ; Gelidiella acerosa; Gracilaria sp; Sargassum sp.*	–	–	(Matteucci 1982)
Zooplankton	*Anfípodos (Gammaridae); Copépodos (Cyclopoida; Harpacticoida); Tintinnina; larvas de peixes*	Zooplankton (58%) and Phytoplankton (42%)	–	(Rosa and Sassi 2002)
Suspensivores Macrobenthos	*Anomalocardia brasiliana; Clibanarius sclopetarius; Iphigenia brasiliana; Mytella charruana; Strombus pugilis*	Sediments (52%) and detritus (48%)	–	(Ferreira da Silva 2006)
Carnivores Macrobenthos	*Aplysia sp; Calappa sulcate; Callinectes bocourti; Callinectes danae; Callinectes exasperates; Callinectes larvatus; Callinectes sapidus; Callinectes sp; Chrysaora láctea; Clibanarius sp; Farfantepenaeus paulensis; Luidia senegalensis; Palaemonetes sp; Penaeus subtilis; Persephona punctata; Turbinella laevigata; Xiphopenaeus kroyeri*	Microbenthos (67%) and others benthos (33%)	–	(Ferreira da Silva 2006)
Epipelagic Suspens Macrobent Fish	*Chloroscombrus chrysurus; Scomberomorus brasiliensis*	Suspensivores Macrobenthos (54%) and little fish (46%)	Species that are typical of epipelagic regions or found along the continental slope can migrate to coastal areas.	(Menezes *et al.* 2003); (Figueiredo and Menezes 2015); Nóbrega, Lessa and Santana 2009; Garcia Júnior *et al.* 2010)
Epipelagic Pisc Fish	*Coryphaena hippurus; Scomberomorus cavala; Sphyraena barracuda; Sphyraena guachancho; Thunnus albacares*	Estuarine fish (50%), Reef fish (33%) and Macrobenthos (17%)		
Estuarine Associated Suspens Macrobent Fish	*Archosargus rhomboidalis; Cathorops spixii; Diapterus rhombeus; Haemulopsis corvinaeformis; Menticirrhus americanos; Micropogonias furnieri; Pomadasys ramosus; Sphoeroides greeleyi;*	Suspensivores Macrobenthos (73%) And others benthos (27%)	Marine fish that depend on estuaries to complete parts of their life cycle such as marine estuarine-	

	Sphoeroides testudineus; Symphurus tessellatus		dependent or marine species that occasionally enter estuaries, especially as juveniles;	
Estuarine Associated Carniv Macrobent Fish	*Cynoscion jamaicensis; Dactylopterus volitans; Eucinostomus argenteus; Eucinostomus gula; Eucinostomus melanopterus; Lutjanus analis; Menticirrhus littoralis; Polydactylus virginicus; Sciades herzbergii; Selene vômer; Stellifer brasiliensis; Stellifer stellifer; Syacium micrurum; Symphurus plagusia; Thalassophryne nattereri*	Carnivores Macrobenthos (70%) And others benthos (30%)		
Estuarine Associated Detrit Fish	*Mugil curema; Trinectes microphthalmus; Trinectes paulistanus*	Detritus (65%), sediments (30%), others (5%)		
Estuarine Associated Pisc Fish	*Caranx latus; Chaetodipterus faber; Centropomus ensiferus; Centropomus parallelus; Centropomus undecimalis; Cetengraulis edentulus; Cynoscion acoupa; Lutjanus jocu; Notarius grandicassis; Pellona harroweri; Sciades parkeri*	Others Estuarine Fish (60%), Reef Fish (25%) and Epipelagic Fish (15%)		
Estuarine Associated Zoo Fish	*Chirocentrodon bleekerianus; Etropus crossotus; Eugerres brasilianus; Larimus breviceps*	Zoobenthos (64%) and Zooplankton (36%)		
Reef Associated Carniv Macrobent Fish	*Lutjanus synagris*	Carnivores Macrobenthos (68%) And others benthos (32%)	Fish that are strictly associated with reefs and do not depend on estuaries or oceanic ecosystems to complete their life cycle	
Reef Associated Pisc Fish	*Rypticus saponaceus*	Small fish (51%), zoobenthos (45%) and others benthos (4%)		

* Data based on prey IRI, obtained after analysis of stomach contents.

Supplementary Table 1- Diet matrix of estuarine and neritic trophic models, in the dry and rainy seasons of the Southwest Tropical Atlantic.

		Prey	**Predator**											
			3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Estuary Dry	**1**	**Phytoplankton**	**0.80**	**0.02**	**0.15**									
	2	**Macroalgae**					**0.04**	**0.01**	**0.00**				**0.00**	**0.00**
	3	**Zooplankton**	**0.10**	**0.11**	**0.00**							**0.92**		
	4	**Suspensivores Macrobenthos**		**0.00**	**0.49**	**0.98**	**0.02**	**0.74**	**0.12**	**0.05**	**0.05**	**0.08**	**0.20**	**0.00**
	5	**Carnivore Macrobenthos**			**0.00**	**0.02**	**0.10**	**0.2**	**0.76**	**0.01**	**0.04**		**0.71**	
	6	**Epipelagic Suspens Macrobent Fish**					**0.37**				**0.11**			
	7	**Epipelagic Piscivores Fish**					**0.17**				**0.02**			**0.01**
	8	**Estuarine Associated Suspens Macrobent Fish**									**0.12**			**0.24**
	9	**Estuarine Associated Carniv Macrobent Fish**									**0.11**			**0.10**
	10	**Estuarine Associated Detritivores Fish**									**0.05**			**0.04**
	11	**Estuarine Associated Piscivores Fish**					**0.15**				**0.10**			**0.30**
	12	**Estuarine Associated Zooplanktivorous Fish**									**0.12**			**0.01**
	13	**Reef Associated Carniv Macrobent Fish**									**0.17**			**0.10**
	14	**Reef Associated Piscivores Fish**					**0.15**				**0.11**			**0.20**
	15	**Detritus**	**0.1**	**0.87**	**0.36**			**0.05**	**0.12**	**0.94**	**0.00**		**0.09**	**0.00**
		SUM	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**	**1.00**

	Prey		Predator											
			3	4	5	6	7	8	9	10	11	12	13	14
Estuary Rainy	1	Phytoplankton	0.45	0.02	0.09									
	2	Macroalgae					0.04	0.01						
	3	Zooplankton	0.10	0.09	0.05	0.98						0.93		
	4	Suspensivores Macrobenthos			0.25	0.02	0.03	0.78	0.09	0.03	0.04	0.07	0.20	
	5	Carnivore Macrobenthos			0.09		0.10	0.20	0.79	0.01	0.05		0.71	
	6	Epipelagic Suspens Macrobent Fish					0.37				0.11			
	7	Epipelagic Piscivores Fish					0.17				0.02			0.03
	8	Estuarine Associated Suspens Macrobent Fish									0.12			0.24
	9	Estuarine Associated Carniv Macrobent Fish									0.10			0.10
	10	Estuarine Associated Detritivores Fish									0.06			0.04
	11	Estuarine Associated Piscivores Fish					0.12				0.08			0.24
	12	Estuarine Associated Zooplanktivorous Fish									0.11			0.01
	13	Reef Associated Carniv Macrobent Fish									0.20			0.12
	14	Reef Associated Piscivores Fish					0.17				0.11			0.22
	15	Detritus	0.45	0.89	0.52			0.01	0.12	0.96			0.09	
	SUM		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

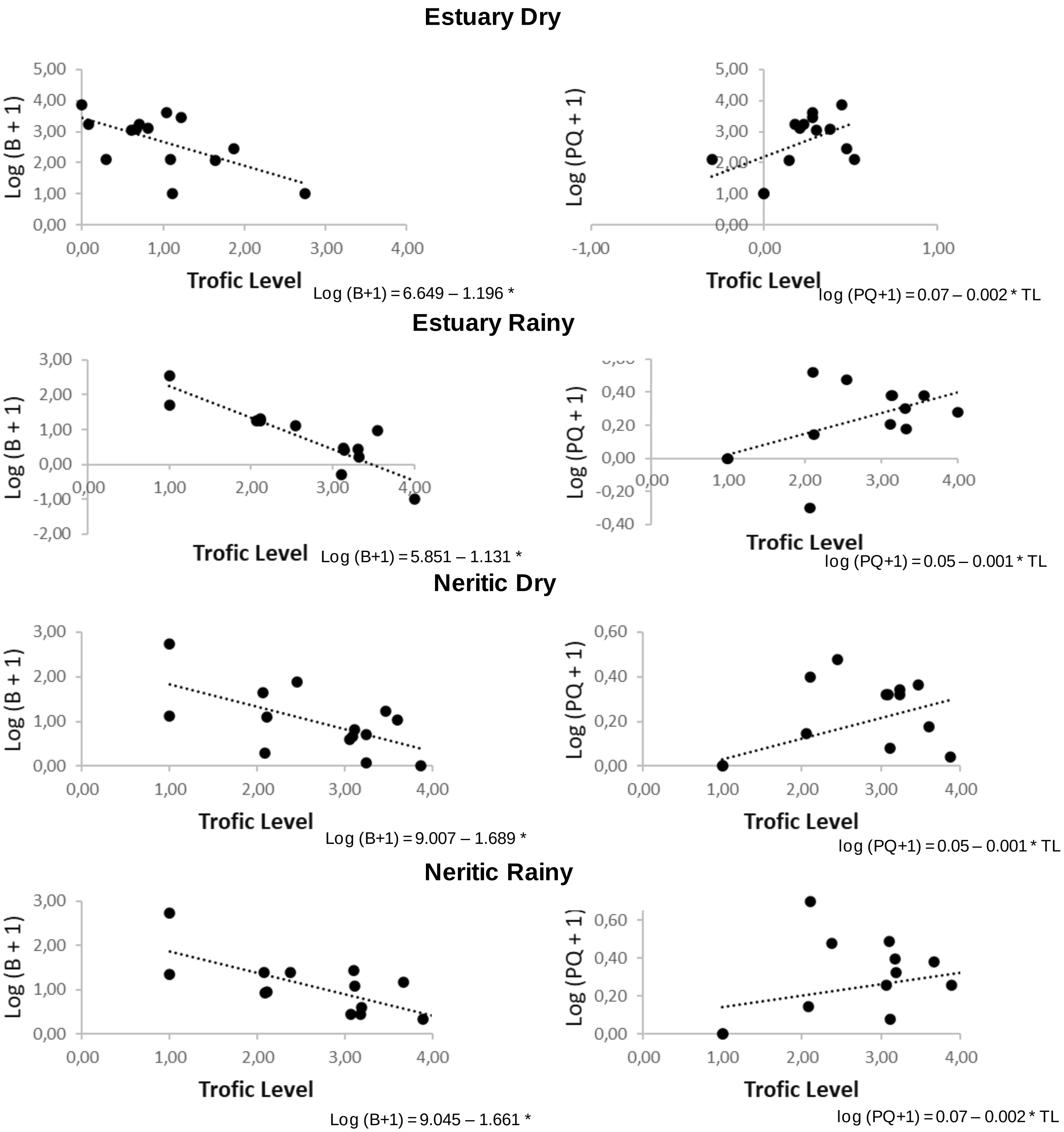
	Prey		Predator											
			3	4	5	6	7	8	9	10	11	12	13	14
Neritic Dry	1	Phytoplankton	0.80	0.02	0.15									
	2	Macroalgae						0.01						
	3	Zooplankton	0.10	0.11								0.93		
	4	Suspensivores Macrobenthos			0.43	0.92	0.02	0.76	0.10	0.07	0.05	0.07	0.21	0.04
	5	Carnivore Macrobenthos				0.08	0.10	0.18	0.78	0.01	0.04		0.70	0.07
	6	Epipelagic Suspens Macrobent Fish					0.37				0.11			0.10
	7	Epipelagic Piscivores Fish					0.06				0.02			0.01
	8	Estuarine Associated Suspens Macrobent Fish									0.12			0.24
	9	Estuarine Associated Carniv Macrobent Fish									0.10			0.10
	10	Estuarine Associated Detritivores Fish									0.04			0.04
	11	Estuarine Associated Piscivores Fish					0.10				0.06			0.10
	12	Estuarine Associated Zooplanktivorous Fish									0.12			0.10
	13	Reef Associated Carniv Macrobent Fish					0.17				0.20			0.10
	14	Reef Associated Piscivores Fish					0.18				0.14			0.10
	15	Detritus	0.10	0.87	0.42			0.05	0.12	0.92			0.09	
	SUM		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

		Prey	Predator											
			3	4	5	6	7	8	9	10	11	12	13	14
Neritic Rainy	1	Phytoplankton	0.56	0.02	0.13									
	2	Macroalgae						0.01						
	3	Zooplankton	0.10	0.07								0.93		
	4	Suspensivores Macrobenthos			0.35	0.92	0.02	0.76	0.10	0.07	0.02	0.07	0.21	0.01
	5	Carnivore Macrobenthos				0.08	0.10	0.18	0.78	0.01	0.02		0.70	0.02
	6	Epipelagic Suspens Macrobent Fish					0.10				0.15			0.10
	7	Epipelagic Piscivores Fish					0.02				0.02			0.01
	8	Estuarine Associated Suspens Macrobent Fish					0.04				0.12			0.24
	9	Estuarine Associated Carniv Macrobent Fish					0.06				0.10			0.15
	10	Estuarine Associated Detritivores Fish					0.08				0.06			0.05
	11	Estuarine Associated Piscivores Fish					0.2				0.01			0.12
	12	Estuarine Associated Zooplanktivorous Fish					0.03				0.12			0.10
	13	Reef Associated Carniv Macrobent Fish					0.17				0.22			0.10
	14	Reef Associated Piscivores Fish					0.18				0.16			0.10
	15	Detritus	0.34	0.91	0.52			0.05	0.12	0.92			0.09	
SUM			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

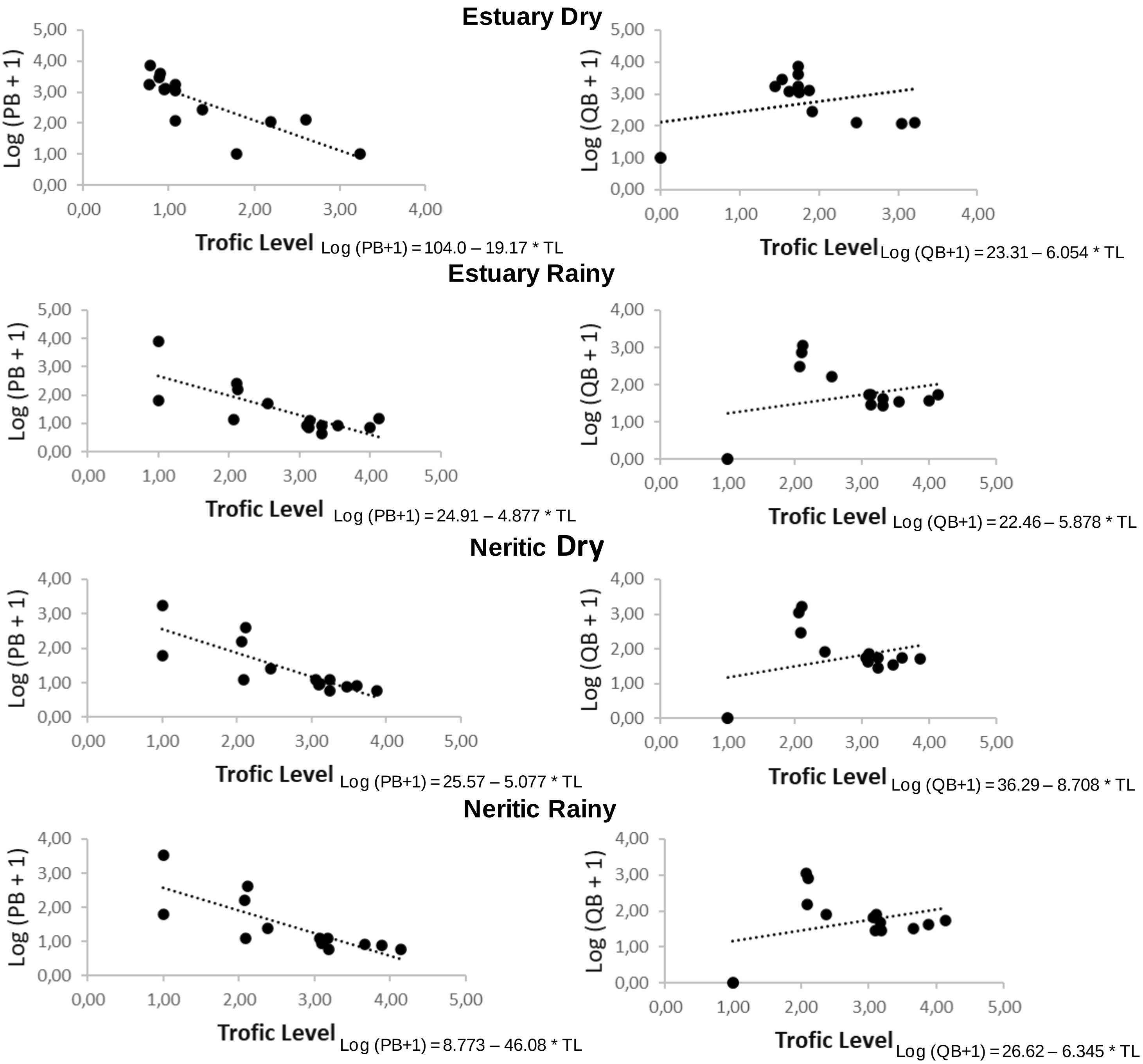
Supplementary Table 2- Model validation rates: P / Q: Production / Consumption Rate (values must be between 0.1 and 0.3); R / A: Respiration / Assimilation Rate (values must be less than 1.0); R/B: Respiration rate/biomass (values should be 1 to 10 for fish and 50 to 100 for groups with higher turnover rates). Values in bold do not meet the requirements.

	Group Names	P / Q	R / A	R / B
Estuary Dry	Phytoplankton			
	Macroalgae			
	Zooplankton	0.33	0.58	35.15
	Suspensivores Macrobenthos	0.14	0.82	72.70
	Carnivores Macrobenthos	0.30	0.62	4.02
	Epipelagic Suspens Macrobent Fish	0.24	0.69	1.59
	Epipelagic Pisc Fish	0.19	0.76	2.23
	Estuarine Associated Suspens Macrobent Fish	0.20	0.75	3.89
	Estuarine Associated Carniv Macrobent Fish	0.17	0.79	3.13
	Estuarine Associated Detrit Fish	**0.05**	0.94	**22.53**
	Estuarine Associated Pisc Fish	0.19	0.76	2.65
	Estuarine Associated Zoo Fish	0.16	0.79	3.33
	Reef Associated Carniv Macrobent Fish	0.15	0.81	1.82
	Reef Associated Pisc Fish	0.28	0.65	2.80
Estuary Rainy	Phytoplankton			
	Macroalgae			
	Zooplankton	0.33	0.58	35.15
	Suspensivores Macrobenthos	0.14	0.82	72.71
	Carnivores Macrobenthos	0.30	0.62	8.04
	Epipelagic Suspens Macrobent Fish	0.24	0.69	1.59
	Epipelagic Pisc Fish	0.19	0.76	2.23
	Estuarine Associated Suspens Macrobent Fish	0.24	0.71	3.12
	Estuarine Associated Carniv Macrobent Fish	0.20	0.75	2.58
	Estuarine Associated Detrit Fish	**0.05**	0.94	**22.53**
	Estuarine Associated Pisc Fish	0.24	0.70	1.91
	Estuarine Associated Zoo Fish	0.16	0.80	3.44
	Reef Associated Carniv Macrobent Fish	0.15	0.81	1.82
	Reef Associated Pisc Fish	0.28	0.65	2.80

	Group Names	P / Q	R / A	R / B
Neritic Dry	Phytoplankton			
	Macroalgae			
	Zooplankton	0.25	0.58	56.00
	Suspensivores Macrobenthos	0.14	0.82	72.70
	Carnivores Macrobenthos	0.30	0.62	4.02
	Epipelagic Suspens Macrobent Fish	0.21	0.74	2.47
	Epipelagic Pisc Fish	0.15	0.82	3.58
	Estuarine Associated Suspens Macrobent Fish	0.21	0.73	3.32
	Estuarine Associated Carniv Macrobent Fish	0.22	0.72	3.14
	Estuarine Associated Detrit Fish	**0.04**	0.95	**22.71**
	Estuarine Associated Pisc Fish	0.23	0.71	1.94
	Estuarine Associated Zoo Fish	0.12	0.85	5.05
	Reef Associated Carniv Macrobent Fish	0.21	0.74	1.65
	Reef Associated Pisc Fish	0.11	0.86	3.70
Neritic Rainy	Phytoplankton			
	Macroalgae			
	Zooplankton	0.50	0.38	24.00
	Suspensivores Macrobenthos	0.14	0.82	72.70
	Carnivores Macrobenthos	0.30	0.62	4.02
	Epipelagic Suspens Macrobent Fish	0.31	0.61	1.40
	Epipelagic Pisc Fish	0.24	0.70	1.90
	Estuarine Associated Suspens Macrobent Fish	0.18	0.77	4.11
	Estuarine Associated Carniv Macrobent Fish	0.25	0.69	2.69
	Estuarine Associated Detrit Fish	**0.08**	0.90	**10.75**
	Estuarine Associated Pisc Fish	0.18	0.77	2.68
	Estuarine Associated Zoo Fish	0.12	0.86	5.39
	Reef Associated Carniv Macrobent Fish	0.21	0.74	1.65
	Reef Associated Pisc Fish	0.11	0.86	3.70



Supplementary Figure 1- Prebal to evaluate the quality of the data entered in the estuarine and neritic models, in the dry and rainy seasons of the Southwest Tropical Atlantic. Biomass (Log B + 1) and Production / Consumption Rate (log (P / Q + 1) in relation to Trophic Level (TL).



Supplementary Figure 2- Prebal to evaluate the quality of the data entered in the estuarine and neritic models, in the dry and rainy seasons of the Southwest Tropical Atlantic. Production / Biomass (Log PB + 1) and Consumption Rate / Biomass (log QB + 1) in relation to Trophic Level (TL).

Supplementary Table 3- Pedigree index values to assess the quality of data entered in the estuarine and neritic models, in the dry and rainy seasons of the Southwest Tropical Atlantic. B: Biomass. P / B: Production / Biomass. Q / B: Consumption / Biomass; DC: Diet composition (1 = highest accuracy. 0 = lowest accuracy).

	Group Names	**B**	**P / B**	**Q / B**	**D / C**
Estuary Dry	Phytoplankton	0.0	0.2		
	Macroalgae	0.0	0.2		
	Zooplankton	0.0	0.2	0.2	0.2
	Suspensivores Macrobenthos	0.0	0.2	0.2	0.2
	Carnivores Macrobenthos	0.0	0.2	0.2	0.2
	Epipelagic Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Epipelagic Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Carniv Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Detrit Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Zoo Fish	1.0	0.5	0.5	1.0
	Reef Associated Carniv Macrobent Fish	0.7	0.5	0.5	1.0
	Reef Associated Pisc Fish	0.7	0.5	0.5	1.0
	Phytoplankton	0.0			
Estuary Rainy	Phytoplankton	0.0	0.2		
	Macroalgae	0.0	0.2		
	Zooplankton	0.0	0.2	0.2	0.2
	Suspensivores Macrobenthos	0.0	0.2	0.2	0.2
	Carnivores Macrobenthos	0.0	0.2	0.2	0.2
	Epipelagic Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Epipelagic Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Carniv Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Detrit Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Zoo Fish	1.0	0.5	0.5	1.0
	Reef Associated Carniv Macrobent Fish	0.7	0.5	0.5	1.0
	Reef Associated Pisc Fish	0.7	0.5	0.5	1.0
	Phytoplankton	0.0			

	Group Names	B	P / B	Q / B	D / C
Neritic Dry	Phytoplankton	0.0	0.2		
	Macroalgae	0.0	0.2		
	Zooplankton	0.0	0.2	0.2	0.2
	Suspensivores Macrobenthos	0.0	0.2	0.2	0.2
	Carnivores Macrobenthos	0.0	0.2	0.2	0.2
	Epipelagic Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Epipelagic Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Carniv Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Detrit Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Zoo Fish	1.0	0.5	0.5	1.0
	Reef Associated Carniv Macrobent Fish	0.7	0.5	0.5	1.0
	Reef Associated Pisc Fish	0.7	0.5	0.5	1.0
	Phytoplankton	0.0			
Neritic Rainy	Phytoplankton	0.0	0.2		
	Macroalgae	0.0	0.2		
	Zooplankton	0.0	0.2	0.2	0.2
	Suspensivores Macrobenthos	0.0	0.2	0.2	0.2
	Carnivores Macrobenthos	0.0	0.2	0.2	0.2
	Epipelagic Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Epipelagic Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Suspens Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Carniv Macrobent Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Detrit Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Pisc Fish	1.0	0.5	0.5	1.0
	Estuarine Associated Zoo Fish	1.0	0.5	0.5	1.0
	Reef Associated Carniv Macrobent Fish	0.7	0.5	0.5	1.0
	Reef Associated Pisc Fish	0.7	0.5	0.5	1.0
	Phytoplankton	0.0			

Supplementary Table 4- A - PERMANOVA using Bray-Curtis similarity matrix for biomass of fish compartments in ecosystems (estuary and neritic) and seasons (dry and rainy), in the tropical southwest Atlantic. DF = Degree of Freedom (values with an asterisk: p <0.05). B – Post-hoc indicating where the differences are. C – Percentage similarity test (SIMPER) for compartments that most contributed to generate dissimilarities between ecosystems (estuary and neritic) and seasons (dry and rainy), in the tropical southwest Atlantic.

A

Factor	**DF**	**Sums of squares**	**Pseudo F-value**	**p**
Ecosystem	**1**	**0.424**	**3.738**	**0.012***
Season	**1**	**0.401**	**3.538**	**0.039***
Interaction	**1**	**0.449**	**3.961**	**0.021***
Residuals	**105**	**11.912**		

B

		Estuary		**Neritic**	
		Dry	**Rainy**	**Dry**	**Rainy**
Estuarine zone	**Dry**	**1**			
	Rainy	**0.901**	**1**		
Neritic zone	**Dry**	**0.342**	**0.467**	**1**	
	Rainy	**0.004***	**0.027***	**0.067**	**1**

C

Compartment	**Average dissimilarity**	**Contribution (%)**	**Cumulative (%)**
Estuarine Associated Carniv Macrobent Fish	**28.47**	**30.30**	**30.30**
Epipelagic Piscivores Fish	**17.95**	**19.10**	**49.40**
Estuarine Associated Suspens Macrobent Fish	**17.05**	**18.15**	**67.55**
Estuarine associated – Piscivores Fish	**11.96**	**12.73**	**80.28**

Supplementary Table 5- (A) Signal changes of the Impact Matrix between environments (neritic-estuary) in the same seasons (dry and rainy) and in the same environment, considering different seasons. The values indicate the number of times (in relative and absolute values) in which there was a change in sign between impacted and impacted groups. (B) List of groups that suffered the most changes between positive (+) and negative (-) signs between environments, in the same seasons and in the same environment, considering different seasons. Bold groups lead the ranking of changes.

A

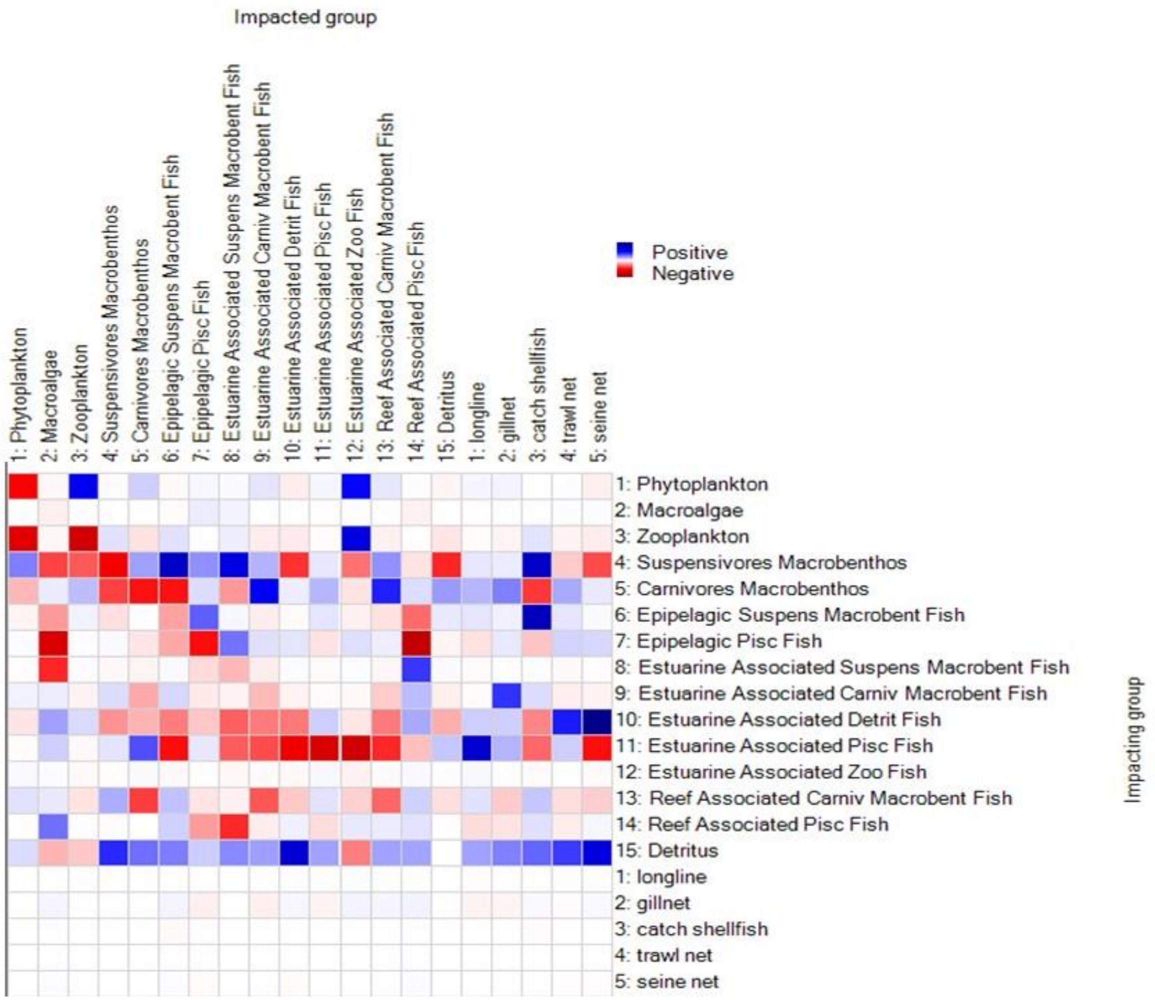
Change of signal (%) in comparisons		**Dry**		**Rainy**
	Estuary		12%	
		31%		32%
	Neritic		20%	
Magnitude of changes in comparisons		**Dry**		**Rainy**
	Estuary		12.14	
		28.38		25.17
	Neritic		20.25	

B

Estuary (dry to rain)		**Neritic (dry to rainy)**	
impacted	**Impacting**	**impacted**	**Impacting**
Macroalgae	**Epipelagic Pisc Fish**	**Estuarine Associated Pisc Fish**	**Estuarine Associated Pisc Fish**
Reef Associated Pisc Fish	Reef Associated Carniv Macrobent Fish	Estuarine Associated Detrit Fish	**Reef Associated Pisc Fish**
Epipelagic Pisc Fish	**Reef Associated Pisc Fish**	Reef Associated Carniv Macrobent Fish	Epipelagic Pisc Fish
trawl net	Estuarine Associated Pisc Fish	**Reef Associated Pisc Fish**	gillnet
Estuarine Associated Suspens Macrobent Fish	**Estuarine Associated Suspens Macrobent Fish**	Estuarine Associated Zoo Fish	Carnivores Macrobenthos

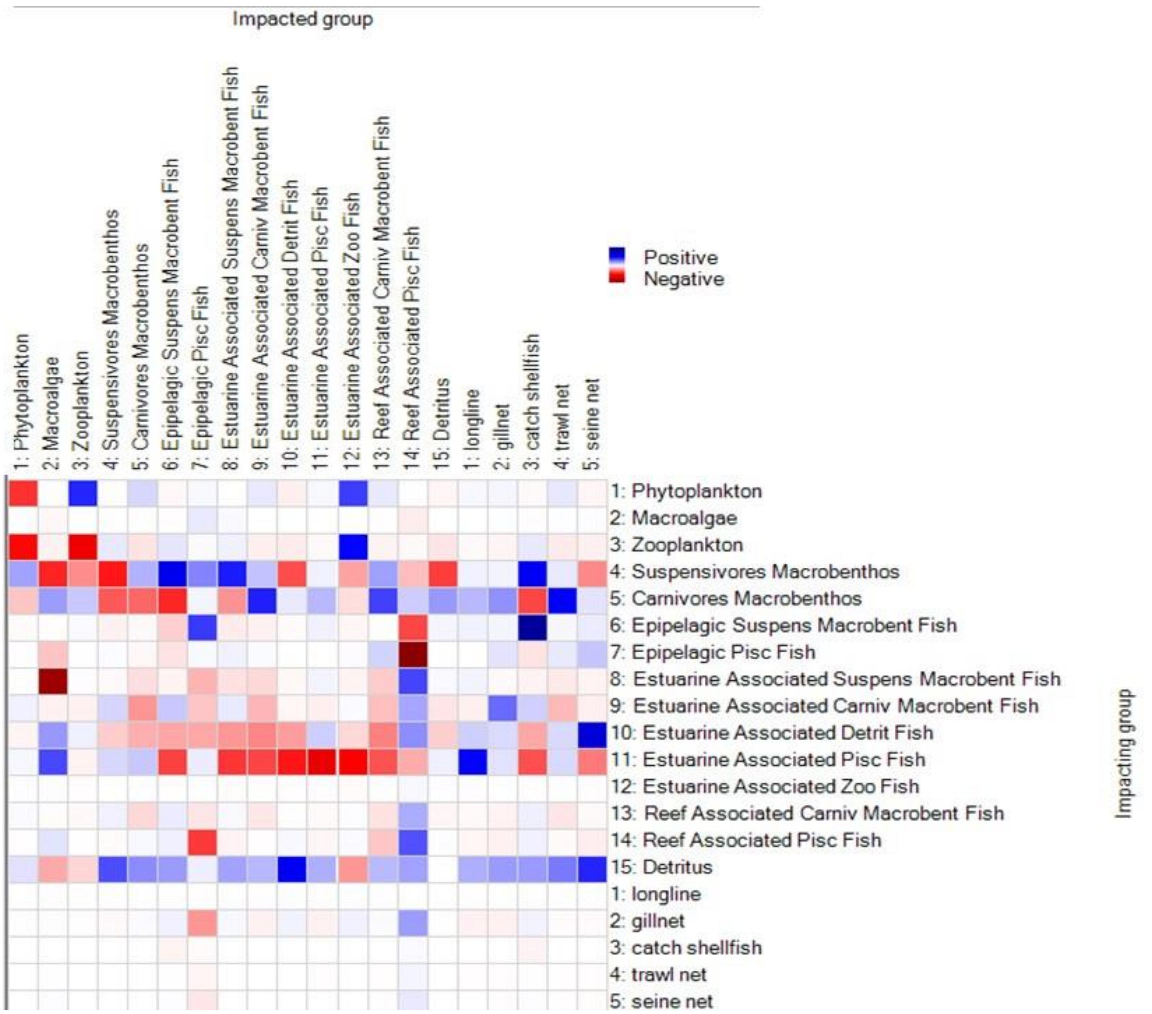
Dry (Estuary and Neritic)		**Rainy (Estuary and Neritic)**	
impacted	**Impacting**	**Impacted**	**Impacting**
Estuarine Associated Detrit Fish	Estuarine Associated Pisc Fish	**Reef Associated Pisc Fish**	Estuarine Associated Pisc Fish
Reef Associated Carniv Macrobent Fish	gillnet	**Epipelagic Pisc Fish**	**Epipelagic Pisc Fish**
Epipelagic Suspens Macrobent Fish	Epipelagic Pisc Fish	catch shellfish	**Reef Associated Pisc Fish**
Reef Associated Pisc Fish	**Estuarine Associated Detrit Fish**	**Epipelagic Suspens Macrobent Fish**	**Epipelagic Suspens Macrobent Fish**
Estuarine Associated Carniv Macrobent Fish	Carnivores Macrobenthos	Estuarine Associated Suspens Macrobent Fish	Estuarine Associated Detrit Fish

Estuary Dry



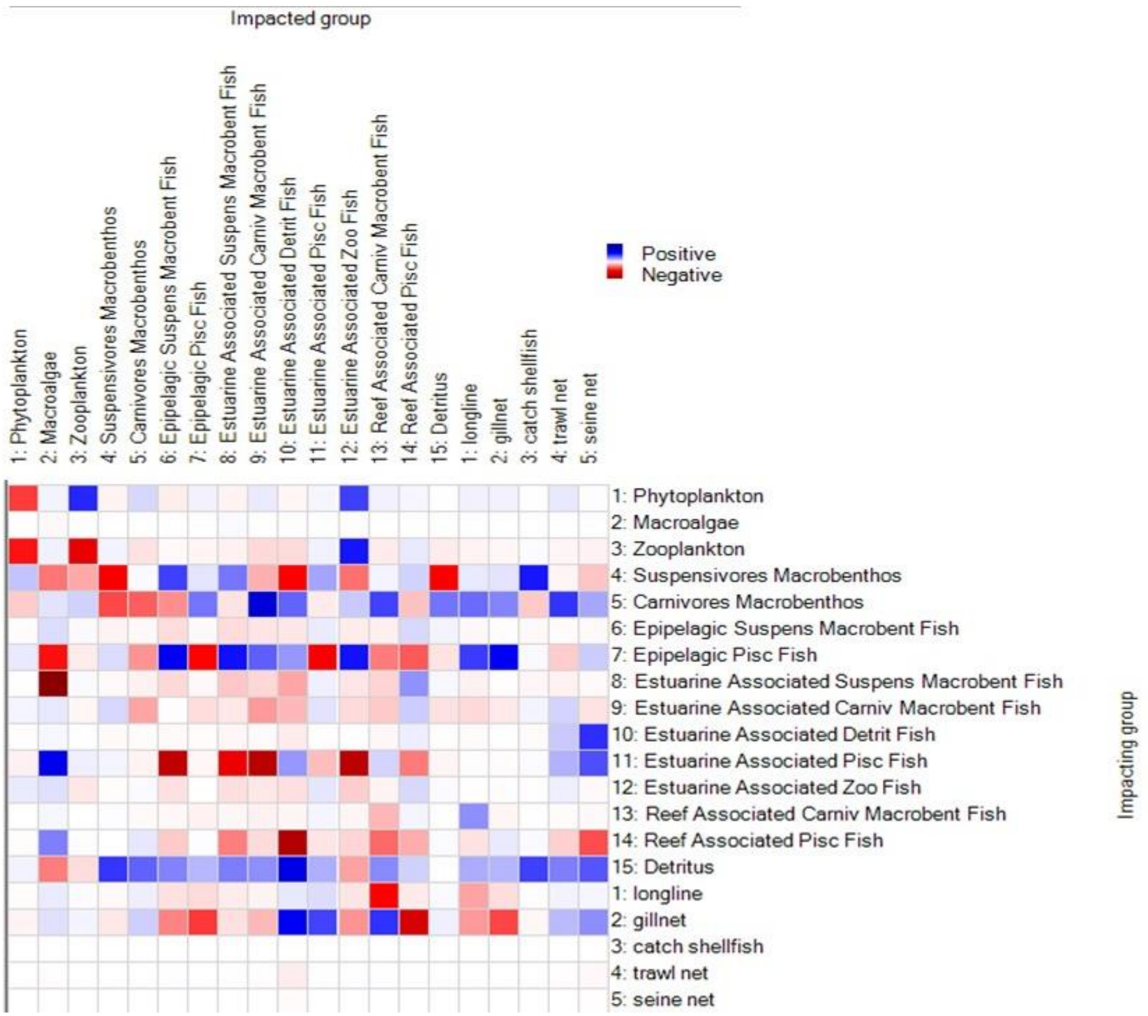
Supplementary Figure 3- Mixed Impact Matrix (MTI) for the estuary during the dry season of the Southwest Tropical Atlantic. The x and y axes represent impacted groups and impacted groups, respectively. The color box shows negative (red) or positive (blue) impacts on the functional groups. The color intensity in the box is proportional to the degree of impacts and its values range from -1 to +1.

Estuary Rainy



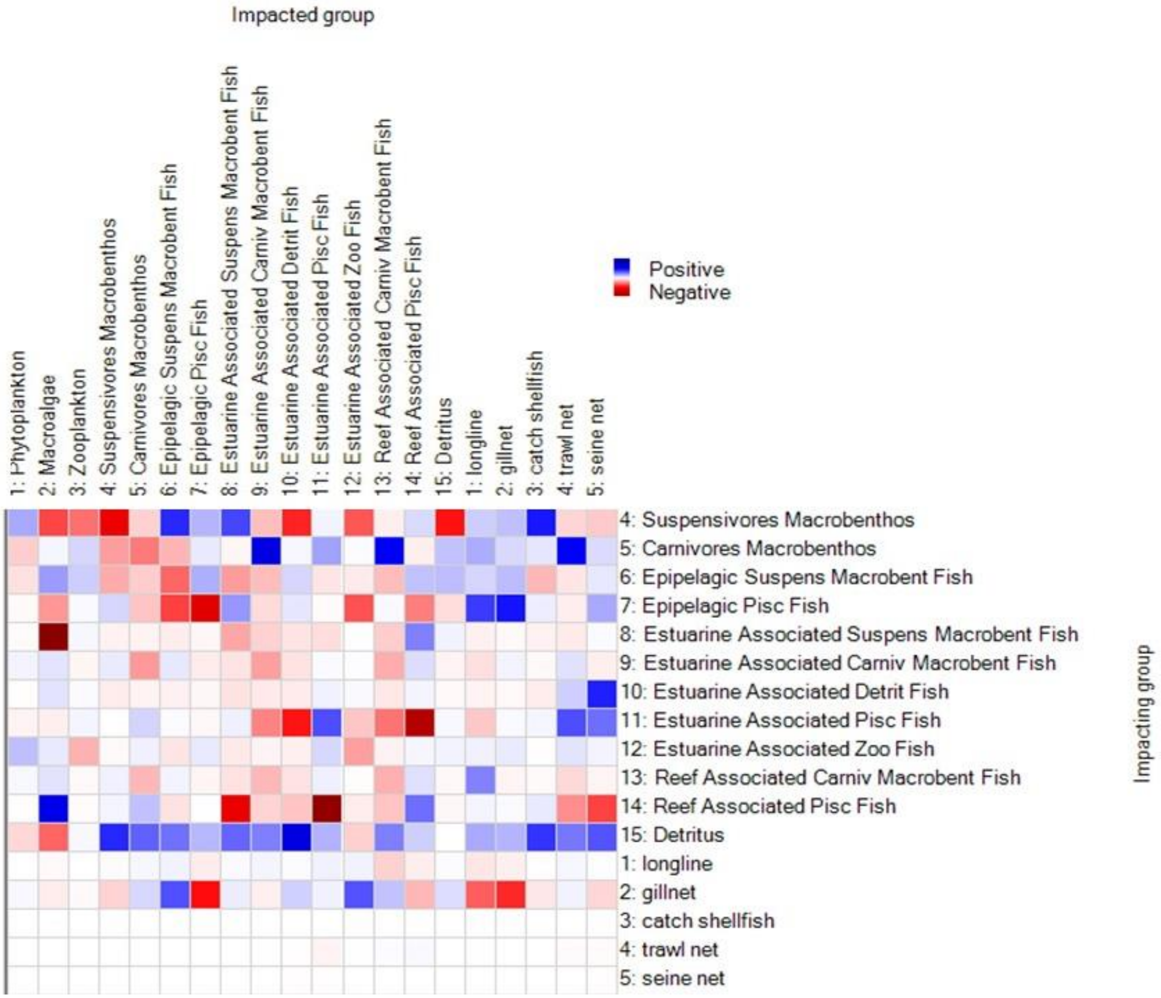
Supplementary Figure 4- Mixed Impact Matrix (MTI) for the estuary during the rainy season of the Southwest Atlantic Tropical. The x and y axes represent impacted groups and impacted groups, respectively. The color box shows negative (red) or positive (blue) impacts on the functional groups. The intensity of the color in the box is proportional to the degree of impacts and its values range from -1 to +1.

Neritic Dry



Supplementary Figure 5- Mixed Impact Matrix (MTI) for neritic during the dry season of the Southwest Tropical Atlantic. The x and y axes represent impacted groups and impacted groups, respectively. The color box shows negative (red) or positive (blue) impacts on the functional groups. The intensity of the color in the box is proportional to the degree of impacts and its values range from -1 to +1.

Neritic Rainy



Supplementary Figure 6- Mixed Impact Matrix (MTI) for neritic during the rainy season of the Southwest Atlantic Tropical. The x and y axes represent impacted groups and impacted groups, respectively. The color box shows negative (red) or positive (blue) impacts on the functional groups. The color intensity in the box is proportional to the degree of impacts and its values range from -1 to +

Supplementary Table 6- Key species of the estuarine and neritic models, in the dry and rainy seasons of the Southwest Tropical Atlantic.

Ranking #3	**Ecosystems**			
	Estuary		**Neritic**	
	Dry	**Rainy**	**Dry**	**Rainy**
1º	**Epipelagic Pisc Fish**	**Epipelagic Pisc Fish**	**Reef Associated Pisc Fish**	**Reef Associated Pisc Fish**
2º	**Estuarine Associated Pisc Fish**	**Estuarine Associated Suspens Macrobent Fish**	**Estuarine Associated Suspens Macrobent Fish**	**Estuarine Associated Pisc Fish**
3º	**Reef Associated Pisc Fish**	**Estuarine Associated Pisc Fish**	**Epipelagic Pisc Fish**	**Estuarine Associated Suspens Macrobent Fish**
4º	**Estuarine Associated Suspens Macrobent Fish**	**Reef Associated Pisc Fish**	**Estuarine Associated Pisc Fish**	**Zooplankton**
5º	**Phytoplankton**	**Carnivores Macrobenthos**	**Zooplankton**	**Epipelagic Pisc Fish**
6º	**Suspensivores Macrobenthos**	**Epipelagic Suspens Macrobent Fish**	**Phytoplankton**	**Suspensivores Macrobenthos**

5 DISCUSSÃO GERAL

Modelos metapopulacionais descrevem um sistema aberto, onde extinção e colonização são eventos dependentes do movimento de indivíduos entre um conjunto de manchas ou habitats irregulares onde as subpopulações estão inseridas (Hastings 1997). Quando os indivíduos se movem com frequência entre subpopulações, as catástrofes locais e flutuações no número de indivíduos são amortecidas. Em contra partida, quando não há movimento entre as manchas, as subpopulações se comportam independentemente, ficando mais susceptíveis a eventos de extinção (Levins 1969, Ricklefs 2003).

Na perspectiva do metaecossistema esses pressupostos continuam sendo respeitados, no entanto, os movimentos de indivíduos passam a ser representados por fluxos de matéria e energia que subsidiam a manutenção e o desenvolvimento desses ecossistemas, garantindo a persistência do metaecossistema em escala mais ampla (REF. LOREAU). A frequência e a intensidade desses fluxos determinarão o grau de conectividade entre seus componentes, enquanto o sentido dos fluxos determina o papel de cada componente na dinâmica fonte-sumidouro.

Apesar do elevado grau de abstração da teoria proposta por Loreau, Mouquet e Holt (2003), os pressupostos para que se estabeleça um metaecossistema foram devidamente evidenciados neste trabalho: (1) Similaridade de compartimentos inter-ecossistêmicos em interação; (2) Restrição de fluxos a compartimentos equivalentes; (3) Conservação da natureza das interações locais.

Em todos os modelos gerados (cap. 2 e 3) houve similaridade entre os grupos funcionais dos ecossistemas estuário e nerítico e um padrão assincrônico na distribuição da biomassa desses grupos, pressupondo a ocorrência de um efeito compensatório, onde a redução da biomassa de um ou mais compartimentos dentro de um ecossistema local resulta no incremento da biomassa desses mesmos compartimentos no outro ecossistema, o que demonstra um elevado grau de interação entre compartimentos inter-ecossistêmicos similares (pressuposto 1). Além disso, a presença dos mesmos grupos funcionais permite a restrição dos fluxos entre compartimentos inter-ecossistêmicos similares (pressuposto 2). Finalmente, a conservação da natureza das interações locais (pressuposto 3) é favorecida pela conectividade. Essa, atenua as perdas de biomassa dentro dos compartimentos, ao permitir o movimento de indivíduos ou grupos entre diferentes ecossistemas frente às flutuações ambientais. Isso reduz a mortalidade e consequentemente as chances de extinções de grupos funcionais, conservando a integridade trófica de cada ecossistema local.

No presente trabalho ficou evidente que a sazonalidade, marcada pela mudança no regime de chuvas, representa a principal força motriz da conectividade entre os ecossistemas e indiretamente determina o sentido dos fluxos no modelo fonte-sumidouro (Loreau, Mouquet and Holt 2003). Com a variação sazonal cria-se uma tendência de alternância funcional entre quem exerce o papel de fonte e quem exerce a função de sumidouro ao longo de um ciclo sazonal. Isso ficou evidente, principalmente no capítulo 2, através da derivada proposta por Loreau, Mouquet and Holt (2003), descrevendo a mudança instantânea no estoque de nutrientes por compartimento, entre estuário e nerítico, adaptada para os períodos seco e chuvoso.

A inclusão de compartimentos não-peixes nos modelos gerados com auxílio do software Ecopath permitiu discriminar o papel de cada ecossistema local dentro do metaecossistema. Durante a estação chuvosa o sistema estuarino exerce o papel de fonte para o nerítico, através do processo de estuarização. Durante esse período ocorre o fluxo de organismos e a descarga de sedimentos ricos em matéria orgânica. Este último, subsidia o incremento da produção primária e a formação dos bancos de lama que predispõe ao aumento da biomassa de organismos bentônicos. Portanto, o sistema estuarino fomenta diretamente a reposição de componentes que formam a base das cadeias tróficas locais. Ao mesmo tempo em que favorece a convergência trófica metaecossistêmica dentro do sistema nerítico (capítulo 2). Isso beneficia indiretamente o sistema oceânico através da disponibilização de recursos para o forrageio de espécies epipelágicas.

Com o fim da estuarização, o sistema nerítico passa a atuar como fonte, no sentido de dissipar a matéria e a energia obtida durante a convergência trófica para os sistemas estuarino e oceânico, por meio do retorno dos organismos aos seus sistemas de origem. Hipotetizamos que a convergência trófica seja crucial para a reposição alimentar de predadores migradores, fornecendo a energia necessária para a reprodução e desova, que deve ocorrer em outros ecossistemas locais, principalmente nos estuários. Além disso, a convergência trófica amortece os efeitos da mortalidade natural e por pesca, ao promover a vinda de novos organismos, em substituição aos que foram predados. Embora não tenhamos analisado a estrutura trófica do ecossistema oceânico, consideramos a entrada de organismos epipelágicos como sendo uma importante fonte de recursos proveniente dessa região, nos permitindo integrar o sistema oceânico ao modelo meta-ecossistêmico composto pelos sistemas estuário-nerítico, tornando-se, portanto, estuário-nerítico-oceano.

Dentre os modelos metaecossistêmicos hipotetizados na literatura, o complexo estuário-nerítico-oceano enquadra-se no modelo baseado no fluxo de recursos (Gounand *et al.* 2018), no qual a finalidade dos fluxos varia entre seus componentes. Entre nerítico e oceano prevalece migrações ligadas ao forrageamento, enquanto estuário e nerítico estabelecem principalmente migrações relacionadas ao ciclo de vida. A adição de predadores de topo ao ecossistema nerítico tende a ocasionar pressões de cima para baixo na região, mas nossos resultados sugerem que a adição simultânea de espécies estuarinas e bentívoras promova um efeito estabilizador.

Embora tenhamos discriminado o tipo de modelo metaecossistêmico mais coerente com nossos resultados, bem como a finalidade dos fluxos, os modelos ainda são demasiadamente abstratos para que possamos compreender como entradas e saídas, de fato, afetam o desenvolvimento de seus componentes em diferentes escalas espaciais e temporais. Neste sentido, até aqui não haviam evidencias sobre como entradas e saídas pulsadas contribuiriam para o aumento da maturidade ecossistêmica.

Os modelos clássico e atual sobre o desenvolvimento dos ecossistemas não preveem a entrada de subsídios externos, tão pouco o efeito das variações temporais sobre a performance dos indicadores da maturidade ecossistêmica, dentre eles, PPB, PPL, Respiração e biomassa. Para nós está evidente que mudanças periódicas na performance desses índices, em função das flutuações ambientais, é incoerente com as ideias de estabilidade e linearidade ecossistêmica, visto que a sazonalidade é uma importante variável explicativa da mudança de performance desses índices, fazendo com que eles oscilem ao longo de um ciclo. A existência de fluxos é incompatível com as ideias de autorregulação e independência ecossistêmica, uma vez que, conectividade torna-se fator chave para manter a estrutura e a funcionalidade dos ecossistemas, em meio aos períodos com menores insumos. Isso torna os ecossistemas dependentes de subsídios adjacentes para sua regulação.

Com base nos resultados obtidos, podemos concluir que na ecologia de metaecossistemas costeiros tropicais, alcançar a estabilidade implica em atingir um estágio de equilíbrio dinâmico, no qual produção e consumo variam em função das flutuações ambientais ocasionadas pela sazonalidade. Nessa situação, o objetivo do metaecossistema é manter elevada a produção líquida de seus componentes locais, seja através dos fluxos de matéria orgânica, que subsidiam o aumento da produtividade primária, ou através da dispersão de organismos, que promove o aumento de biomassa, mesmo quando as condições ambientais são menos favoráveis, mantendo a homeostase dos sistemas. Dessa maneira, o metaecossistema não só persiste, tornando-se mais resistente e resiliente, mas evolui, ao facilitar, através dos subsídios, que seus componentes possam armazenar energia para empregar em possíveis mudanças e diversificações ao longo do tempo.