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

JORDANA RANGELY ALMEIDA SANTOS DE OLIVEIRA

PLASTICIDADE INDIVIDUAL E INTERESPECÍFICA NA HISTÓRIA DE VIDA DE ESPÉCIES DE *MUGIL* (TAINHAS) QUE CO-OCORREM EM AMBIENTES TROPICAIS: IMPLICAÇÕES PARA O MANEJO E CONSERVAÇÃO.

MACEIÓ - ALAGOAS
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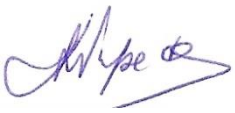

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Efésios 3:20

RESUMO

A plasticidade individual e variabilidade interespecífica desempenham um papel crucial na capacidade dos peixes de responder a mudanças ambientais o que influencia o ciclo de vida, como crescimento e maturação sexual. Em espécies congenéricas e morfologicamente semelhantes, esses mecanismos de plasticidade podem permitir a coexistência, gerando divergências sutis nas características da história de vida. O objetivo geral desta tese foi avaliar os traços de história de vida de forma interespecífica e a plasticidade individual no uso do habitat de espécies de *Mugil* que co-ocorrem em ambientes tropicais, verificando as implicações para o manejo e conservação. Para tanto, indivíduos de três espécies de *Mugil* foram capturados em quarto estuários tropicais e os seus otólitos foram utilizados, tanto para mensurar a idade quanto para fazer uma cronologia química dos primeiros estágios de vida. A pesquisa foi estruturada em quatro capítulos complementares que abordam diferentes aspectos da ecologia populacional e pesca. No primeiro, foram discutidos mecanismos de coexistência entre as espécies, relacionados a fatores abióticos. Verificou-se que *M. curema* é influenciada por fatores como temperatura, oxigênio dissolvido e turbidez e ocupa três ambientes durante a primeira fase do ciclo de vida enquanto *M. rubrioculus* é mais afetada pela variação na salinidade e se restrige à parte externa do estuário e ao mar. Então, apesar de filogeneticamente próximas, as duas espécies exibem diferentes padrões de uso do habitat. O segundo capítulo investiga o crescimento polifásico alométrico em otólitos, que se mostrou um bom indicador de eventos críticos do ciclo de vida, como a maturação sexual. As espécies de *Mugil* exibiram diferentes padrões de crescimento e maturação, sugerindo uma assincronia nos ciclos de vida que facilita a coexistência, sendo que *M. rubrioculus* (K = 0,31) apresenta maior velocidade de crescimento e *M. liza* um crescimento mais lento (K = 0,21), enquanto *M. curema* (K=25) é a espécie intermediária. Foi observado que a velocidade de crescimento possui dois pontos de mudança ao longo da vida, sendo o segundo associado a migração reprodutiva para o mar. No terceiro capítulo, foi analisada a dependência estuarina e a plasticidade no uso do habitat. *M. liza* foi a espécie que passou mais tempo na fase inicial de vida no estuário. Por outro lado, *M. rubrioculus*, apresentou menor dependência estuarina. *M. curema* destacou-se pela maior plasticidade individual no uso de habitats, exibindo maior migração parcial. O quarto capítulo conclui que *M. liza* é a espécie mais vulnerável à pesca, com uma redução para apenas 20% do estoque original. Essa vulnerabilidade pode ser relacionada à sua menor plasticidade e maior permanência no estuário. O estudo destaca a importância de incluir o Conhecimento Ecológico Local (LEK) no manejo sustentável das espécies, por meio de uma abordagem participativa que envolva pescadores, gestores e cientistas. Assim, conclui-se que a coexistência das espécies de Mugilidae é sustentada por complexos mecanismos ecológicos, nos quais o uso do habitat e a plasticidade fenotípica desempenham papéis cruciais. A gestão adequada desses recursos deve considerar a variabilidade ambiental, as peculiaridades de cada espécie e as interações entre diferentes agentes sociais, como pescadores, gestores e cientistas pesqueiros, para promover a sustentabilidade dos estoques pesqueiros de forma horizontal e participativa.

Palavras-chave: *trade-off*. otólito. crescimento. migração parcial.

ABSTRACT

Individual plasticity and interspecific variability play a crucial role in the ability of fish to respond to environmental changes which influence the life cycle such as growth and sexual maturation. In congeneric and morphologically similar species, these plasticity mechanisms can allow coexistence, generating subtle divergences in life history characteristics. The general objective of this thesis was to evaluate interspecific life history traits and individual plasticity in habitat use of Mugil species that co-occur in tropical environments, verifying the implications for management and conservation. To this end, individuals of three *Mugil* species were captured in four tropical estuaries and their otoliths were used, both to measure age and to make a chemical chronology of the first stages of life. The research was structured into four complementary chapters that address different aspects of population ecology and fishing. In the first, mechanisms of coexistence between species were discussed, related to abiotic factors. It was found that *M. curema* is influenced by factors such as temperature, dissolved oxygen and turbidity and occupies three environments during the first phase of its life cycle, while *M. rubrioculus* is more affected by variations in salinity and is restricted to the external part of the estuary and to the sea. Therefore, despite being phylogenetically close, the two species exhibit different patterns of habitat use. The second chapter investigates allometric polyphasic growth in otoliths, which has been shown to be a good indicator of critical life cycle events such as sexual maturation. *Mugil* species exhibited different growth and maturation patterns, suggesting an asynchrony in life cycles that facilitates coexistence, with *M. rubrioculus* (K = 0.31) showing a higher growth speed and *M. liza* showing slower growth (K = 0.31) K = 0.21), while *M. curema* (K=25) is the intermediate species. It was observed that growth speed has two points of change throughout life, the second being associated with reproductive migration to the sea. In the third chapter, estuarine dependence and plasticity in habitat use were analyzed. *M. liza* was the species that spent the most time in the initial phase of life in the estuary. On the other hand, *M. rubrioculus* showed less estuarine dependence. *M. curema* stood out for its greater individual plasticity in habitat use, exhibiting greater partial migration. The fourth chapter concludes that *M. liza* is the species most vulnerable to fishing, with a reduction to just 20% of the original stock. This vulnerability may be related to its lower plasticity and longer stay in the estuary. The study highlights the importance of including Local Ecological Knowledge (LEK) in the sustainable management of species, through a participatory approach that involves fishermen, managers and scientists. Thus, it is concluded that the coexistence of Mugilidae species is sustained by complex ecological mechanisms, in which habitat use and phenotypic plasticity play crucial roles. The appropriate management of these resources must consider environmental variability, the peculiarities of each species and the interactions between different social agents, such as fishermen, managers and fisheries scientists, to promote the sustainability of fishing stocks in a horizontal and participatory way.

Key-word: trade-off. otolith. growth. partial migration.

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1 APRESENTAÇÃO

A história de vida de um organismo compreende o padrão de crescimento, a diferenciação morfológica, a armazenagem de energia e a reprodução (Begon *et al.*, 2009, Rochet 2000). A variação no ciclo de vida frequentemente está correlacionada com esses parâmetros, assim como, com o ambiente em que esse organismo se desenvolve (Winemiller, 1989, Phillips *et al.,* 2010). Considerando que os organismos vivem em um mundo finito, o conceito de alocação limitada dos recursos durante o ciclo de vida permite sustentar hipóteses sobre o destino dos recursos investidos pelo organismo para uma dada atividade implicarará em tornam-se indisponíveis para outras (Roff, 1992; Stearns, 1992; Ricklefs, 2003, Begon *et al.,* 2007).

Sendo assim, a alocação de energia para reprodução e crescimento pode influenciar o desempenho individual e consequentemente a dinâmica populacional (Roff, 1992; Stearns, 1992). Essa relação negativa entre dois traços da história de vida é chamada de *trade-off*, e possui um ponto de inflexão de alocação, justamente quando o indivíduo diminui ou cessa a alocação de energia para um dos traços e investe em outro, como uma gangorra de alocação. A plasticidade individual também afeta a dinâmica populacional, permitindo respostas adaptativas às mudanças ambientais por meio de alterações na fisiologia e comportamento. (Begon, *et al*., 2007, Wooton, 1990).

Compreender a plasticidade individual e interespecífica da história de vida de espécies de peixes do género *Mugil* é fundamental, principalmente se tratando de espécies congenéricas que co-ocorrem em ecossistemas estuarinos. São espécies de peixe estuarino-dependentes obrigatórias, que possuem uma área de criação (estuário) e uma área de reprodução (mar) (Able, 2005, Fowler *et al*., 2016, Santana *et al*., 2018). Dessa forma, essas espécies podem ter o ponto de inflexão do *trade-off* intimamente relacionado ao uso de habitat e impactando o desempenho desses organismos. Se partimos do pressuposto de que a estuarino dependência gera um ponto de inflexão no ciclo de vida, já que o organismo sai da área de crescimento e parte para a área de reprodução, seria o momento onde as espécies de *Mugil* sofrem o impacto do *trade-off*. Quanto maior a estuarino-dependência, ou seja, quanto mais tempo eles passam no

estuário, maior é o pré ponto de inflexão e isso poderá se traduzir em maior tamanho. Assim sendo, a estuarino-dependência poderá explicar diferenças interespecíficas no crescimento das espécies, pois está relacionada com o pré ponto de inflexão, que segundo Sousa e colaboradores (2015) é a etapa do ciclo de vida com investimento em crescimento. Esse uso diferenciado de habitat, bem como traços de história de vida, pode ser rastreados por meio dos otólitos, pois são estruturas conservativas que fornecem uma cronologia química da vida do peixe, (Albuquerque *et al*., 2010; Avigliano & Volpedo, 2013)

Ressaltamos ainda a importância dos Mugilidae enquanto recurso pesqueiros, visto que compõem 20% da captura no Brasil (MPA, 2011), o que os qualifica como espécies cujo manejo e conservação é de interesse socio-econômico para o país, em especial no Nordeste, onde coexistem pelo menos seis espécies do gênero (Menezes *et al*., 2015, Neves *et al.* 2021) e todas são explotadas pela pesca, sendo conhecidas como tainhas. Neste contexto, o objetivo geral dessa tese é avaliar os traços de história de vida de forma interespecífica e a plasticidade individual no uso do habitat de espécies de *Mugil* que co-ocorrem em ambientes tropicais, verificando as implicações para o manejo e conservação. Para atingir esse objetivo geral, a tese foi organizada em quatro capítulos independentes e complementares, cada um gerou um artigo científico.

Capítulo 01 - Objetivo: identificar padrões temporais e espaciais na distribuição de *M. curema* e *M. rubrioculus* em ambiente tropical estuário do Atlântico Sudoeste. Pergunta: qual é o papel da variabilidade ambiental na formação dos padrões de distribuição destes peixes em um local escala? Hipótese: espécies congenéricas morfologicamente semelhantes apresentam segregação temporal impulsionada por diferentes respostas a fatores ambientais como mecanismo para permitir a coexistência.

Capítulo 02 – Objetivo: fornecer parâmetros de crescimento com base nas relações comprimento-idade de três espécies de tainhas tropicais exploradas (*M. curema, M. liza, M. rubrioculus*) e integrar informações de idade e crescimento polifásico alométrico de otólitos e reprodução. Hipótese: (1) a alometria polifásica otolítica pode com precisão prever a idade de maturação; (2) seguindo a teoria de história de vida, a espécie menor e de crescimento mais rápido exibirá maturação mais precoce e mudança

na velocidade de crescimento em idades mais jovens, enquanto que a espécie de crescimento mais lento apresentará maturação e alterações alométricas tardias.

Capítulo 03: Objetivo: Determinar a variabilidade individual na estuarino-dependência para as espécies de Mugilidae relacionada a primeira fase do seu ciclo de vida. Hipótese: A maior estuarino-dependência implica em uma menor plasticidade individual nas estratégias de utilização de habitats estuarinos e costeiros por Mugilideos.

Capítulo 04: Objetivo: integrar Conhecimento Científico Convencional (CSK) e Conhecimento Ecológico Local (LEK) como meio de promover a melhor gestão pesqueira de tainhas. Especificamente, foi avaliado a situação dos estoques de três espécies de tainha (*M. curema*, *M. liza* e *M. rubrioculus*). Além disso, empregamos LEK como método complementar para reunir informações importantes sobre a história de vida e a pesca, bem como identificar os pontos fortes, fraquezas, oportunidades e ameaças associadas às pescarias estudadas.

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2 REVISÃO DA LITERATURA

2.1 História de vida

A história de vida não é uma propriedade fixa que o organismo exibe, mas sim o resultado de forças evolutivas de longo prazo acrescida das respostas imediatas de um organismo ao ambiente no qual ele está inserido (Begon et al., 2007, Phillips et al., 2010). A variação em um traço de história de vida, como crescimento, fecundidade ou maturidade, está frequentemente correlacionada a variação em outro traço e com o ambiente em que esse organismo ocupa, ou seja, é como um complexo conjunto de traços co-evoluídos, que estão diretamente ligados ao *fitness* (Roff 1984, Ricklefs, 2003, Stearns 1992, Rochet 2000).

Esses traços também variam em níveis biológicos, por exemplo, entre as espécies (Winemiller & Rose, 1992) entre os indivíduos (Heins & Baker, 1987; Fowler *et al.*, 2016) e entre as populações (Soeth *et al*., 2019). A variação em uma característica de história de vida pode ser vista de maneira diferente dependendo do nível organizacional biológico de comparação. Comparar os traços de duas ou mais espécies e buscar entender as diferenças entre eles, à luz dos ambientes que as espécies ocupam é imperativo (Wooton, 1990; Devine *et al*., 2012; Midway & Peoples, 2019). Nesse sentido, os principais traços de história de vida a serem analisados são: tamanho/idade na maturidade, tamanho/idade máxima, taxa de crescimento e fecundidade (Winemiller, 1989).

O tamanho corporal, traço de história de vida mais evidente, é um indicador da necessidade energética e superioridade inter e intraespecífica e, desta forma, é esperado que indivíduos e/ou espécies maiores tenham acesso aos melhores recursos disponíveis, como alimento e espaço (Letourneur, 2000). Combinando o tamanho corporal (comprimento total) com a idade é possível avaliar o crescimento somático, outro importante traço de história de vida. A estimativa dos parâmetros de crescimento é uma importante ferramenta para avaliação da dinâmica de populações, e também essencial para o entendimento dos eventos do ciclo de vida, aspectos comportamentais e a conservação e manejo de espécies (Fabré & SaintPaul, 1998; Sousa *et al*., 2015). Nas

regiões tropicais, as taxas de crescimento são influenciadas pelo período sazonal, o habitat ocupado pela espécie, as fases do ciclo de vida e os recursos alimentares (Boujard *et al*., 1991, Lowe-McConnel, 1991).

O padrão reprodutivo pode ser conceituado como o conjunto de atributos que uma espécie possui para obter sucesso reprodutivo e manter populações estáveis (Winemiller, 2005). Este padrão engloba: tamanho de primeira maturação, desenvolvimento gonadal, tamanho do ovócito, tipo de desova e fecundidade (Vazzoler, 1996; Winemiller, 2005). A reprodução está adaptada, principalmente, às condições ambientais e a pressão de predação (Stearns 1976, Winemiller, 1989, Wilson *et al*., 2019). Por exemplo, o aumento da disponibilidade de alimentos, ou seja, um ambiente que propicie um forrageamento de qualidade, aumentou o crescimento, reduzindo a idade na maturidade e aumentando a expectativa de vida reprodutiva do adulto para o peixe *Salvelinus namaycush* (Wilson et al. 2018). Além disso, para muitos animais, a seleção sexual e/ou os custos reprodutivos levam a taxas de crescimento diferenciais e/ou tamanhos corporais máximos divergentes entre machos e fêmeas (Andersson 1994; Love *et al.* 1990).

No contexto dos peixes, a estimativa dos parâmetros de crescimento frequentemente emprega a função de crescimento de von Bertalanffy (VBGF), e as interações entre esses parâmetros são utilizadas como indicadores das estratégias de história de vida (Beverton & Holt, 1957; Ricker, 1975). Por exemplo, espécies com taxas de crescimento relativamente rápidas costumam ser caracterizadas por atingir a maturidade sexual em idades e tamanhos reduzidos, o que se reflete em alta produtividade reprodutiva, expectativa de vida curta e tamanho corporal máximo limitado (Roff, 1984; Stearns & Crandall, 1984; Stearns, 1992). Dessa forma, a mesma espécie pode apresentar diferentes padrões de crescimento em diferentes ambientes, por exemplo, ambientes com maior ou menor disponibilidade de recursos, com maturidade sexual sendo atingida em diferentes tamanhos ou em diferentes idades (Stearns *et al.* 1986). A maturação precoce pode resultar em populações densas de indivíduos pequenos e incorrer em um custo na forma de redução da fecundidade futura (Williams 1966; Bertschy & Fox, 1999). A forma mais recomendada, de estimar o crescimento, por

causa da precisão, é por meio de estruturas rígidas como escamas, espinhos e otólitos, pois são estruturas conservativas.

Muitas espécies de peixes realizam migrações para completar seu ciclo de vida, pois os habitats necessários para reprodução, crescimento e alimentação muitas vezes estão separados por vários quilômetros (Northcote, 1978). A migração, pode ser conceituada como movimentos que resultam em uma alternância entre dois ou mais habitats separados, com um eventual retorno ao habitat original, ocorre com periodicidade regular e envolve uma grande proporção da população (Northcote, 1978). Vários são os padrões migratórios conhecidos, como por exemplo: vertical ou horizontal, descendente (para jusante, rio abaixo) ou ascendente (para montante, rio acima). A migração também pode ser parcial, onde uma população é composta tanto por migrantes quanto por residentes, possui implicações ecológicas e evolutivas (Swingland, 1984; Chapman et al., 2011). Isso foi verificado por Fowler e colaboradores (2016), com a espécie *Mugil cephalus* na costa leste Australiana, onde indivíduos que compõe a população permanecem no mesmo ambiente de salinidade por longos períodos (residentes), enquanto outros se deslocam regularmente entre ambientes de salinidades diferentes (migrantes). Sendo assim, existe uma diversidade de fenótipos migratórios entre e dentro das populações, podendo levar à sobrevivência diferencial através da exposição a diferentes predadores, além da resiliência à pressão por pesca, demonstrando plasticidade nesse comportamento.

2.2 Plasticidade individual em peixes

A plasticidade fenotípica representa a capacidade intrínseca de um determinado ser vivo de expressar diferentes fenótipos em resposta a variações temporais ou espaciais em seu ambiente biótico ou abiótico, e pode ser estudada a nível individual ou populacional (Schlichting & Pigliucci 1998, Sultan 2003, Dingemanse *et al*., 2010). Podendo ser aplicada a uma série de características fenotípicas expressas a nível comportamental, fisiológico, morfológico ou do desenvolvimento (De Witt e Scheiner, 2004; Fusco e Minelli, 2010). Essa adaptabilidade individual, que é um fenômeno epigenético, pode ser desencadeada por diversas causas e, quando persistente ao longo

do tempo, pode ter implicações evolutivas significativas para a sobrevivência das populações em ambientes dinâmicos (Nussey *et al*., 2007; Stamps, 2016). O estudo da plasticidade fenotípica teve início com a elaboração das “curvas fenotípicas”, que demonstram o gradiente de respostas fenotípicas de uma ou mais características submetidas a variações de fatores ambientais, conhecidas como de normas de reação (Woltereck, 1909, Sarkar, 2004). A norma de reação de uma característica fenotípica morfológica, fisiológica, comportamental ou de história de vida pode ser representada graficamente em coordenadas cartesianas, que facilitam a compreensão desse conceito.

A plasticidade do desenvolvimento em peixes é particularmente pronunciada em suas respostas às flutuações ambientais (Karjanailen *et al*. 2016). Por exemplo, a taxa de crescimento, a idade na maturidade e a fecundidade são altamente influenciadas pela temperatura e pela disponibilidade de alimentos (Stearns, 1977). Os peixes têm a capacidade de ajustar seu crescimento e o momento de atingir a maturidade sexual em resposta a mudanças na disponibilidade de recursos, na temperatura da água e em outros fatores ambientais, o que os destaca como exemplos notáveis de plasticidade fenotípica (Reed *et al*., 2010; Coulson *et al*., 2001). Essa capacidade adaptativa é essencial para sua sobrevivência e reprodução em ambientes que são variáveis e muitas vezes imprevisíveis. Nesse sentido, a variação temporal no clima pode impactar o desempenho individual, os padrões e a intensidade da seleção natural e as interações dependentes da densidade, conduzindo a mudanças físicas no habitat e alterando a distribuição e abundância das espécies interativas (Grant & Grant, 2002; Stenseth *et al*., 2002).

Outro exemplo da alta plasticidade ambiental em termos de habitat, salinidade, residência e movimento nos peixes, temos os juvenis de *Centropumus paralelus* (Daros *et al*. 2016). Essa alta plasticidade nos primeiros estágios do ciclo de vida poderia permitir maiores taxas de sobrevivência, uma vez que os sistemas de natação das larvas e pós-larvas não estão totalmente desenvolvidos e elas flutuam passivamente nas correntes de água durante o início de sua história de vida (Daros *et al*. 2016).

A plasticidade individual associada ao comportamento reprodutivo se torna mais previsível com o envelhecimento do indivíduo (Nettle & Bateson, 2015; Fischer *et al*.,

2014), e com a redução da incerteza ambiental (Fawcett & Frankenhuis, 2015; Polverino *et al*., 2019). Isso sugere que os custos dessa plasticidade podem ser mitigados, correlacionados com a manutenção sensorial e regulatória necessária para uma alta capacidade de resposta ao ambiente (DeWitt *et al*., 1998; Urszan *et al*., 2018). Portanto, a capacidade de um organismo em se adaptar às mudanças ambientais é uma estratégia fundamental para atenuar os efeitos das variações no ambiente, maximizando seu desempenho (DeWitt *et al*., 1998; Urszan *et al.*, 2018).

A compreensão das origens e das consequências dessa plasticidade é crucial para os estudos do comportamento de peixes e torna-se ainda mais urgente em contextos de exploração populacional, nos quais a pesca seletiva com base no tamanho pode alterar a história de vida das espécies (Wilson *et al*., 2019). Pois as populações naturais sob regime de exploração, como no caso da pesca, geralmente enfrentam algum tipo de restrição nas características fenotípicas desejadas (Allendorf e Hard, 2009). Como exemplo temos a diminuição do tamanho médio de captura dos peixes expostos a sobrepesca de exemplares de maior tamanho (Law, 2000; McClenachan, 2009). O que é relevante considerando que a adaptação das populações em escalas de tempo ecológico e evolutivo é fornecida pela evolução genética e também pela plasticidade fenotípica.

2.3 *Trade-off* em peixes

A teoria da história de vida preocupa-se com *trade-offs* estratégicos com relação à alocação de energia entre várias funções biológicas e os efeitos desta alocação na dinâmica populacional (Roff, 1992; Stearns, 1992; Arendt, 1997, Begon *et al*., 2007). Segundo o conceito de trade-off, os recursos destinados para uma atividade tornam-se indisponíveis para outras atividades, dessa forma um *trade-off* é uma relação negativa entre duas características da história de vida, como uma gangorra de alocação de recursos (Roff, 1992; Stearns, 1992; Begon, *et al*., 2007).

O *trade-off* entre o crescimento e reprodução é um dos mais importantes estudados (Roff *et al*., 2006; Tsikliras *et al*., 2007; Roff & Fairbairn, 2007), já que são processos complementares (Wooton, 1990). Sendo assim, um indivíduo, ao aumentar sua alocação de energia para atividades reprodutivas, tenderá a diminuir sua

sobrevivência/ou taxa de crescimento corporal, diminuindo, consequentemente, seu potencial para a reprodução no futuro. O aumento da reprodução conduzirá ao tamanho reduzido e consequentemente uma diminuição no Valor Reprodutivo Residual - VRR (Begon *et al*., 2007). O VRR combina a sobrevivência futura esperada com a fecundidade futura esperada, levando em conta a contribuição de cada indivíduo para as futuras gerações (Begon *et al*., 2007).

Tsikliras e colaboradores (2007) testaram o *trade-off* entre a taxa de crescimento e a fecundidade dentro de uma única população de *Sardinella aurita*. Foi concluído que a fecundidade individual está negativamente relacionada com taxa de crescimento específico individual, demostrando que *S. aurita*, com a idade, aloca cada vez menos energia para o crescimento e mais para a reprodução e que essa alocação relacionado ao crescimento determina a fecundidade presente, sendo a fecundidade reduzida com o custo de crescer mais rápido. Isso indica que qualquer aumento no crescimento está associado a uma diminuição no número de descendentes. Consequentemente, a reprodução é trocada por maior crescimento.

Levando em consideração as diferenças observadas nos padrões de crescimento e desova devido à idade, indivíduos mais jovens parecem investir sua energia adquirida em seu próprio crescimento, enquanto indivíduos mais velhos a investem na desova (Tamura *et al*., 2019). A seleção nas taxas de crescimento via *trade-off* entre sobrevivência à maturidade sexual e longevidade para *Xiphophorus multilineatus* foi estudada, e demostrarou um custo de crescimento mais rápido para os juvenis, tendo assim longevidade reduzida na idade adulta (Weinstein *et al*., 2019). Também foi observada uma relação negativa entre a taxa de crescimento das primeiras idades para as fêmeas, suportando ainda mais um custo de longevidade para um crescimento mais rápido.

Outro exemplo de plasticidade de crescimento é o da truta, *Salvelinus namaycush*, na América do norte da América, resultando da adaptação local e *trade-offs*, que impulsionam a variação em características associadas ao crescimento ao longo do ciclo de vida (Wilson *et al*., 2019). Para essa espécie, a alocação reprodutiva foi explicada pela evolução dos *trade-offs* com mortalidade e outros traços de história de vida. Um *trade-off*

entre crescimento e mortalidade tem sido detectado para algumas espécies e apoia fortemente a hipótese de que a taxa de crescimento mais rápida pode não sempre ser ideal (Mangel & Stamps 2001).

2.4 Mugilidae

Os peixes da família Mugilidae estão distribuídos nas regiões tropical e subtropical de todos os continentes, principalmente nas águas estuarinas e marinhas costeiras, onde são conhecidos popularmente como tainhas, curimã e paratis (Thomson, 1997; Harrison, 2002, Menezes, *et al*., 2015). Essa família é constituída por 17 gêneros e 72 espécies, sendo que sua taxonomia tem sido amplamente discutida e é bastante problemática, principalmente devido ao fato de serem muito semelhantes morfologicamente (Nelson, 2006, Menezes *et al*, 2010; Menezes *et al*., 2015). Na América do Sul, até o presente, foram identificadas oito espécies de Mugilidae, todas do gênero *Mugil*, são elas: *M. brevirostris* Ribeiro, 1915; *M. curema* Valenciennes, 1836; *M. curvidens* Valenciennes, 1836; *M. incilis* Hancock, 1830; *M. margaritae* Menezes, Nirchio, Oliveira & Ramirez; *M. rubrioculus* Harrison, Nirchio, Oliveira, Ron & Gavíria, 2007; *M. trichodon* Poey, 1875 e *M. liza* Valenciennes, 1836 (Menezes *et al*., 2015). Sendo que em Alagoas foram identificadas apenas cinco linhagens mitocondriais de *Mugil* (figura 1).

Apesar dos mugilídeos compreenderem um complexo de espécies estuarinas morfoecologicamente similares, sua história evolutiva é notavelmente longa e distintiva. Este gênero se destaca por sua diversificação ao longo de milhões de anos, sem uma divergência morfológica e ecológica pronunciada (Neves *et al*., 2020). *Mugil curema* e *M. rubrioculus* são exemplos de espécies que divergiram há cerca de 23 milhões de anos, e apesar disso, mantêm uma notável semelhança morfológica, sugerindo um conservadorismo extremo nesta característica, possivelmente influenciado por similaridades no uso do habitat e traços de história de vida (Neves *et al*., 2020).

O ciclo de vida dos indivíduos do gênero *Mugil* possuem uma influência sazonal, marcada pela pluviosidade nos ambientes aquáticos tropicais (Lowe-McConnell, 1991; González Castro *et al*., 2009). Nesses ambientes duas estações sazonais são definidas, são elas: seca e chuvosa (Figueroa & Nobre 1990). Na estação chuvosa, o fluxo de água

doce que entra nos estuários aumenta a produtividade biológica e disponibiliza alimento, afetando assim todos os níveis da cadeia trófica, aumentando os teores de clorofila-a favorecendo o crescimento e a sobrevivência dos peixes da região estuarina (Grego et al., 2004, Robins et al., 2006, Gillson, 2011).

O uso do estuário e dos habitats marinhos adjacentes pode ser compreendido como um *continuum* para os peixes do gênero *Mugil* o grau de dependência é obrigatório, pois eles passam pelo menos uma fase do seu ciclo de vida nesse ambiente, com grande relevância nos fluxos de matéria orgânica entre esses habitats (Able, 2005; Lebreton *et al*., 2011). São necessários novos estudos que incorporem o papel das variáveis bióticas, como por exemplo: o padrão de uso do estuário pelas coortes de desova e a variação anual na abundância de peixes. Dessa forma, será possível melhorar a compreensão do significado funcional e do grau de dependência estuarina dessas espécies (Simenstad *et al*., 2000; Able, 2005). A explotação simultânea dos Mugilidae é devido ao fato de ocorrem em simpatria e apresentando segregação temporal e espacial (Ibáñez Aguirre, 1993; Albieri *et al*., 2010, Mai *et al*., 2018). Essa segregação se dá, por exemplo com diferentes períodos de desova entre as espécies, com ocupação de áreas com alta salinidade ou menor salinidade. Então, de forma geral, não ocupam o mesmo nicho ecológico simultaneamente (Ibáñez Aguirre, 1993; Albieri *et al*., 2010, Mai *et al*., 2018).

Segundo Menezes e colaboradores (2015) As espécies do gênero *Mugil* apresentam variações morfológicas distintas, permitindo sua diferenciação taxonômica. *M. brevirostris* possui corpo fusiforme, cabeça curta e larga, focinho arredondado e escamas grandes, enquanto *M. curema* é mais robusto, com faixa prateada, focinho pontiagudo e escamas menores. *M. curvidens* diferencia-se pelos dentes curvados bem desenvolvidos, corpo menos robusto, nadadeira dorsal mais alongada e um sulco bem definido entre os olhos. *M. rubrioculus* tem olhos avermelhados, corpo esbelto e boca menor. *M. liza* destaca-se pelo corpo fusiforme e otólitos com bordas irregulares, sendo a espécie mais divergente do grupo em análises morfológicas e genéticas (figura 1).

Figura 1 - Espécies do gênero *Mugil* que coexistem em estuários tropicais. De cima para baixo: *M. curvidens, M. brevirostris*, *M. curema, M. rubrioculus e M. liza.* Fotos: equipe do Laboratório de Ecologia de Peixes e Pesca da UFAL.

Os Mugilídeos de forma geral são considerados detritivoros, convertendo energia potencial dos detritos em energia aproveitável para outros níveis tróficos (Yañez-Arancíbia, 1976). Dessa forma, apresentam um importante papel ecológico e econômico para as regiões onde ocorrem. Os indivíduos de *M. curema* habitam principalmente regiões estuarinas de fundo com lodo e águas turvas e os juvenis são encontrados em praias arenosas, próximo aos estuários (Vieira & Scalabrin, 1991). *M. curema* possui uma alta capacidade de adaptação alimentar, sendo considerada detritívora, iliófaga, herbívora, onívora, fitófaga e zooplanctófaga (Franco & Bashirullah, 1992).

2.4.1 Reprodução e migração de *Mugil*

Em termos gerais, o ciclo reprodutivo das espécies estuarino-dependentes, como os Mugilidae, é caracterizado por uma fase de maturação gonadal nos estuários, configurando uma história de vida bipartida, sendo classificados como catádromos. Durante a época reprodutiva, os peixes adultos empreendem uma migração em direção às águas marinhas costeiras para a desova, com os ovos e as larvas sendo dispersos pelos processos oceanográficos físicos até os estuários, onde as larvas em estágio avançado estabelecem-se e desenvolvem-se como juvenis (Moore, 1974). Após a metamorfose, os juvenis permanecem nos estuários para completar seu desenvolvimento e, à medida que amadurecem, participam na migração reprodutiva, encerrando o ciclo (Vieira & Scalabrin, 1991) (Figura 2). Então, em sua maioria, as tainhas utilizam os estuários como berçários, aproveitando as condições favoráveis, como o influxo de nutrientes e os habitats estruturados, para seu desenvolvimento durante os primeiros anos de vida (Santana *et al*., 2018).

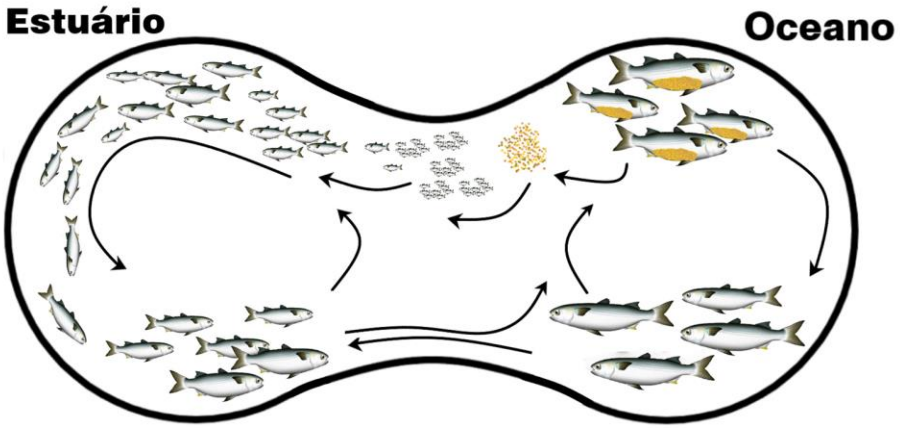

Figura 2 – Esquema representativo do ciclo de vida dos *Mugil*. Fonte: equipe do Laboratório de Ecologia de Peixes e Pesca da UFAL.

No entanto, os Mugilidae do gênero *Mugil* possuem uma alta variabilidade intraespecífica e interespecíficas nos padrões de migração (Chang *et al*., 2004; Chang & Iizuka, 2012; Ibáñez-Aguirre *et al*., 2012; Avigliano *et al*., 2015; Fowler *et al*., 2016). Esta variação no uso do habitat estuarino indica um comportamento migratório mais complexo que o previsto inicialmente para tainhas (Fowler *et al*., 2016; Mai *et al*., 2018). Dessa forma, *M. curema* está associada a águas de alta salinidade podendo ser classificada como marinho migrante sub-categoria marinha estuarina-oportunista. Já *M. liza* está associada a águas menos salinas, devendo ser classificada como marinha migrante sub-categoria estuarina dependente (Mai *et al*., 2018). *Mugil cephalus,* uma das espécies mais estudadas desse gênero, apesenta uma migração diádroma parcial, possuindo uma diversidade considerável na história migratória entre os indivíduos (Fowler *et al*. 2016). Não há estudo que analise esse traço de história de vida para as demais espécies do gênero.

Os Mugilidae, em sua maioria, são peixes gonocóricos e de alta fecundidade (Alvarez-lajonchere, 1982; Fazli *et al*., 2008). Essa fecundidade está relacionada com o tamanho do peixe, assim, indivíduos com 32 cm de comprimento total possuem cerca de 1.082.200 ovos e 2.632.000 ovos foram encontrados em indivíduos com 54 cm de comprimento total, conforme descrito por Lawson e Jimoh (2010) para a espécie *M. cephalus*. A maturidade sexual em mugilídeos ocorre entorno de 3-4 anos nos machos,

e as fêmeas alcançam entre 4-5 anos, e o tamanho total de maturidade sexual depende da espécie, no caso de *M. liza* na Baía de Sepetiba, o tamanho varia de 55 a 57 cm (Okumus & Basçmar, 1997).

Em seu estudo sobre *M. curema*, Santana e colaboradores (2018) observaram que os indivíduos analisados nascem em áreas de salinidade características do estuário, onde eles se desenvolvem até aproximadamente um ano de idade, quando migram para áreas de maior salinidade até atingir a maturidade sexual (3 anos) no mar. Após a desova ocorrer, os indivíduos de *M. curema* podem permanecer no mar ou retornar ao estuário até a próxima desova. O período reprodutivo de *Mugil curema* ocorre de diferentes formas e de acordo com a distribuição geográfica, muitas vezes com ocorrência de dois picos reprodutivos (Marin *et al*. 2003).

No Atlântico Ocidental subtropical *M. liza*, apresenta desova única e desenvolvimento oocitário sincrônico em dois grupos, ou seja, a cada período de reprodução evidenciam-se dois lotes de ovócitos dentro dos ovários, o dos ovócitos do estoque de reserva e aquele dos ovócitos que serão eliminados no período de desova (Vieira & Scalabrin, 1991; Sousa *et al*., 2015). Já *M. curema* apresenta desova parcial, desenvolvimento oocitário assincrónico, consistindo na liberação de apenas parte dos oócitos por vez, em lotes (Santana *et al*., 2018).

Ibáñez e colaboradores (2012) observaram que *M. cephalus* e *M. curema* na costa do México podem desovar tanto em águas marinhas quanto em ambientes estuarinos. Nos que desovam em ambientes marinhos os ovos são transportados para ambientes costeiros estuarinos. Foi verificado que a migração reprodutiva para o mar de *M. cephalus* ocorre no inverno e de *M. curema* na primavera, evidenciando a segregação temporal e espacial que ocorre quando duas espécies intimamente relacionadas são simpátricas (Mai *et al*., 2018).

O processo reprodutivo e a abundância das espécies de *Mugil* estão sujeitos a interferências negativas decorrentes do aquecimento global, considerando que a temperatura da superfície do mar constitui o principal fator que limita a distribuição geográfica dessas espécies, e os ambientes estuarinos e costeiros marinhos são altamente sensíveis às mudanças climáticas (Hung & Shaw, 2006; Lan *et al*., 2014). Além

disso, o aumento do nível do mar e a acidificação dos oceanos, ambos associados ao aquecimento global, podem impactar os habitats costeiros, reduzindo a disponibilidade de alimentos para os indivíduos e, consequentemente, afetando sua capacidade de sobrevivência e crescimento. É importante ressaltar que o período de adaptação da tainha a essas mudanças ainda não é completamente compreendido, o que pode resultar em uma menor disponibilidade desse importante recurso em um futuro próximo (Rijnsdorp *et al*., 2009; Durand & Whitfield, 2016).

2.4.2 Crescimento, idade e microquímica de otólitos

Os otólitos são estruturas mineralizadas, acelulares, formadas por carbonato de cálcio (97-99%), em sua maioria sob forma de aragonita, embutido em uma matriz proteica, denominada otolina (Campana & Neilson, 1985, Campana 1999, Cousseau, 2010). Eles estão localizados no aparelho vestibular do ouvido interno de peixes ósseos e estão presentes em três pares: *sagittae, lapilli* e *asterisci* (Thresher, 1999; Popper *et al.*, 2005). Em Perciformes, os *sagittae* são os mais utilizados para diversos estudos, por serem os mais fáceis de remover e localizar, além de possuírem o maior eixo de crescimento e a maior massa (Secor *et al*., 1992; Thresher, 1999).

As estruturas otolíticas são altamente conservadoras, não sofrendo reabsorção e permanecendo intactas ao longo da vida do peixe (Tuset *et al*., 2008). Elas representam as primeiras estruturas calcificadas a se formarem nos estágios embrionários ou larvais (Domingues & Hayashi, 1998). Sendo a forma dos otólitos de cada espécie única (figura 3), é possível até a identificação da espécie pela sua morfometria (Dahl *et al*. 2024). Mas, como essa forma sofre influência de um componente genético e também há uma variabilidade hormonal e ambiental (fatores como sexo, idade, dieta, temperatura da água, profundidade, tipo de substrato, salinidade e fonte de alimento), a forma dos otólitos pode ser utilizada para diferenciação de estoques pesqueiros (Moralles-Nin *et al*. 1998, Secor & Rooker, 2000, Ibañez *et al*. 2022).

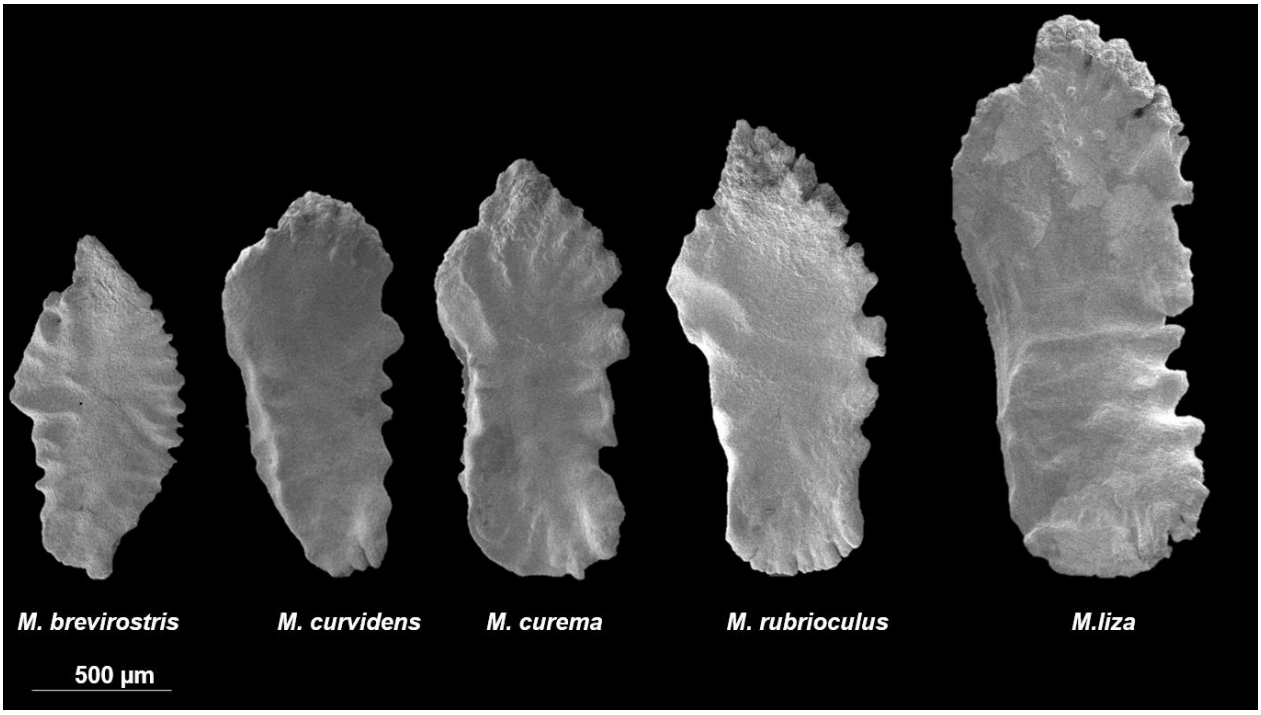

Figura 3 - Micrografia eletrônica de otólitos *sagittae* de *M. brevirostris, M. curvidens, M. curema, M. rubrioculus* e *M. liza*. Fotos: equipe do Laboratório de Ecologia de Peixes e Pesca da UFAL.

O crescimento dos otólitos é caracterizado pela adição de camadas concêntricas de carbonato de cálcio sobre uma base proteica, resultando em uma estrutura na qual diferentes taxas de deposição de matéria orgânica e inorgânica ao longo do tempo se traduzem em marcas com propriedades ópticas distintas, sendo elas opacas ou hialinas. As opacas são zonas mais calcificadas, mais largas e escuras, que corresponde ao período de crescimento rápido e as hialinas, também conhecidas como translúcidas, são zonas menos calcificadas e mais estreita, período de crescimento lento, que juntas formam um anel de crescimento (Panfili & Tomas 2001, Campana, 2004, Volpedo & Vaz-dos-Santos, 2015). Tais marcas são o resultado de uma interação complexa de fatores endógenos e exógenos, como alterações no crescimento, flutuações na temperatura, doenças, atividade reprodutiva, migração, disponibilidade e consumo de alimento, e estresse ambiental (Campana, 2004). A contagem do número dessas marcas opacas e hialinas (figura 4) é amplamente empregada para estimar a idade e o crescimento de

grande parte dos teleósteos (Rufino, 2004; Fabré & Saint-Paul, 1998). As primeiras pesquisas utilizando essa abordagem foram realizadas em regiões temperadas, onde as flutuações de temperatura entre verão e inverno são bem marcadas (Ricker, 1975). Posteriormente vieram as pesquisas em regiões tropicais, que apresentam variações sazonais, como períodos secos e chuvosos (Morales-Nin & Panfili, 2005, Sousa *et al.* 2015).

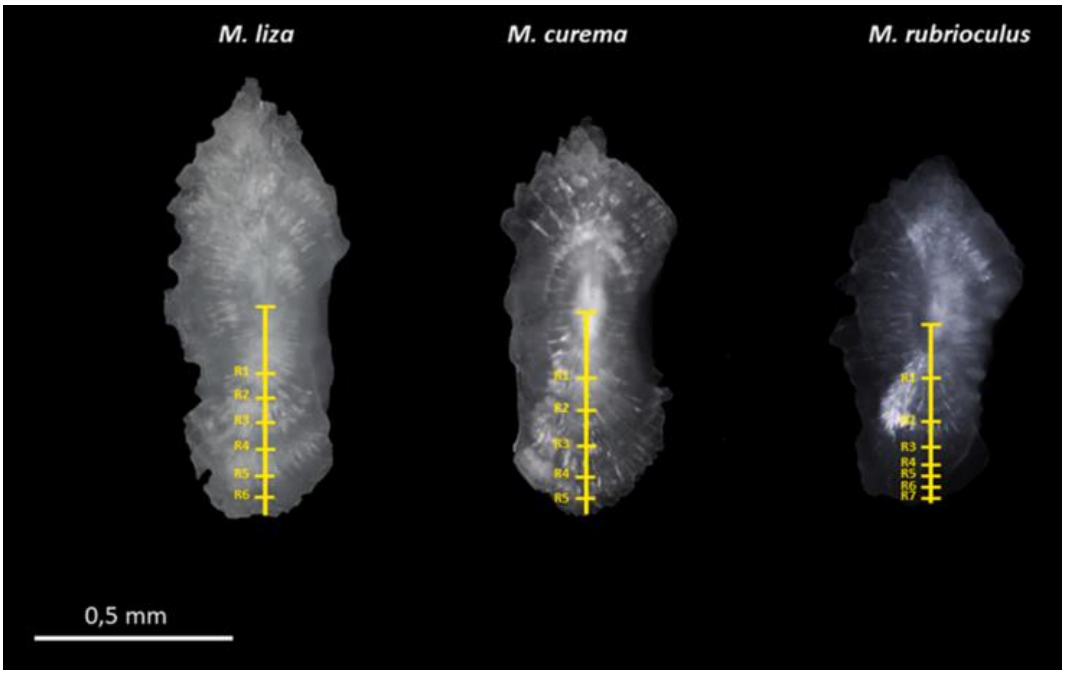

Figura 4 - Otólitos *sagittae* inteiros de *M. liza, M. curema* e *M. rubrioculus*. Mostrando o núcleo opaco (seta) e as sucessivas zonas translúcidas e opacas que formam os anéis de crescimento. Fotos: equipe do Laboratório de Ecologia de Peixes e Pesca da UFAL.

No entanto, durante o estágio inicial da vida, como a transição do estágio larval para o juvenil e as mudanças ambientais que podem deixar marcas nos otólitos (Chang *et al*., 2000), a validação da marca de idade pode se tornar confusa. Por exemplo, foram registradas marcas nos otólitos de *Mugil curema* antes do primeiro ano de vida, possivelmente correspondendo à mudança de habitat, do local de nascimento marinho para a região estuarina (Santana *et al*., 2018). Nesse sentido, é fundamental validação, ou seja, a determinação da periodicidade e época de formação dos anéis nos otólitos

(Campana, 2001, Green *et al*. 2009, Volpedo & Vaz-dos-Santos, 2015). Assim como também é fundamental, anteriormente, a escolha da técnica de visualização de anéis, por exemplo, se os anéis serão visualizados inteiros ou seccionados, se serão polidos ou não, se é preciso aplicar alguma técnica de coloração para melhorar o contraste entre as zonas opacas e hialinas (Figura 05) (Stevenson e Campana 1992).

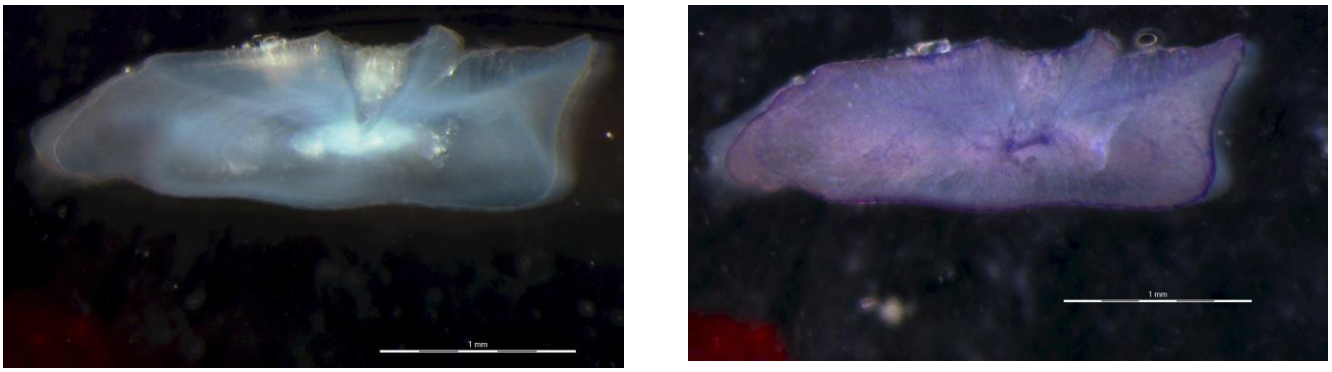

Figura 5 – Otólito *sagitae* de *M. curema* seccionado pelo isomet, emblocado em resina, e posteriormente polido (A) e corado (B) com azul de metileno. Fotos: Jordana Rangely.

Esses dados de crescimento desempenham um papel crucial em uma variedade de cálculos essenciais para a ciência pesqueira, como por exemplo: longevidade, taxa de mortalidade, modelos de avaliação de estoques, além da modelagem ecológica (Sparre e Venema 1988, Beverton e Holt 1957, Methot e Wetzel 2013).

Durante um certo tempo de sua vida, o crescimento do peixe é acompanhado de mudanças na forma do corpo, que são atreladas a mudanças anatômicas ou fisiológicas, que são conhecidas como relações alométricas, (Begon *et al*., 2006). Da mesma forma, os otólitos também podem apresentam alometrias morfométricas relacionadas com a ontogenia (Volpedo & Echeverría, 1999; Pérez & Fabré, 2013). Diversos modelos podem ser utilizados para identificar essa alometria, sendo um dos mais aceitos o proposto por Huxley (1924). Esse modelo foi aplicado por Bervian e colaboradores (2006) que identificaram pontos de mudança do crescimento ao longo do ciclo de vida do peixe, indicativas de alocação de energia diferenciada, registradas em mudanças morfológicas e morfométricas no otólito.

Além dessas informações trazidas pelo otólito também é possível gerar um perfil da história de vida e obter informações sobre as características ambientais de cada espécime por meio da microquímica de otólitos (Campana & Thorrold, 2001). Conforme os peixes crescem, os otólitos incorporam em sua composição material proveniente dos ambientes em que estão inseridos. Existem pelo menos 50 tipos de elementos presente nos otólitos, entre eles: cálcio (Ca), carbono (C), oxigênio (O), nitrogênio (N), cloro (Cl), enxofre (S), magnésio (Mg), sódio (Na), fósforo (P), estrôncio (Sr), potássio (K), lítio (Li), manganês (Mn), cobre (Cu), cobalto (Co), cádmio (Cd), bário (Ba), chumbo (Pb), silício (Si) e zinco (Zn) (Sturrock *et al*., 2012).

Alguns desses elementos, como o lítio, manganês, bário e estrôncio, apresentam concentrações variadas para diferentes ambientes (marinho e estuarino) e estação (seca e chuvosa), formando marcadores naturais que refletem o ambiente físico-químico e consequentemente as mudanças sofridas pelo indivíduo durante o seu ciclo de vida (Campana e Thorrold, 2001; Campana, 2005; Elsdon *et al*., 2008).

Dessa forma, a microquímica de otólitos fornece uma cronologia química da vida do peixe, sendo uma técnica precisa e cada vez mais utilizada em pesquisas de alto impacto, como por exemplo, em relação a migração (Thresher, 1999, Albuquerque *et al*., 2010; Sturrock *et al*., 2012; Avigliano & Volpedo, 2013; Mai *et al*., 2019, Koochaknejad *et al.* 2024), reprodução (Fowler *et al*., 2016; Avigliano *et al*., 2016), idade e crescimento (Santana *et al*., 2018) e ontogenia (Walther *et al*., 2010), fornecendo informações para responder questões ecológicas aplicadas em diferentes escalas temporais e espaciais, que podem ser utilizadas para fins de gerenciamento e conservação de espécies de peixe (Campana, 2005; Elsdon *et al*., 2008; Avigliano *et al*., 2016). Além disso, combinando a análise dos elementos com os anéis de crescimento é possível um arquivo importante que registra com organização temporal as informações do ambiente frequentado pelos peixes, as mudanças ambientais e a exposição a poluentes em toda a ontogenia (Halden & Frierich, 2008).

Pesquisas recentes indicam o potencial desta técnica em avaliar a estuarinodependência e uso diferenciado de habitat (Albuquerque *et al*. 2010, 2012, Condini *et al.,* 2016, Mai *et al*. 2019, Almeida et al. 2024), já que os ambientes estuarinos

passam por processos constantes de input e output de nutrientes que afetam, espacial e temporalmente, os processos biológicos, físicos e químicos dos peixes (Elsdon & Gillanders, 2005). A heterogeneidade química dentro dos estuários, devido às descargas fluviais e antropogênicas, cria variabilidade espacial entre os ambientes estuarinos e costeiros adjacentes, que podem ser quimicamente identificadas nos otólitos dos peixes (Elsdon *et al*., 2008; Walther & Thorrold, 2009).

A variabilidade da concentração de Sr e Ba nos otólitos é principalmente devido à composição química da água (Campana 1999, Wells *et al*. 2003). A concentração de Sr está positivamente relacionada à salinidade enquanto Ba está negativamente relacionada à salinidade, dessa forma, na região estuarina é encontrada uma menor concentração de Sr e uma maior concentração de Ba em relação a região marinha, o que ficará registrado no otólito dos peixes (Secor *et al*., 2001; Zimmerman, 2005; Labonne *et al*., 2009; Tabouret *et al.* 2010; Avigliano & Volpedo, 2013).

Dessa forma, é possível verificar a conectividade entre a região marinha costeira e o estuário para as espécies utilizando Sr e Ba. Por exemplo, para *M. curema,* a maior salinidade na estação seca leva a uma maior assinatura Sr: Ba no otólito entre os indivíduos gerados nesta temporada desde o nascimento até um ano de vida (Santana *et al*. 2018). Por outro lado, a menor salinidade na estação chuvosa leva a uma menor assinatura Sr:Ba no otólito entre os indivíduos gerados nesta temporada (Ibañez *et al*. 2012). Esta relação direta entre a salinidade e a relação Sr: Ba no otólito também foi encontrada para *M. liza* (Callicó Fortunato *et al*., 2017).

A metodologia mais utilizada para análise microquímica dos otólitos nos dias atuais é a ablação a laser e espectrometria de massas por plasma acoplado indutivamente (LA-ICP-MS) (Mai *et al.* 2014, Avigliano *et al.* 2015, Ferreira *et al.* 2023). Essa técnica determina elementos traço de forma pontual sobre cortes de otólitos, em um *raster* que vai do núcleo à borda do otólito (Volpedo & Vaz-dos-Santos, 2015). Sendo assim, segue os seguintes passos: limpar com água MiliQ logo após sua extração, colocar os otólitos em resina cristal epóxi, seccioná-los transversalmente através do núcleo, colar em lâmina de vidro e submeter a LA-ICP-MS (Albuquerque *et al.* 2012, Avigliano *et al.* 2015).

2.5 Pesca Artesanal

Há uma crise global na indústria pesqueira nas últimas décadas (FAO 2022, Pauly, 2008, 2019). A estagnação vivida recentemente está principalmente ligada a um ligeiro declínio na captura de pesca, que diminuiu 4,5 por cento em 2019 e 2,1 por cento em 2020, (FAO 2022). Esta queda deveu-se a vários fatores, incluindo grande exploração dos recursos pesqueiros sem uma gestão adequada, os impactos do COVID-19, a degradação ambiental e a questão do aquecimento global (FAO 2022, Paniagua & Rayamajhee, 2024).

A pesca de pequena escala (SSF) vem recebendo crescente atenção internacional por desembarcar cerca de 50% das capturas globais de pesca marinha e empregar cerca de 51 milhões de pessoas ao redor do mundo, 90% das pessoas envolvidas na pesca, muitas delas nos países mais pobres do mundo (FAO/ WorldFish Centro 2010, Mills *et al.* 2011, FAO, 2018). Suas contribuições para a segurança alimentar e a redução da pobreza, especialmente nos países em desenvolvimento, são cruciais para os Objetivos de Desenvolvimento Sustentável da ONU (ODS) (FAO, 2015). Centenas de milhões de pessoas em toda a cadeia de produção dependem dessa indústria para sua subsistência, sendo ela uma força motriz econômica e social (Stobutzki *et al*., 2006 a,b; Hilborn *et al*., 2020). Consequentemente, a SSF contribui diretamente para a segurança alimentar, redução da pobreza, nutrição global, emprego e melhoria das condições socioeconômicas de grande parte da população (Batista *et al.,* 2014). No entanto, essas pescarias frequentemente carecem de dados históricos importantes, o que resulta na falta de avaliação adequada e no subgerenciamento dos estoques pesqueiros (Stobutzki *et al.,* 2006 a,b; Hilborn *et al*., 2020).

No Brasil, a atividade pesqueira é regulamentada pela Lei Nº 11.959, de 29 de junho de 2009, que dispõe sobre a Política Nacional de Desenvolvimento Sustentável da Aqui-cultura e da Pesca, visando o desenvolvimento sustentável da pesca, o desenvolvimento e a fiscalização da atividade pesqueira e o desenvolvimento socioeconômico, cultural e profissional dos que exercem a atividade pesqueira. Neste documento, a pesca comercial artesanal é “aquela praticada diretamente por pescador

profissional, de forma autônoma ou em regime de economia familiar, podendo utilizar embarcações de pequeno porte” (Brasil, 2009).

2.5.1 Pescarias com dados limitados

A estatística global de pescarias existe desde 1950, em um esforço das Nações Unidas de monitorar o desenvolvimento da economia mundial (Ward, 2004, Pauly, 2008). No entanto a maioria das pescarias no mundo é considerada de “dados limitados” (Costello *et al*., 2012), o que significa que há uma escassez de informações sobre a dinâmica populacional das espécies, como comprimento máximo, idade, tamanho/idade na maturidade e fecundidade (Walters & Martell, 2004). Essa limitação de dados impede a definição de estratégias eficazes para o desenvolvimento sustentável da pesca, utilizando os modelos de avaliação baseados em métodos convencionais, que utilizam séries temporais de dados (Dowling *et al.*, 2015, 2017, 2023). Para essas situações, foram desenvolvidos os modelos de avaliação com dados limitados (DLMs), que oferecem métodos alternativos focados em espécies com dados escassos. Os DLMs podem ser divididos em modelos baseados em comprimento e modelos baseados em capturas, ambos são utilizados para estimar o estado dos estoques de espécies e desenvolver uma gestão pesqueira viável (Kuo *et al.,* 2023). Esses modelos foram testados, tanto em países desenvolvidos, quanto em desenvolvimento, fornecendo estimativas comparáveis às das avaliações convencionais e oferecendo uma visão mais abrangente dos estoques (Zhou *et al.,* 2017, Sagarese et al. 2018, van Germet *et al*., 2022).

Vários DLMs foram desenvolvidos, como: indicadores baseados em comprimento (LBI; Froese 2004), razão potencial de desova baseada em comprimento (LBSPR; Hordyk et al. 2015) e abordagem de biomassa bayesiana baseada em comprimento (LBB; Froese *et al*., 2018). O LBB estima simultaneamente todos os parâmetros relevantes com uma abordagem bayesiana da Cadeia de Markov de Monte Carlo (MCMC), que é recomendado para quantificar a incerteza na avaliação dos estoques pesqueiros (Magnusson *et al.*, 2013, Froese *et al.*, 2018). Este método relaciona as taxas de história de vida dependente de comprimento e como essas taxas interagem para

produzir uma determinada distribuição de frequência de comprimento, fornecendo: mortalidade natural, mortalidade por pesca, comprimento assintótico, comprimento na primeira captura, comprimento ótimo, biomassa atual explorada e a biomassa inexplorada, consequentemente o status do estoque. LBB pode ser modelado com traços de história de vida então, primeiro ele estima o comprimento assintótico L_{inf}, mas, se uma boa estimativa de L_{inf} está disponível a partir de um estudo independente anterior, este valor pode ser introduzido, diminuindo assim a incerteza nos resultados do LBB (Froese *et al.*, 2018).

2.5.2 Conhecimento Ecológico Local (LEK)

Para se ter um entendimento completo do processo pesqueiro e um consequente manejo adequado dos recursos, para além do status do estoque, é preciso considerar as relações humanas (Marrul-Filho, 2003, Diegues, 2001). Para gerar um plano de manejo adequado, é fundamental o ordenamento da atividade pesqueira, como um sistema resultante de uma combinação complexa, que avalia e integra os efeitos das dinâmicas ambiental, social, econômica, tecnológica e política, com vistas ao uso sustentável do recurso (Marrul-Filho, 2003, Diegues, 2001, Beddington *et al*., 2007). No geral, a pesquisa e gestão da pesca está mudando de foco para colocar a pesca em um contexto mais amplo que coloca mais ênfase nas interações entre pessoas, poder, perturbação externa e incerteza e dinâmica de governança mais ampla (Andrew *et al*., 2007, Jentoft 2007; Mahon *et al.*, 2008).

Neste contexto, surge o conceito de Conhecimento Ecológico Local (LEK), que consiste em um conjunto de crenças e conhecimentos empíricos acumulados sobre o ambiente (Berkes *et al*., 2000). Esse conhecimento é baseado principalmente nas observações e experiências dos moradores locais, que possuem uma compreensão profunda e abrangente sobre conservação, transmitidos culturalmente através de gerações (Kohl & Yli-Pelkonen, 2005; Braga *et al*., 2018). O LEK tem sido amplamente utilizado em estudos de pesca (Silver & Campbell, 2005; Grant & Berkes, 2007), pois os pescadores podem fornecer informações específicas sobre as espécies, como tamanho, abundância, hábitos alimentares e reprodutivos, além de dados históricos e

contemporâneos das capturas (Pauly, 1995; Grant & Berkes, 2007; Rasalato *et al*., 2010). Portanto, o LEK pode ser utilizado para reconstruir ou complementar tendências de longo prazo em populações fortemente exploradas ou em espécies mal avaliadas com baixa biomassa (linhas de base históricas), além de melhorar o planejamento, as práticas de conservação e detectar extinções (Saenz-Arroyo *et al*., 2005; Thornton & Scheer, 2012; Leduc *et al*., 2021).

Morril (1967) foi um dos pioneiros em pesquisa etnoictiológica, descrevendo a compreensão dos pescadores das Ilhas Virgens (“Cha-Cha”) sobre taxonomia, ecologia, comportamento e toxidade dos organismos marinhos. Poizat e Baran 1997 observaram que existe uma sobreposição das informações recolhidas dos pescadores (LEK) sobre a distribuição espacial e temporal dos peixes com os resultados de um levantamento ictiológico (CSK) em um estuário africano. Sáenz-Arroyo e Revollo-Fernández (2016) notaram uma forte sobreposição de dados históricos de capturas com as memórias dos pescadores no México. No Brasil, em Alagoas, Marques (1991) também observou uma forte sobreposição de LEK e CSK ao analisar o conteúdo estomacal de bagre no Complexo Estuarino Lagunar Mundaú Manguaba.

Os estudos que incorporam o LEK também trazem benefícios significativos para os próprios pescadores. Por exemplo, fortalecem seus valores culturais, proporcionam maior voz política e reconhecimento por parte dos gestores, auxiliam na resolução de disputas de manejo, aprimoram o diálogo entre os pescadores e as agências de gestão, promovendo uma gestão participativa e horizontal dos recursos pesqueiros (Ruddle 1995; Berkes 1999).

Como exemplo de LEK aplicado a pesca das tainhas, temos o trabalho de Herbst e Hanazaki (2014), que investigaram o conhecimento ecológico local dos pescadores ao longo de um gradiente latitudinal no litoral de Santa Catarina, sobre o ciclo de vida da tainha *Mugil liza,* dando ênfase aos aspectos migratórios, alimentares, reprodutivos e comportamentais. Foi concluído que pescadores possuem um conhecimento detalhado sobre o ciclo de vida da tainha e identificam variações intra e interanuais nas rotas migratórias, e esse padrão precisa ser considerado no manejo da pescaria.

2.5.3 Pesca de tainhas

Essa gestão participativa é especialmente importante para espécies de *Mugil*, pois são um dos recursos mais consumidos no Brasil, representando cerca de 20% da pesca comercial, uma das maiores pescarias de Mugilideos do mundo (MPA, 2011). As espécies mais abundantes nas capturas são *M. liza* e *M. curema*. Na região Sul do país, *M. liza* é responsável pela mobilização de uma frota industrial de traineiras e frotas de média escala como o emalhe anilhado, além de milhares de pescadores artesanais em todas as regiões das lagoas e estuários (Vieira & Scalabrin, 1991). Já na região Nordeste a pesca é artesanal, possuindo uma grande importância econômica, social e cultural, com volume de captura muito mais baixo, porém existe a exploração simultânea de várias espécies, sendo *M. liza* substituída por *M. curema*, que é a espécie mais capturada na região (Santana da Silva, 2007).

As condições de mercado interferem nos desembarques, pois, dependendo da época, o esforço de pesca é direcionado para peixes mais rentáveis, causando redução nos desembarques de tainha (Steele & Bert, 1998, Mendonça & Machado 2010). Sendo assim, as capturas de tainha mais baixas em alguns meses do ano e mais altas em outros. Assim, as oscilações na produção devem-se principalmente ao aumento da presença de pescadores em busca de melhores fontes de renda.

O comércio das ovas de *Mugil* é histórico no Brasil. Na região sul do país as gônadas de *M. liza* são colhidas na época reprodutiva e exportadas como ‘Bottarga’ para mercados internacionais. Essa pesca ocorre quando imensos cardumes estão em direção norte, para se reproduzir, sendo um momento de grande vulnerabilidade para a espécie, aumentando a sobrepesca. Esse comércio representa uma ameaça significativa à conservação desta espécie, e a Instrução Interministerial Brasileira (MPA/MMA nº 7 de 2011) proibiu o desembarque de ovas de *M. liza* sem suas carcaças. Na região nordeste esta prática histórica de consumo de ovas de *Mugil* também ocorre e é potencialmente negativa para o manejo do estoque, uma vez que capturam os peixes durante o período reprodutivo, especificamente antes da desova (Marques *et al*., 2005, Cascudo, 1984). Esse comercio era intensificado no período da quaresma, onde a quantidade de *Mugil* capturada era muito numerosas porque os pescadores procuram apenas as ovas, não

utilizando todos os peixes para alimentação. (Cascudo, 1984). Marques e colaboradores (2005) relatam que uma cena comum era observar corpos de curimãs deixados às margens da Lagoa Mundaú, pois a população local não conseguia utilizar todos aqueles peixes, mas ovas necessárias para suprir o consumo tradicional da população local era muito alto. Atualmente, as ovas de curimãs e tainhas ainda são um alimento tradicional em Alagoas (Marques *et al*., 2005). No entanto, esta prática já não é comum como antigamente, devido à baixa oferta pelo declínio drástico dos estoques em certa forma, devido à consciência dos pescadores em face ao declínio do estoque, ou pela educação ambiental conduzida por ONGs, escolas e academia (Santos & Sampaio, 2013; Siemer & Knuth, 2001; Patterson *et al*., 2009).

Mugil liza foi recomendada para classificação como Quase Ameaçada (NT) sob a recente revisão da IUCN no Brasil, e em 2004 a espécie foi classificada como superexplorada pelo Ministério da Pesca e Aquicultura do Brasil (IBAMA/ICMBIO/CEPSUL, 2007). Esse problema de sobrepesca para *M. liza* já foi reconhecida pelo governo federal, que em 2015, instituiu o Plano de Gestão da Pesca da Tainha. Já as outras espécies do gênero são considerados deficiente em dados pela IUCN. Já que raramente são relatadas nas estatísticas, porque geralmente ocorre nos desembarques da pesca artesanal. Então o seu rendimento é normalmente subestimado nas estatísticas e também no número de embarcações registadas (Mendonça & Miranda, 2008; Mendonça & Machado, 2010).

Os Mugilideos são muito vulneráveis à atividade de pesca pois possuem relativamente alta longevidade, maturação sexual tardia, são capturada em todos os estágios da vida, e principalmente durante o período reprodutivo em cardumes (safra). Apesar dessa importância para os desembarques, no nordeste do Brasil não existe plano de manejo, nem período de defeso para este grupo (Sousa *et al*., 2015).

As tainhas possuem uma forte conexão com a história, a cultura e a economia de Alagoas. Tanto é que sua relevância está eternizada na bandeira do estado, que exibe três tainhas, representando não apenas a riqueza dos recursos pesqueiros, mas também a importância da pesca artesanal para o sustento das comunidades costeiras. As tainhas foram durante décadas o recurso pesqueiro mais importante do estado. Em 2005, a

produção de tainhas em Alagoas alcançou 1.766,4 toneladas, representando 18,1% de toda a produção de pescado marinho e estuarino no estado (IBAMA, 2006). Em 2007, as tainhas corresponderam a 13% dos desembarques pesqueiros totais, destacando sua relevância para a economia local (IBAMA, 2007). Após 2007, as estatísticas oficiais sobre a pesca de tainha em Alagoas tornaram-se escassas.

As pescarias na região são realizadas utilizando oito principais aparelhos de pesca: rede de espera, rede de cerco, tarrafa, linha, arrasto duplo, a rede de caceia, a rede de cerco e o arrastão de praia. Cada uma dessas técnicas resulta em capturas de diferentes espécies de tainhas, além de incluir outras espécies da fauna acompanhante associada a essa atividade. A pesca com rede de cerco concentra-se predominantemente na captura de *Mugil curvidens* e *M. curema*, enquanto a rede de espera e a linha são mais eficazes para capturar *Mugil liza*. Já a tarrafa é mais utilizada para capturar *Mugil curema* e *Mugil curvidens*. Essa diversidade de métodos reflete a adaptação das práticas de pesca às características comportamentais e ecológicas de cada espécie (Torres *et al.* 2007; Rangely 2011).

A captura das tainhas nos rios, lagunas e no litoral sempre foi uma atividade essencial, fornecendo alimento e renda para inúmeras famílias que dependiam diretamente da pesca para sobreviver. Seu comércio movimentava mercados locais e desempenhava um papel importante na identidade cultural de Alagoas, marcando presença em pratos típicos e celebrações regionais (Cascudo, 1984; Marques *et al*., 2005).

Preservar as tainhas vai além de garantir a continuidade da pesca; trata-se de valorizar a história de Alagoas, suas tradições e o sustento das futuras gerações. O cuidado com os ecossistemas costeiros, como estuários e manguezais, é crucial para a sobrevivência das tainhas e para manter viva a ligação entre esse peixe icônico e o povo alagoano.

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3 CONGENERIC, SYMPATRIC TROPICAL MULLETS RESPOND DIFFERENTLY TO ENVIRONMENTAL VARIABILITY: INSIGHTS INTO COEXISTENCE

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Abstract

Context: Disentangling mechanisms influencing the seasonal and spatial distribution of fish is essential to understanding population dynamics. In the Southwestern Atlantic, the sympatric mullets *Mugil curema* and *M. rubrioculus* are closely related and use habitat similarly. However, which processes allows their coexistence is unknown.

Aim: We tested the hypothesis that the species exhibit different habitat use patterns that are temporally decoupled to allow sympatry due to different responses to environmental drivers. **Methods:** Bayesian zero-inflated models were used to unravel spatial and temporal distribution patterns of those species in a Southwestern Atlantic lagoon.

Key results: The two species display different distribution within the estuary, being spatially and temporally segregated, with *M. curema* mostly inhabiting inner portions and *M. rubrioculus* inhabiting the outer estuary.

Conclusions: This decoupling in habitat use might be driven by distinct responses to environmental variability: *M. curema* is influenced by factors such as temperature and dissolved oxygen, while *M. rubrioculus* by variations in salinity. We suggest that the studied species evolved divergent responses to environmental variation to allow coexistence.

Implications: This study suggests that environmental factors drive the abundance of mullets inside estuaries, and are therefore useful in predicting their spatial and temporal distribution.

Keywords: ecology, fish, *Mugil*, habitat use, fisheries, salinity, estuary, temperature

Introduction

Mechanisms underlying the spatial co-occurrence of species have always drawn the attention of ecologists (Dufour *et al.,* 2015; Winston, 1995). Because sympatric congeneric species tend to be ecologically similar, presenting similar habitat requirements and feeding on roughly the same available resources (Schoener, 1974), insights into which mechanism allows their coexistence are considered to be of great importance to understand ecological differentiation and processes behind the structuration of biological communities (Ackerly *et al.* 2006), as well as to provide useful insights to management and conservation (Davidson-Watts *et al.* 2006; Di Bitetti *et al.* 2008; Jirapunpipat *et al*. 2009). Historically, many drivers of species coexistence such as habitat selection (Davidson-Watts *et al.,* 2006), trait divergence (Ackerly *et al*. 2006; da Silva *et al*. 2019) and niche differentiation (da Silva & Fabré, 2019) have been identified. However, the astonishing variability in strategies adopted by co-occurring species warrants a closer species-specific examination of its drivers, especially when it comes to closely related and commercially important species.

At a local scale, ecologically similar species are expected to exhibit morphological differences, as well as spatial and/or temporal segregation in microhabitat and resource use to reduce competition (Ackerly *et al.* 2006). However, for a few congeneric species, these assumptions appear to be in contradiction. The family Mugilidae, for example, contains a substantial number of co-occurring species, which are abundantly present in estuaries and other coastal regions in tropical and subtropical regions (Blaber, 2000). Despite showing highly conservative morphological features (Menezes *et al.* 2015) and similar ecological traits such as feeding habits (Garcia *et al*. 2018), habitat requirements have been demonstrated to significantly overlap between species (Ibáñez *et al*. 2012), with factors such as temperature and salinity being able to influence their habitat use patterns (Cardona *et al.* 2008; Lemos *et al*. 2021). However, there is scant evidence of habitat partitioning in congeneric species as a mechanism to allow for coexistence through changing niche amplitude (Garcia *et al.* 2018).

In the Tropical Western Atlantic, mullets are represented by the abundant and commercially important genus *Mugil*, with eight species (Menezes *et al.* 2015). Out of

these, *M. curema* and *M. rubrioculus* are closely related and the most morphologically similar species (Neves *et al.* 2020, 2021). *M. curema* and *M. rubrioculus* live in sympatry and have very similar life cycles (Avigliano *et al*. 2021; Ibáñez *et al*. 2012; Menezes *et al.* 2015). Although data for *M. rubrioculus* is highly scarce in the literature (da Silva *et al.* 2017a), *M. curema* was previously suggested to be in a state of overfishing or population decline (Mendonça and Bonfante, 2011), highlighting the need of gathering relevant ecological information that may aid future management decisions.

Classical ecological niche theory states that species with similar ecological requirements and life history need to partition resources to maintain coexistence, and habitat heterogeneity plays a crucial role in niche differentiation (Jenkins *et al*. 2019; Schoener, 1974). Recent studies revealed that *M. curema* and *M. rubrioculus* display significant interspecific variation in some life-history traits such as length-at-age, maturity and allometry, possible evidence of niche differentiation reflected on ecological traits (Rangely *et al.* 2023). However, it is still not known how such species arrange themselves spatially and temporally in relation to each other. The aim of this study was to identify spatial and temporal patterns in the distribution of the white mullet *M. curema* and redeye mullet *M. rubrioculus* in a tropical estuary of the Southwestern Atlantic. We addressed the following question: what is the role of environmental variability in shaping the distribution patterns of these fish at a local scale? We hypothesized that those morphologically similar, congeneric species may exhibit some degree of spatial and temporal segregation driven by different responses to environmental factors as a mechanism to allow coexistence.

Materials and methods

Study area and sampling

Sampling was executed in the Mundaú Lagoon, located in a tropical and semi-humid region of the Southwestern Atlantic coast. The area has two well-defined seasons characterized by rainfall patterns: a dry season from October to March and a rainy season from April to September. There, eight sampling sites were placed to cover the whole estuarine gradient: from the upper estuarine to the surf zone at the sea, with two sampling points in each region (upper, middle, lower estuary, and sea) (Fig. 1). Each site was monthly sampled from November 2013 to October 2014 with a 1000 m long and 3 m wide seine net with 35 mm of mesh opening, a traditional local fishing gear usually utilized to capture mugilids (Torres *et al*. 2007). This net was deployed in the water by artisanal fishers using two small boats to enclose the sampling site for about 20 minutes, forming a semicircle with a set of baited hooks attached at the end of the net. All sampling procedures were executed systematically by the same fishing team to reduce potential effects of different fishing skills. In this way, we could assume absolute count data represents abundance since the effort was standardized. The two fishing sets from each region are more than 1 km distant from one another, which ensures independence between samples (e.g. de Barros *et al*. 2023). Two fishing sets per site/month were deployed, which totals 96 sets for the whole year. More replication would be necessary to obtain a more accurate picture of the spatial variability on mullet abundance, but we were limited by logistical constraints such as the need for the tides to be below a certain level. While our sampling is limited regarding the spatial variability in mullet abundance, we argue the data is still sufficient to answer the main question posed in this study about how environmental factors influence mullet abundances because of sufficient temporal coverage. At each sampling point, the following physicochemical and environmental variables were recorded in situ from water samples: temperature (◦ C), turbidity (NTU), salinity (parts per thousand - ppt), dissolved oxygen (mg/l), conductivity (µmhos/cm), and primary productivity (µg/l of chlorophyll a). Abiotic variables were recorded with a Multiparameter Sonde (YSI 6600 V2). In addition, mean monthly rainfall (mm) for the corresponding region was retrieved from http://www.semarh.al.gov.br/ (SEMARH, 2024).

Then, fish were identified in the laboratory by specialized taxonomic keys and processed. Sampling and transport were authorized by the Biodiversity Information and Authorization System - SISBIO (license number 56293-1).

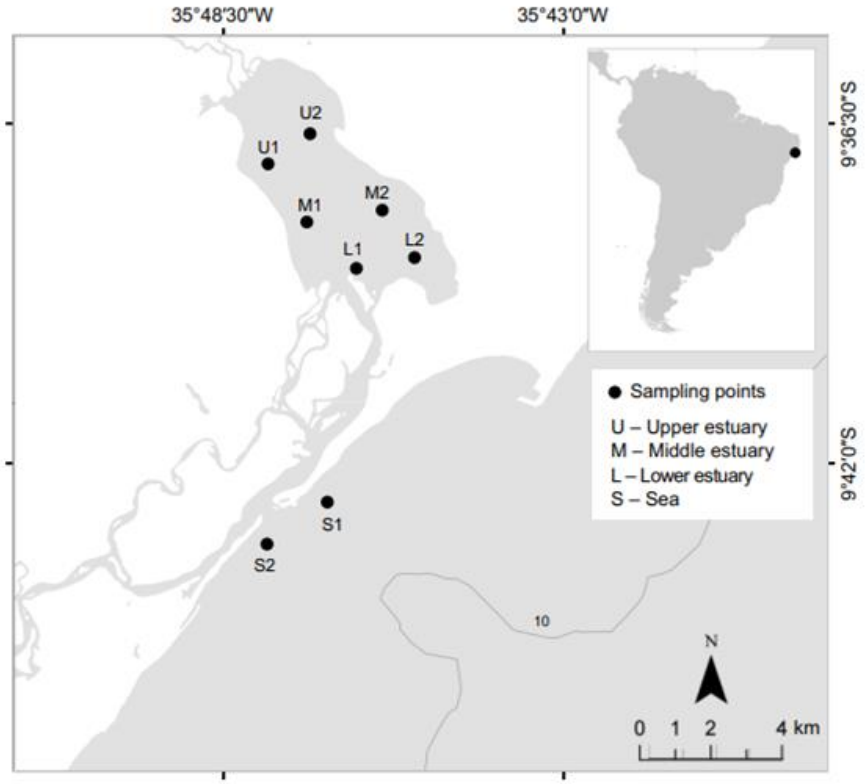

Figure 1. Map showing the sampling points within the Mundau Lagoon, Northwestern Atlantic.

Data analysis

Because of the high proportion of zeros in the mullet count data, log-transformation was not effective in producing normally-distributed data. Then, we compared fish counts with a non-parametric Mann-Whitney U test. Effects of environmental variability on the abundance of *M. curema* and *M. rubrioculus* were modeled using Bayesian zero-inflated, random-effects models with Monte Carlo Markov Chains (MCMC) algorithms. A zero-inflated model was considered the most appropriate after checking if a conventional generalized linear model (GLM) was underfitting zeros in the R package “performance”

(Lüdecke *et al*. 2021). The number of iterations was set to 500K and 10K burn-ins in the "r2jags" R package, an implementation of the JAGS (Just Another Gibbs Sampler) for the R statistical software (Su and Yajima, 2012). A complete description of the modeling framework is as follows:

Let Y = {y_i, i = 1,…, N} be a N-dimensional variable denoting the counts of *M. curema* and *M. rubrioculus* in the study area. We assume Y is generated by a mixture of two distinct processes as follows:

$$p(y_{[i]} \vee \theta, \lambda) = \begin{cases} \theta + (1-\theta)e^{-\lambda} for y_i = 0 \\ (1-\theta)(\frac{\lambda^{y_{[i]}}}{y!})e^{-\lambda} for y_i > 0 \end{cases}$$

where θ is the overall probability of observing zeros in the data. We model θ as a function of covariates using the logit link:

$$\theta = \frac{e^{(\gamma 0 + \gamma_{[\kappa]} X)}}{1 + e^{(\gamma 0 + \gamma_{[\kappa]} X)}}$$

$$\gamma_0 N(0, \sigma_{\gamma_0})$$

$$\sigma_{\gamma_0} half_{Cauchy}(0,1)$$

$$\gamma_{[\kappa]} N(0, \sigma_{\gamma_{[\kappa]}})$$

$$\sigma_{\gamma_{[\kappa]}} half_{Cauchy}(0,1)$$

where γ_0 is an intercept and γ_k is a K-dimensional vector of coefficients for each *k*-th covariate, while X represents a K x N-dimensional matrix of covariates. Coefficients follow non-informative prior distributions centered at zero with half-Cauchy standard deviations. For data points that are not zero, Y is assumed to follow a Poisson distribution with rate parameter λ:

$$Y Poisson(\lambda)$$

$$\lambda = e^{(\beta 0 + \beta_{[\kappa]} X)}$$

$$\beta_0 N(0, \sigma_{\beta_0})$$

$$\sigma_{\beta_0} half_{Cauchy}(0,1)$$

$$\beta_{[\kappa]} N(0, \sigma_{\beta_{[\kappa]}})$$

$$\sigma_{\beta_{[\kappa]}} half_{Cauchy}(0,1)$$

where β0 is an intercept and β[k] is a K-dimensional vector of coefficients for each *k*-th covariate, and X is the same K x N-dimensional covariate matrix as in above. The covariates included in the model are environmental data on salinity (ppt), temperature (Celsius), Dissolved Oxygen (mg/L), turbidity (NTU), Chlorophyll concentration (mg/L), and rainfall (mm), as well as the abundance of the other mullet (number of individuals), and collection site (Figure 1). The coefficient for collection site is random, while the other parameters are fixed for both count and presence-absence models. The resulting log-likelihood function for the Poisson Zero-inflated model may be then written as follows:

$$logL(\beta, \gamma) = \sum_{y_{[i]=0}} \log$$

$$+ \sum_{y_{[i]>0}} [y_{[i]} X\beta - e^{(X\beta)} - log(y_{[i]}!)] - \sum_{i=1}^{N} \log[1 + e^{(X\gamma)}]$$

Posterior predictive checks were conducted by sampling from the posterior predictive distributions for the models from both species and comparing these graphically to the observed data. We evaluated all possible model combinations taking into consideration the list of explanatory variables considered in this study and identified the set of most adequate models according to the smallest BIC (Bayesian Information Criteria) and DIC. Explanatory variables were previously examined for collinearity using the Spearman's rank correlation test at a threshold of r > 0.7 for highly correlated variables (Dormann *et al.* 2013). If collinearity was detected, the models were executed separately with each variable to examine their respective BIC and DIC values. Then, the variable that generated a model with the lowest predictive error was selected for the general model, while the other was excluded. As a result, only water conductivity was excluded because

of an expected high correlation with salinity (r = 0.78). For model diagnostics, MCMC chain convergence was checked with the potential scale reduction factor, which compares within and between-chain variances to test the null hypothesis of homogeneity of variances of posterior distribution among parallel chains (Brooks and Gelman, 1998). The models were considered to converge when the upper limit of the convergence diagnostic is close to unity. Posterior predictive checks were executed by analysing model residual distribution after comparing predicted and simulated data (Gelman *et al*. 2000). Effects of explanatory variables were considered significant if 80% of the posterior distributions did not overlap zero, following standard procedures that require defined criteria for hypothesis tests within a Bayesian framework (Kruschke, 2021).

Results

All measured environmental factors varied spatially and temporally within the study area. Temperature was at its highest (> 30 Celsius) during the dry season, and at its lowest during the wet season (< 26 Celsius). The inner lagoon appeared to have hottest temperatures, while the sea was colder. Expectedly, salinity was highest at the sea and lowest at the upper and middle lagoon regions, and varied seasonally at all sampled regions with peaks during the dry season. Turbidity was spatially similar, but peaked inside the lagoon at the end of the wet season. Primary productivity was higher inside the lagoon, at which there were peaks during the wet season. Finally, dissolved oxygen was the lowest at the sea (Fig. 2).

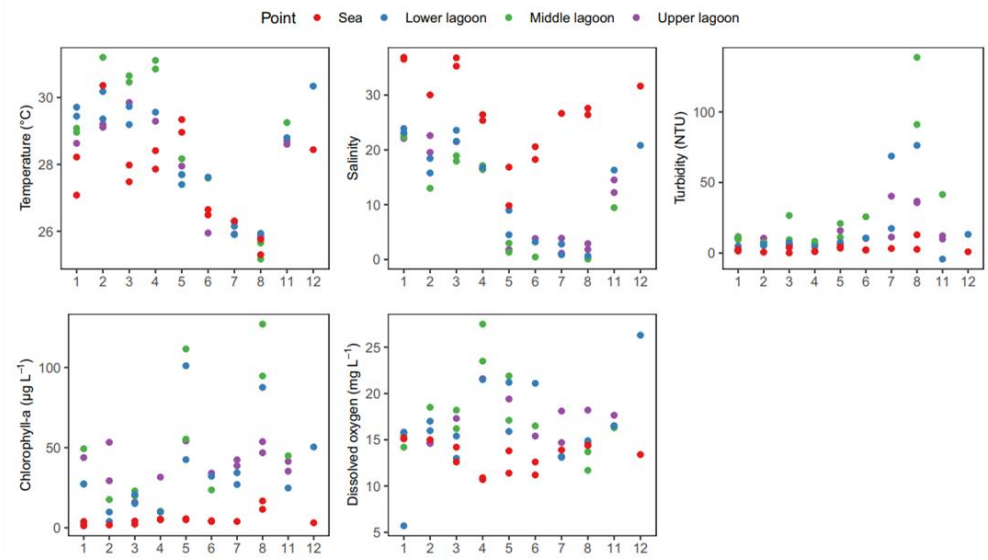

Figure 2. Monthly variation in environmental parameters measured at different regions of the Mundau Lagoon, Northwestern Atlantic.

A total of 1167 individuals were collected during the sampling period in 96 replicate net hauls, with 985 being *M. curema* and 182 *M. rubrioculus*. Evidently, the white mullet *M. curema* was far more abundant than the redeye mullet *M. rubrioculus* (Mann Whitney U test, $p < 0.0001$). Even though, the species appeared to exhibit substantial differences in their patterns of abundance within and outside the estuary, which also seems to vary seasonally (Figure 3). Specifically, the white mullet is evenly distributed inside the estuary and less abundant at the sea during the dry season. In the rainy season, the white mullet is more abundant in the upper lagoon. The redeye mullet is much more abundant at the sea than inside the estuary in the rainy season, while it seems to enter estuarine regions with the advent of the dry season (Fig. 3).

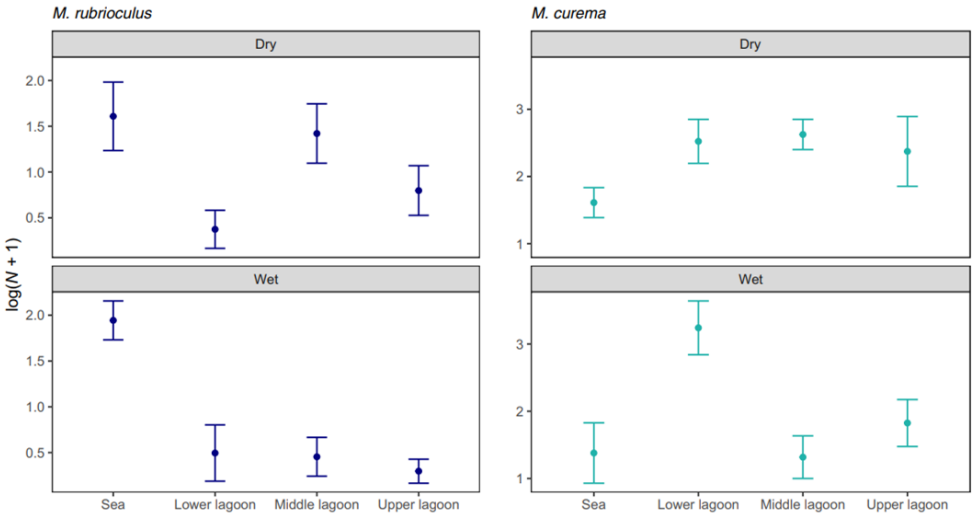

Figure 3. Spatial and temporal variation in abundance (counts) of white and redeye mullets at the Munda Lagoon, north-western Atlantic. The vertical axis shows the log-transformed means and two standard errors of mullet counts.

According to the traceplots for the three MCMC chains and the potential scale reduction factor, Bayesian zero-inflated model outputs showed full convergence to the posterior for almost all model parameters after 500K iterations and 10K burn-ins. The regression coefficient for temperature was the only parameter that exhibited slight signs of non-convergence on the models for both species, possibly due to multiple local minima on the negative log-likelihood profile. Posterior predictive checks show that the model for *M. curema* can accurately predict the observed data, with a normal residual distribution. The model for *M. rubrioculus* was not as good on predicting all the variation and spread of the data, but still useful to describe its general trends (Fig. 4). In fact, after including all variables and random effects in the models, predictive error (DIC statistic) was reduced from more than 2000 to about 250 – 300 for both models. Posterior distributions and credible intervals of model parameters show that the examined species exhibit different responses to environmental variability. The abundance of the white mullet is positively influenced by temperature and primary productivity, and negatively by dissolved oxygen, turbidity, and rainfall. Conversely, abundances of the redeye mullet are only positively

influenced by salinity. Both species also seem to negatively respond to increased abundance of their congeneric (Fig. 5, Table 1).

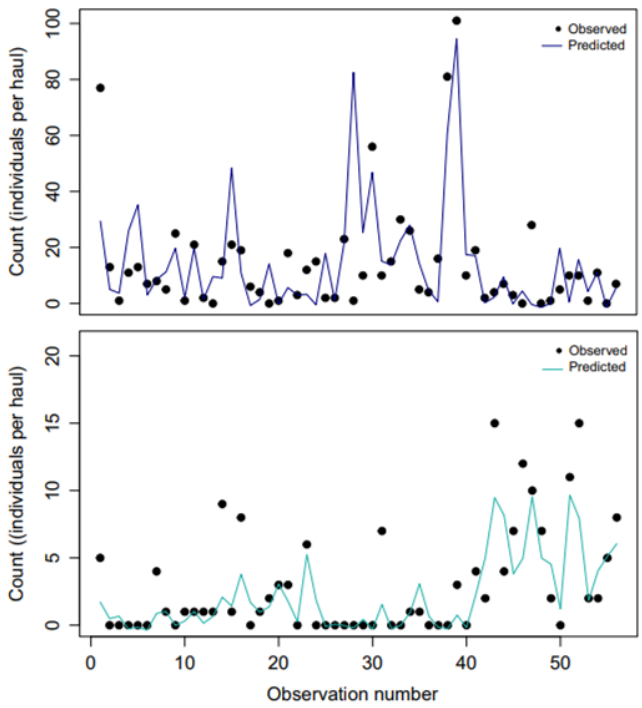

Fig 4. Posterior predictive check for the Bayesian zero-inflated generalised linear models fit to count data of white (top) and redeye (bottom) mullet species sampled at the Mundaú Lagoon, north-western Atlantic. Individual data points represent observed quantities and coloured lines are median model fits.

Table 1. Summary of posterior distributions for the random-effects zero-inflated model parameters for predicting the abundance of *M. curema* and *M. rubrioculus.* 80% credible intervals were selected according to criteria for hypothesis testing within a Bayesian framework. Values highlighted in bold denote a “significant” effect. “Mullet” refers to the coefficient for the abundance of the congeneric species affecting the other.

	M. curema		*M. rubrioculus*	
Parameter	Median estimate	80% credible interval	Median estimate	80% credible interval
Probability of Encounter	0.93	0.90 to 0.96	0.67	0.089 - 0.1
Temperature	**0.408**	**0.286 to 0.545**	0.115	-0.151 to 0.478
Salinity	0.002	-0.036 to 0.042	**0.072**	**0.044 to 0.104**
Turbidity	**-0.035**	**-0.044 to -0.026**	0.004	-0.029 to 0.018
Chlorophyll	**0.034**	**0.026 to 0.041**	-0.0014	-0.011 to 0.046
Mullet	**-0.024**	**-0.012 to -0.036**	**-0.047**	**-0.028 to -0.062**
Dissolved O2	**-0.11**	**-0.149 to -0.072**	-0.042	-0.153 to 0.065
Rainfall	**-0.049**	**-0.077 to -0.01**	-0.001	-0.012 to 0.01

80% credible intervals were selected according to criteria for hypothesis testing within a Bayesian framework. Values highlighted in bold denote a 'significant' effect. 'Mullet' refers to the coefficient for the abundance of the congeneric species affecting the other.

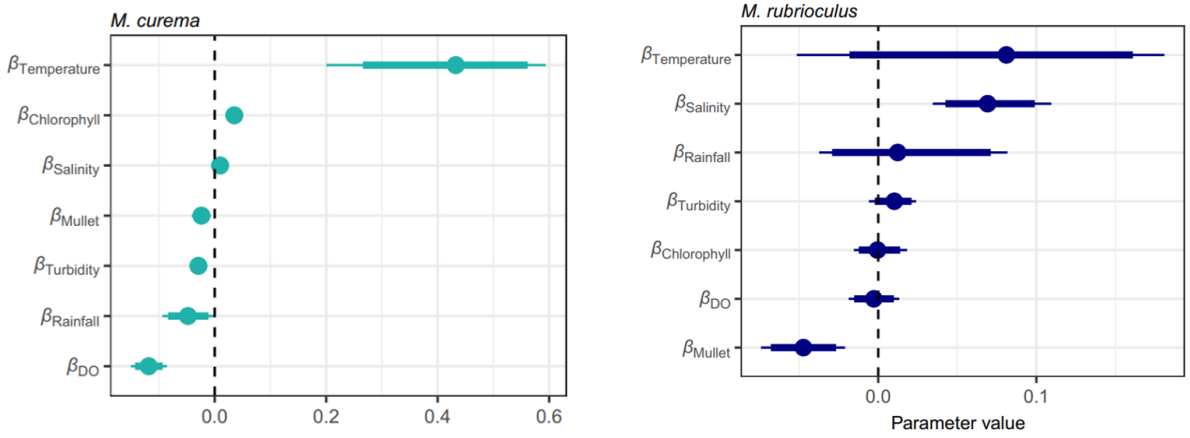

Fig 5. Influence of environmental parameters on the abundance of white and redeye mullets within the Mundaú Lagoon, north-western Atlantic. Points represent Bayesian

posterior medians from the zero-inflated models and lines represent the 80% credible intervals after 500,000 iterations. DO, dissolved oxygen.

Discussion

Current ecological theory states that sympatric, morphologically alike species with similar life-history traits such as *M. rubrioculis* and *M. curema* (Rangely *et al.* 2023) are expected to exhibit mechanisms to allow for coexistence and reduce overlap in resource use that often result in subtle trait divergences (Holt *et al.* 1994; Porreca *et al*. 2017). Our results suggest that the habitat use patterns of the studied species are spatially and temporally decoupled (Figure 6) due to different responses to environmental variability. Specifically, *M. rubrioculus,* driven by salinity, occupies outer estuarine reaches and the sea, only penetrating inner estuarine areas during the dry season. *M. curema* is driven by temperature, dissolved oxygen, chlorophyll, and turbidity, being able to occupy the inner estuary.

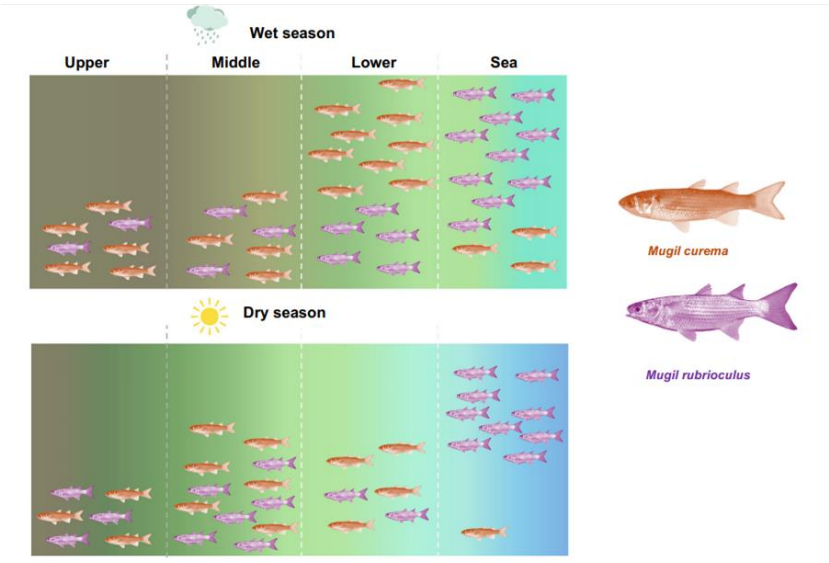

Fig 6. Infographic illustrating the spatial-temporal movements of white and redeye mullet *M.curema* and *M. rubrioculus* in the Mundaú Lagoon, north-western Atlantic.

Evolutionary responses to coexistence leading to niche differentiation can vary considerably from mechanisms such as dietary mismatches and different life-histories to

distinct responses to varying environmental conditions (da Silva *et al*. 2017b; Rangely *et al.* 2023; Ulrich and Tallman, 2021). The advent of different responses to abiotic factors in sympatric species has long been acknowledged as an evolutionary tool that makes each species have optimal competitive fitness in different environments, hence contributing to ecological partitioning (Lombarte *et al.* 2000). Therefore, one of the mechanisms that could have led to such decoupled life histories in tropical mullets is character displacement, acknowledged as a common process when sympatric species are found to differ in resource use (Goldberg and Lande, 2006). Ecological character displacement can be explained as competition-induced differences in life-history traits through phenotypic plasticity, causing differential selection to take place (Slatkin, 1980). This process is a key driver of species diversity, also often associated with sympatric speciation (Schluter and McPhail, 1992; Tyerman *et al*. 2008). Despite being previously seen as relatively rare in nature because the presence of gene flow usually slows down trait divergence, sympatric speciation is now acknowledged as one of the main mechanisms leading to the formation of species with similar ecological requirements but with fine-scale divergences due to the presence of assortive mating among individuals with a particular trait (Barluenga *et al.* 2006; Bird *et al.* 2012; Jiggins, 2006). Therefore, such process is thought to select individuals that perform better in certain environmental conditions (see Johannesson, 2001 for a review on sympatric/parallel speciation and its mechanisms). In fact, phylogenetic studies on the genus *Mugil* found that *M. curema* and *M. rubrioculus* are the most closely related among tropical mullets, and their lineages have diverged more recently (Neves *et al.* 2020, 2021), which supports the occurrence of sympatric speciation.

Complex interactions between biotic and abiotic variables come into place to explain variations in fish habitat use over time and space (da Silva *et al.* 2021, 2022). An important density-dependent effect on fish populations is interspecific competition, which can be particularly strong on sympatric, closely-related species and influences factors such as growth and habitat use (Andersen *et al.* 2017; Hasegawa, 2016). As a response, the overlap in niche between populations of competing species tends to decrease to minimize competition (Johannesson, 2001; Lombarte *et al.* 2000). The white mullet *M.*

curema, ubiquitous inside the estuary, is a generalist predator able to adapt to various prey community structures (Garcia *et al.* 2018), which is usually favored inside estuarine regions due to the commonly higher diversity and abundances of potential prey in its productive waters. Unfortunately, such information is not yet available for the redeye mullet. Even so, we speculate that this species may present less variable feeding habits and, consequently, a stricter ecological niche when compared to *M. curema* because of the less variable spatial distribution found in this study. Then, an apparent resource partitioning, apart from the evident spatial segregation, should be another mechanism allowing such species to coexist (when and where they do), which was previously observed in the study of Garcia *et al.* (2018) between *M. curema* and *M. liza* in a subtropical estuary.

The spatial and temporal decoupling showed by the studied species follows common dynamics of tropical coastal habitats. Estuaries are one of the most dynamic systems among coastal habitats, with marked variations in environmental conditions due to its connection with both terrestrial and oceanic systems (Macedo *et al.* 2023; Ram *et al.* 2003). Accordingly, biological communities are highly affected by such considerable environmental changes, including nekton (Jaureguizar *et al.* 2021; Childs *et al.* 2008). Unlike temperate regions, where temperature variations control most environmental changes and ecological cycles, nekton on tropical estuarine environments are usually driven by seasonal variations in rainfall (wet/dry seasons) (da Silva *et al.* 2018; de Barros *et al*. 2022; Macedo *et al.* 2021), which affect water mixing and nutrient dynamics on estuaries (Burford *et al*, 2012; Medeiros and Kjerfve, 1993). The tropical rainy season drives allochthonous entrances from upstream that increase primary productivity, reduces salinity, dissolved oxygen and enhances water turbidity (Carrillo *et al.* 2009; Kress *et al.* 2002), while conditions in the dry season include the penetration of sea-like conditions inside the estuary (Azhikodan *et al*. 2021). Our results suggest *M. rubrioculus* might be more adapted to higher salinities (Figure 5), being mostly restricted to occupy areas outside the estuary during the rainy season (Figure 3). Conversely, the advent of the dry season allows this species to penetrate the estuary due to increased saltwater intrusion. *M. curema*, not restricted by salinity, was evenly distributed inside the estuary during the

rainy season (Figure 2), where dissolved oxygen is lower, but turbidity and primary productivity are higher. In the dry season, when *M. rubrioculus* can penetrate estuarine regions, *M. curema* showed higher abundances on the upper estuarine region, which could be attributed to effects of interspecific competition.

Mullets are an important fishery resource in South America, but few mullet stocks are assessed in the region since those fisheries are artisanal and small-scale. With some reports of overfishing (Mendonça and Bonfante, 2011) and increasing fishing pressure due to population growth in the region (Blaber and Barletta, 2016), assessment and management efforts will be vital to ensure the long-term sustainability of these resources. Fisheries stock assessments primarily rely on abundance indexes to infer trends in the population over time (Maunder and Punt 2004). However, raw abundance indexes often do not reflect the true abundance since variations in the index can also reflect numerous other factors such as sampling artifacts, variations in environmental conditions at the time of sampling, and fishing behaviour (Maunder *et al.* 2006). Therefore, data standardization (*i.e.* 'removing' the influence of factors other than abundance) is necessary for the index to be used as a reliable indicator of population trends (Hinton and Maunder 2004). In our study, we demonstrate that the abundances of *M. curema* and *M. rubrioculus* are significantly impacted by variations in environmental conditions, which should therefore be accounted for in future assessments. We also highlight the usefulness of modelling frameworks that can handle overdispersed characteristics in the data such as zero inflation, being therefore highly useful for species with patchy distributions. In fact, zero-inflated models have been extensively used in CPUE standardization procedures, and produce reliable results when the right explanatory variables are accounted for (Alvarez-Berastegui *et al.* 2018, Brodziak and Walsh 2013, Hiraoka *et al.* 2015).

Conclusions

The studied species showed significant spatial segregation in the Mundaú Lagoon Estuary, which appears to be a result of divergent adaptation resulting in distinct responses to environmental conditions between species. As a result, the white mullet, which is more abundant, is substantially widespread inside the lagoon. Conversely, the

redeye mullet exhibits a remarkably low abundance inside the estuary, whereas it is much more present at the sea, where salinity is at its highest. The inherent seasonality of tropical estuaries appears to rearrange the species distribution within the different estuarine regions. Management decisions towards improving mullet conservation and stock productivity should incorporate the small-scale variability in spatial distribution assessed here into future species distribution models. Further, the influence of predicted shifts in abiotic parameters due to climate change on the studied species should be explored.

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Conflict of interest

The authors have no conflict of interest to declare.

Data availability statement

The dataset used for analyses in this study can be made available upon reasonable request to the corresponding author.

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4. ASSESSING INTERSPECIFIC VARIATION IN LIFE-HISTORY TRAITS OF THREE SYMPATRIC TROPICAL MULLETS USING AGE, GROWTH AND OTOLITH ALLOMETRY

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Highlights

- Validation of annuli deposition for three sympatric, tropical mullets is provided.
- Otolith allometry is integrated with age, growth and reproduction.
- Otolith allometry is a potential predictor of key life cycle events.
- The studied species adjust their life-history traits to allow for coexistence.
- Information provided here allows for further look into possible management options.

Abstract

Life history theory predicts that organisms optimize their life-history traits according to evolutionary context and environmental constraints. Sympatric estuarine-dependent fish are intriguing subjects for studying life-history variation, as their traits are molded by their complex habitat use and co-occurrence with ecologically similar species. In this study, we investigated life-history traits of three tropical mullet species (*Mugil curema*, *M. liza* and *M. rubrioculus*) using otolith age, growth, and allometry. Our results indicate that otolith allometric patterns are useful predictors of specific life history traits: the faster-growing species *M. rubrioculus* (K = 0.31) was characterized by earlier stanza changing points (SCPs), with 0.8 years of life. In contrast, the slower-growing species, *M. liza* (K = 0.21) was characterized by later changing points, 1.3 years of life. *M. curema* is intermediate (K = 0.25), with 0.95 years of life. The first SCP may register juvenile movements between estuarine and coastal habitats before the first year of life, and the second SCPs appear to reflect the migration to the sea and age at maturation. More generally, our study species exhibit fine-scale temporal differences in life cycle events that may be negatively related to growth rates and body size that can be predicted by otolith allometry, as well as a gradient of interspecific divergences in life-history traits. These are likely to be driven by differences in their migratory behavior and habitat use that permit coexistence.

Keywords: fish, fisheries, *Mugil*, sympatry, estuarine-dependent, life cycle

1 Introduction

Life-history theory predicts that organisms make optimal decisions about how to best allocate energy to mutually exclusive processes such as growth, reproduction and migration (Marquet et al., 2014; Reiners et al., 2017; Winemiller, 2011). As a result, a unique and optimal set of traits emerge that maximize fitness in the species' evolutionary and ecological context (Stearns, 2015). Recent developments in life-history theory suggest that a species' life-history traits can be used to accurately predict its responses to environmental constraints such as seasonality, abiotic variability and habitat use (Perkin et al., 2016; Hitt et al., 2020).

Connectivity within a seascape is often conceptualized as the product of complex interactions among different biophysical elements such as coastal and estuarine ecosystems (Ray, 2005; Taylor et al., 1999, Macedo et al, 2021). Some opportunistic marine or freshwater species utilize estuarine habitats for early growth or reproduction (Able, 2005; Ray, 2005), despite the additional costs associated with osmoregulation (Cardona, 2000). Among estuarine-dependent fish, the family Mugilidae (mullets) is one of the most representative, with the genus *Mugil* being particularly pervasive in tropical and subtropical coastal environments (Froese & Pauly, 2008; Menezes et al., 2015). Mullets usually exhibit complex migratory behaviors, with particularly variable habitat use patterns in different life cycle stages (Avigliano et al., 2021; Mai et al., 2018). According to Avigliano et al. (2021), the most common habitat use pattern for mullets is estuarine migratory, in which the estuary is vital at some point of their life cycle. Mullets typically use estuaries as nurseries, where juveniles take advantage of the higher nutrient input and structured habitats to rapidly develop in their first year(s) of life. After that, they typically migrate to coastal seas, where reproduction takes place (Santana et al., 2018). In this sense, mullets are potential model species for studying life-history traits because of their complex migratory behavior, wide commercial importance, and a high degree of sympatry (Ibáñez et al., 2022; Mai et al., 2018; Morado et al., 2021; Whitfield et al., 2012).

Fish otoliths, hard calcified structures located in their inner ear, have been widely used by scientists due to their capacity to store information about a fish's life history (Campana, 2005; Miller et al., 2010; Schulz-Mirbach et al., 2019; de Queiroz et al., 2018). As the fish grows, the otolith incorporates calcium and other elements, a process that is usually controlled by environmental variation (Morales-Nin, 2000). As such, otoliths are very useful in disentangling life-history traits such as age, growth and allometric patterns (Bervian et al., 2007; Jakes-Cota et al., 2021; Medeiros et al., 2021; Xieu et al., 2021). For example, Medeiros et al. (2021) described polyphasic allometric growth patterns in otoliths of snook (genus *Centropomus*), finding that changes in allometric growth rates are associated with critical events in their life cycle, such as age at maturity and sex change. Such findings highlight a potential new, cost-effective, and practical tool for evaluating critical aspects of fish life histories, potentially providing important baseline information for management purposes. However, it is mandatory that such methodology undergoes species-specific testing.

For estuarine-dependent species such as mullets, spending less time in estuaries in the early years of their life may be related to faster growth rates, with faster-growing species being able to migrate earlier because of reduced size-selective mortality risks (Able, 2005; Ray, 2005). According to life-history theory, such fast-growing species may reach sexual maturity earlier, but also attain smaller maximum sizes (Thorson et al., 2014, 2017). In this study, we aim to provide growth parameters based on length-at-age relationships of three exploited tropical mullet species (*Mugil curema* – white mullet, *Mugil liza* – lebranche mullet, *Mugil rubrioculus* – redeye mullet) to aid management of such poorly studied resources. In addition, we integrated age and growth information with polyphasic otolith allometry and reproduction to address the following hypotheses: (1) otolith polyphasic allometry can accurately predict age at maturation; and (2) the studied species exhibit a gradient in life-history parameters according to life-history theory. Specifically, we hypothesize that the faster-growing and smaller species will exhibit earlier maturation and change allometric growth patterns at younger ages, while the slowest-growing species will exhibit late maturation and allometric changes. In addition, crucial

population parameters are provided for the first time for the extremely under-studied mullet *M. rubrioculus*.

2 Materials and methods

2.1 Study area and sample collection

Sampling activities were carried out in two tropical Southwestern Atlantic estuaries; Mundaú Lagoon, (9° 380 15″ S 35° 460 20″ W) and the estuary of the Santo Antônio river (9º24’50”S e 35º30’24”W), Alagoas, Brazil (Figure 1). These areas exhibit a semi-humid tropical climate, with rainy periods from March to August (rainfall 242.9 - 94.2 mm) and dry periods between September and February (100.7 - 63.9 mm). Rainfall (in mm) was recorded monthly based on data from the Brazilian National Weather Institute.

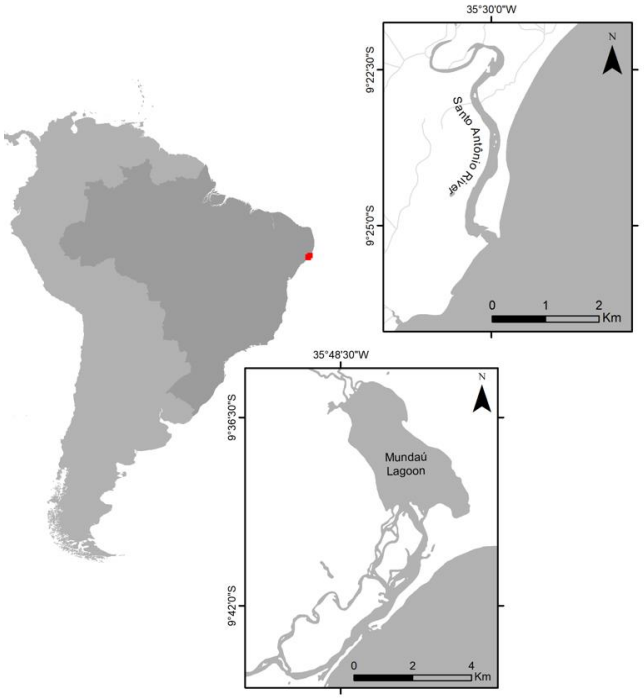

Figure 1. Map of the sampling locations in the tropical Southwestern Atlantic: Mundau Lagoon (lower panel), and Santo Antonio River (upper panel).

Monthly samples were obtained for one year for the three species: white mullet in 2009-2010; lebranche mullet in 2011-2012, and redeye mullet in 2018. Different fishing gear (e.g., gillnets, trawl, longline, casting nets, and hand line) was used to obtain representative samples in terms of size composition, as certain gears tend to select individuals of different sizes. Individuals were then taken to the laboratory, identified following dichotomic keys by Menezes et al. (2015), and processed according to standard fish sample processing procedures. Each individual was measured (total length (TL in cm) and individual gonad developmental stages were assigned by macroscopic examination. Gonad developmental stages were defined as immature, developing virgin, mature, post-spawning and spent or resting (Vazzoler, 1996). Next, the otoliths were removed and washed with distilled water and a 2% sodium hydroxide solution. In addition, to visualize growth rings, the otoliths were decalcified by submersion in a 4% xylene solution and read while submersed in a 70% ethanol solution. Each otolith was photographed with a digital camera attached to a stereoscopic microscope and had its radius (distance from the nucleus to the rostrum) measured with the aid of the ImageJ software (Schneider et al., 2012).

2.2 Otolith polyphasic allometric patterns

The first step in fitting poly or multiphasic growth models is to validate the assumption of non-linear growth patterns, which would take form of a non-random residual distribution in a linear fit of the data (Bervian et al., 2006). For that, the relationship between otolith radius (OR) and total length (TL) for the three species were analyzed by fitting the Huxley (1950) power equation. The standardized residuals of the fitted power equation were plotted against the explanatory variable (OR) and checked for non-random patterns by a normality test. A non-normal residual distribution implies that the fitted model fails in explaining a considerable amount of variation in the data.

Once non-linear growth patterns were identified, several power regressions with invariant intercepts (a) for data grouped into size classes of 5 mm were fitted to extract allometric coefficients (bsc, i.e. the *b* parameter in the Huxley power equation). These allometric coefficients were plotted against the explanatory variable (OR) and a third-

degree polynomial model was fitted for the relationship between fish total length and allometric coefficients (bsc) (Bervian et al. 2006). To determine the rate of change of the allometric coefficients as the fish grows, the polynomial models were differentiated for their first derivatives. Then, the inflection points for the polynomial fits (i.e. stanza changing points (SCP) – when the rate of change for the allometric coefficient is equal to zero were determined by plotting the first derivatives against OR observations. Finally, the SCPs were transformed into predicted ages according to the best-fit growth model.

2.3 Otolith macrostructure and age determination

After decalcification with a 5% xylol solution, whole otolith ring demarcation patterns were evaluated by quantitative methods to ensure robust growth ring identification and to detect potential false marks. Quantitative evaluation was based on the distance from the otolith core to each mark called, the radius of each ring. Each radii were evaluated for conformation with a normal distribution (Shapiro-Wilk's test) and to check if the mean radius of each mark decreased with increasing otolith size, under the assumption that the growth rate decreases as the fish grows. A particular mark was considered false (and not considered in further age estimation) if it did not follow these criteria.

After eliminating ‘false’ rings, otolith growth increments were identified by two researchers in an independent, double-blind process (no prior knowledge of individual fish morphometric characteristics that could bias age determination, as well as no knowledge of which age the paired researcher attributed to the fish) (Jakes-Cota et al., 2021). The otoliths were read under transmitted light at 10x magnification. Then, reading accuracy was assessed by the coefficient of variation (CV) with a threshold of 10% (Allman et al., 2014; Chang, 2011). To confirm the annual formation of growth rings, we utilized the Marginal Increment Ratio (MIR) (Fabré & Saint-Paul, 1998), defined by the following equation:

$$MIR(\%) = \frac{R_t - R_n}{R_n - R_{n-1}} * 100$$

where R_t is the otolith radius, R_n is the distance from the nucleus to the last growth ring, and R_{n-1} is the distance from the nucleus to the penultimate growth ring. We applied a one-way analysis of variance (ANOVA) followed by the Tukey post-hoc test to check for significant differences in the MIR between months, showing the periodicity of ring formation. The month with significantly smaller MIR, as determined by a *post-hoc* Tukey test, was considered as the month of ring formation.

Otolith macrostructures are the result of alternating periods of faster and slower growth rates which are, in turn, a consequence of seasonal growth that is usually driven by variations in environmental parameters. To investigate if seasonal tropical rainfall and fish condition are related to fish growth, a generalized linear model (GLM) was used. MIR, the response variable, was used as an indicator of seasonal growth rate (Fabré and Saint-Paul, 1998; Hauser et al, 2018) and used as response variable, while condition factor and monthly rainfall (mm) were considered explanatory. Here, condition factor was defined as the ratio between the observed and predicted length, as defined by the previously fitted least-squares length-weight relationships (Froese, 2006). Model assumptions such as residual normality and homogeneity of variances were previously verified before accepting test results.

A total of 953 otoliths (364 for *M. curema*, 380 for *M. liza* and 209 for *M. rubrioculus*) were processed for age estimation (size ranges were 5 – 42.5 cm for the white mullet, 11.5 – 75 cm for lebranche mullet, and 8 – 39 cm for redeye mullet). Sagittal otoliths of the three species after decalcification were characterized by a very dense opaque core, followed by a large hyaline band and subsequently alternating growth rings. Following the quantitative criteria of decreasing between-ring distances and unimodal fitting, the first two rings were not considered to be annuli for all species (Figure 2).

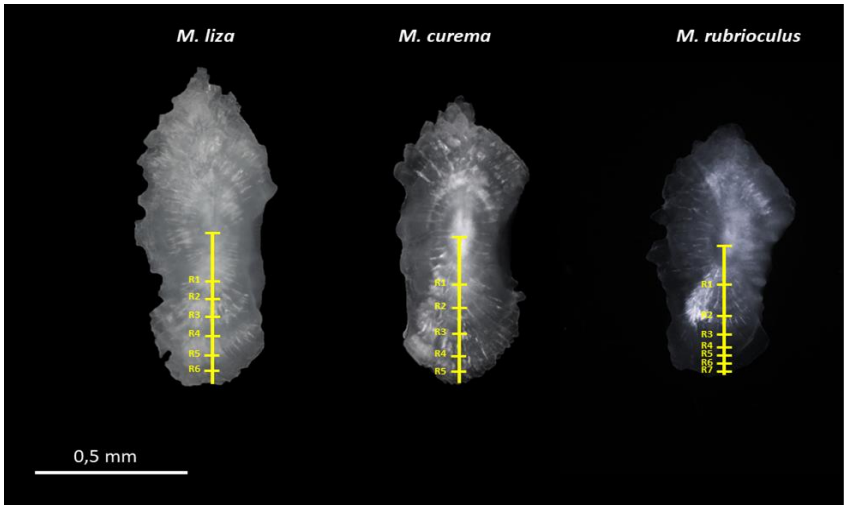

Figure 2. Sagitta otoliths from *Mugil liza, M. curema* and *M. rubrioculus* and their annual growth rings.

2.4 Growth rate and asymptotic size

We utilized the back calculation method to estimate fish length at previous ages through correspondent growth ring measurements towards improving the accuracy of length-at-age data. This is based on the relationship between otolith size and fish size, using the radius of each growth ring as a proxy to calculate fish size at its respective age (Morat et al., 2020). We used the back-calculation model from Morita & Matsuishi (2011), which uses the following multiple regression model:

$$TL = \alpha + \beta * + \gamma * Age$$

where α is the intercept, β is the coefficient of variation for OR (otolith radius), and γ is the coefficient of variation for fish age.

Then, the coefficients of the best-fit model are applied to the following equation:

$$TL_t = \frac{-\alpha}{\beta} + \frac{(TL_c + \frac{\alpha}{\beta} + \frac{\gamma}{\beta} * t) *}{c}^{t} - \frac{\gamma}{\beta} * t$$

where TL_t is the length at age t, TL_c is the length at capture, OR_t is the otolith radius at age t, OR_c is the otolith radius at capture, and α, β and γ are the coefficients obtained by the multiple regression analysis.

Length-at-age data (observed and back-calculated) were utilized as input to estimate the growth parameters of the three species by fitting the von Bertalanffy growth model (VBGM) in the R package "FSA" (Ogle et al., 2021). It utilizes non-linear least-squares regression analysis to search for optimal parameters such as k, L_∞ and t_0 and their respective standard errors. The following equation define the VBGM:

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

where L_t is the length at age t, L_∞ is the asymptotic size, k is the growth rate and t_0 is the theoretical age when length is set to zero, i.e., the x-intercept.

2.5 Hypothesis testing

To test if otolith allometry can be used to accurately describe important life history events in the three species, we first converted the SCPs to relative age according to the best-fit von Bertalanffy growth model. We then utilized the R package "sizeMat" to calculate the age at first maturity (A_{50}) using the data on individual gonad developmental levels for each species. Then, we verified if the A_{50} 95% confidence intervals overlap with any SCP. We also analyzed the 95% posterior distributions of growth parameters k and L_∞ and compared them between species. All statistical analyses were carried out with predefined, fixed seed values to allow for reproducible results in the R software version 4.1.2.

3 Results

Lebranche mullet had the highest mean (31.41 ± 19.2 cm) and maximum total length (75 cm), followed by white (28.5 ± 7.67 and 45 cm) and redeye mullet (27.08 ± 6.19 and 39.6 cm) (Figure 3). Age estimates ranged from 0 to 9 years for white mullet (only 4.78% or error between readers), 2 to 8 years for lebranche mullet (6.37% error) and 1 to 10 years for redeye mullet (5.43% error).

The monthly marginal increment ratio (MIR%) variation confirmed that one annulus is formed per year for each species. The smallest MIR values indicated that the hyaline zone was formed in the month of February for both lebranche and white mullet (Tukey *post-hoc* pairwise test, $p < 0.0001$ and $p = 0.031$, respectively). For the redeye mullet, ring formation appears to take place in August (Tukey *post-hoc* pairwise test, $p = 0.028$) (Figure 4). Generalized linear models indicated that the relative condition factor and monthly rainfall are closely related to annuli formation. More specifically, we detected significant positive influence of rainfall on the marginal increment ratio of lebranche and white mullets. Condition factor was also positively related to the MIR for the white and redeye mullets (Table 1).

Table 1. Output of the generalized linear models (GLMs) for the influence of rainfall and condition factor on the annuli formation (IMR) for the three species

Specie	Effect	Estimate	Standard error	t value	p value
Lebranche mullet	Condition factor	-0.160	0.136	-1.178	0.24
	Rainfall	0.00024	0.000115	2.098	0.0373*
White mullet	Condition factor	13.83	5.115	10.4	0.005*
	Rainfall	0.022	4.884	2.832	0.042*
Redeye mullet	Condition factor	0.731	0.360	2.031	0.043*
	Rainfall	0.00019	0.053	0.004	0.99

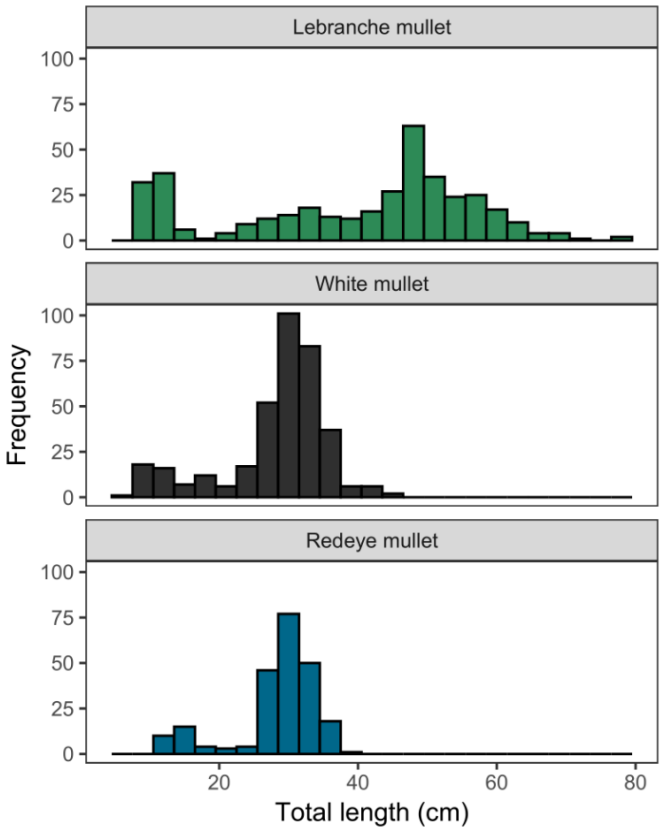

Figure 3. Size structures for the lebranche mullet *M. liza*, white mullet *M. curema*, and redeye mullet *M. rubrioculus* caught in the study locations.

According to the non-random residual distributions, the OR / TL relationship for all three species showed polyphasic allometric growth ($p < 0.001$). As demonstrated by the polynomial fit, there was significant variation of the allometric coefficient with increasing otolith radius. Differential equations for the polynomial models, which denote the rate of change for the fitted model as the independent variable changes, indicate two sequential stanza changing points (SCPs) for the three species. The redeye mullet achieves the SCPs at smaller ORs, while the lebranche mullet achieves it at larger ORs (Figure 5). According to the length-at-age plots, the first SCPs take place at around one year of age for all three species. However, the redeye mullet had the earliest (about 0.8 years), followed by white (0.95 years) and lebranche mullets (1.3 years). Similarly, despite

occurring at roughly 3 years of age for the three species, the second SCP also exhibited a similar gradient: approximately 2.7 for the redeye mullet, 3.1 for the white mullet, and 3.5 years for the lebranche mullet. According to the macroscopic gonadal maturation models, the second SCP for the three species greatly overlapped with the age at maturation, hence confirming our 1st hypothesis (Figure 6).

Not surprisingly, fitted growth parameters also show the same gradient pattern found for the SCPs: the lebranche mullet was the slowest-growing (k = 0.21) and had the greatest asymptotic length (L_∞ = 70.37), the redeye mullet was the fastest-growing (k = 0.31) and exhibited the smallest asymptotic length (L_∞ = 36.38), and the white mullet exhibited intermediary growth parameters (k = 0.25, L_∞ = 39.45). The growth curves of the three species were similar, but 95% confidence intervals did not overlap (Table 2 and Figure 6).

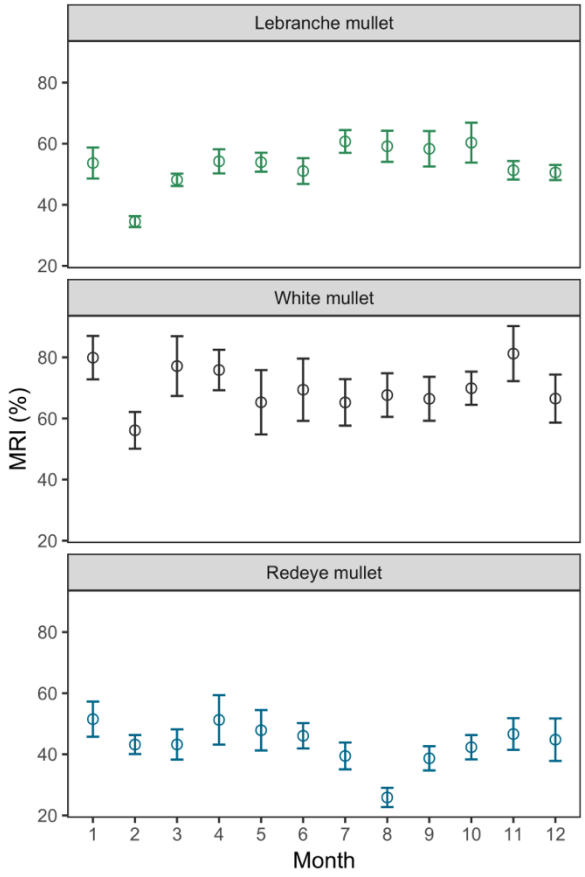

Figure 4. Monthly marginal relative increment (MRI %) for the lebranche mullet *M. liza*, white mullet *M. curema*, and redeye mullet *M. rubrioculus* caught in the study locations. *A posteriori* multiple comparisons indicate significant differences in the month of February for the lebranche and white mullets, and in August for the redeye mullet.

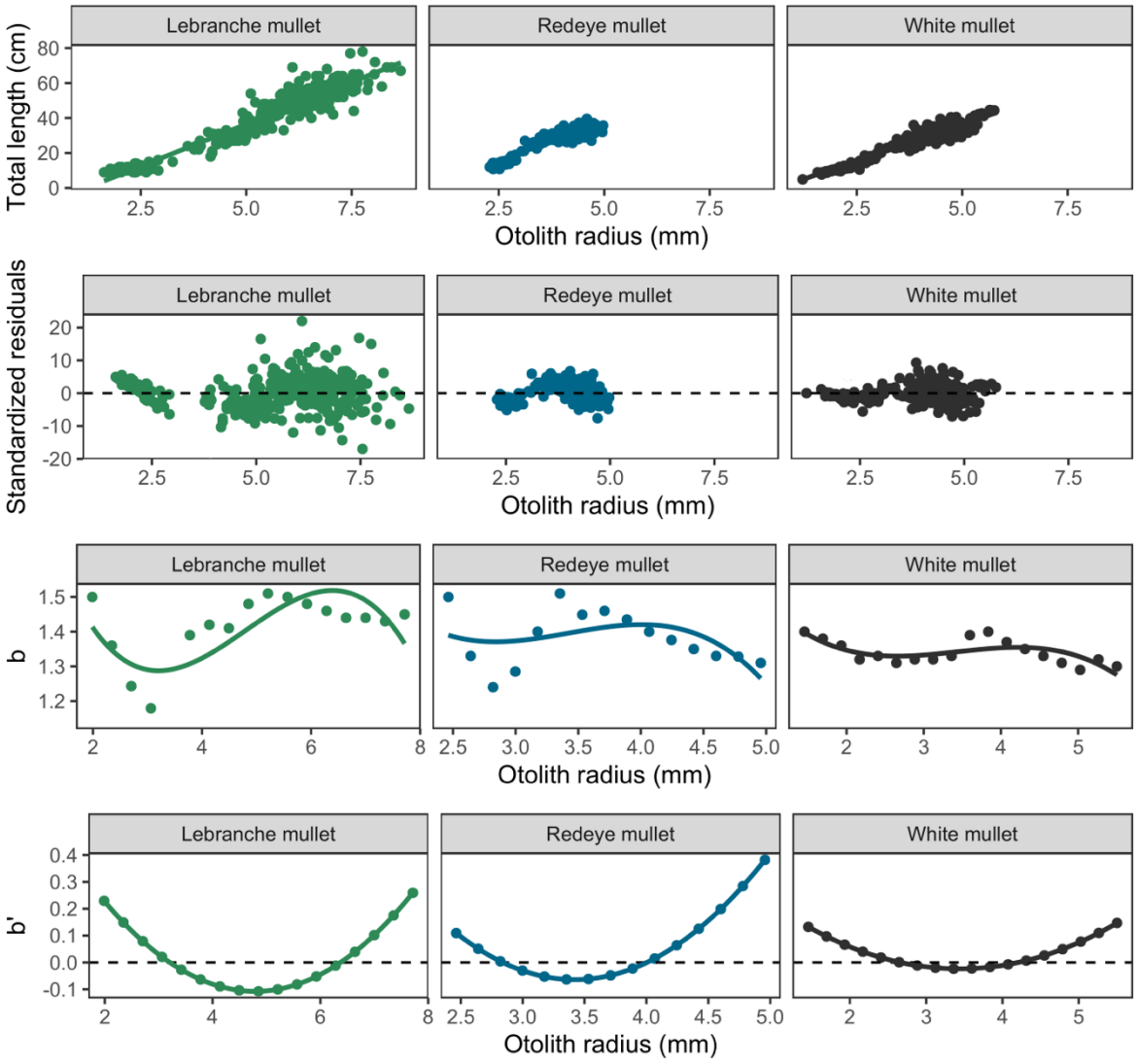

Figure 5. From top to bottom, for the lebranche mullet *M. liza*, white mullet *M. curema*, and redeye mullet *M. rubrioculus*: relationship between otolith radius (OR)- mm) and total length (TL), standardized residuals of the power regression between OR and TL, polynomial fit of the relationship between OR and the allometric coefficient (b), and relationship between the derivative of the polynomial model (b') and OR.

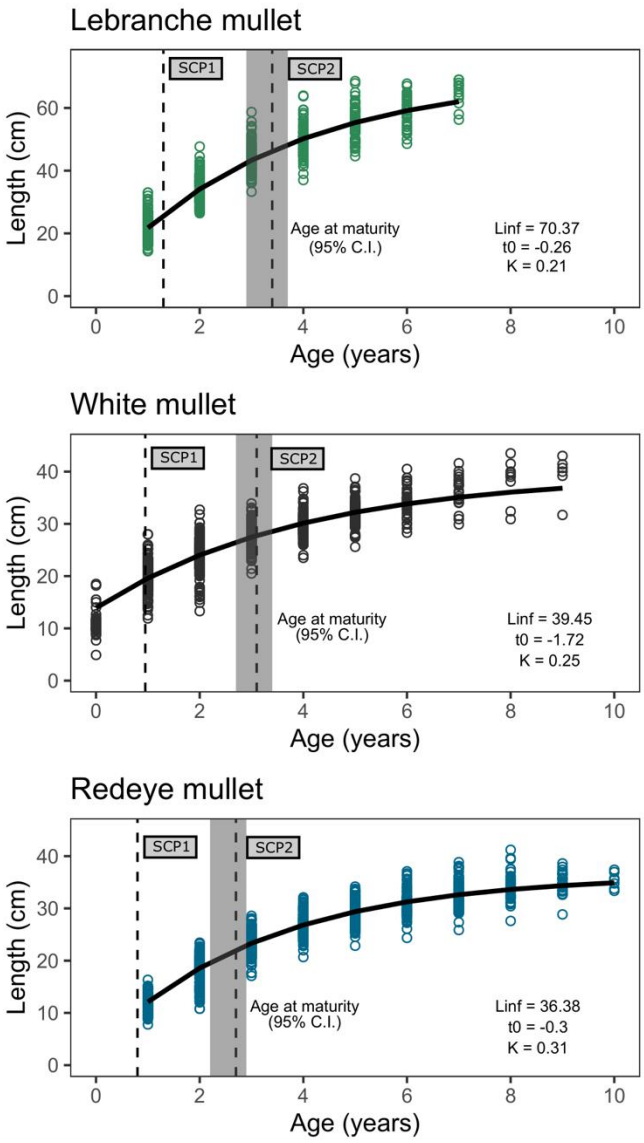

Figure 6. Length-at-age plots, von Bertalanffy growth curves fitted to back-calculated lengths, age-converted SCPs from the polyphasic growth models and 95% confidence intervals for the age at maturity (A_{50}) for the three studied species. Note the different y-axis scales because of significant size differences between lebranche mullet and the other species.

Table 2. Life history parameters and 95% confidence intervals obtained for the studied species. A_{50} = age at first maturity, A_{95} = longevity, L_{50} = size at first maturity, L_{∞} = von Bertalanffy asymptotic length, k = von Bertalanffy growth rate.

	Lebranche mullet	White mullet	Redeye mullet
A_{50} (Years)	3.4 (3.2 – 3.5)	3.1 (2.9 – 3.3)	2.5 (2.2 – 2.6)
A_{95} (Years)	14 (13 – 15)	13 (11.5 – 14)	10 (9 – 11)
L_{50} (cm)	42.5	28.4	24.6
L_{∞} (cm)	70.37 (67.33 – 74.1)	39.45 (38.05 – 41.17)	36.38 (35.73 – 37.1)
t_0	-0.26 (-0.21 – -0.29)	-1.72 (-1.69 – -1.75)	-0.3 (0.27 – 0.33)
k	0.21 (0.19 – 0.22)	0.25 (0.23 – 0.28)	0.31 (0.29 – 0.33)

4 Discussion

This study is the first to combine data on age, growth, maturity, and polyphasic allometric growth patterns. We also provide annuli validation and growth parameters for three highly exploited mullet species, especially for the data-poor redeye mullet. On joining data on age, growth and reproduction with allometry, we demonstrate that polyphasic otolith allometric variation can be a powerful tool to understanding variation in life-history traits in exploited fish, as well as providing insights on important events in their life cycle such as age at migration and maturation. In addition, our results show significant variation in life-history traits among species that follow the expected ecological theory predictions, as stated in our second hypothesis: the fastest-growing species reached the smallest asymptotic sizes and exhibited earlier changes in allometry and maturation, and the slowest-growing showed larger sizes and later changes in allometric patterns and maturity. Multiple implications for management of such data-poor species can be drawn from our results, such as the use of the new parameters in further population and ecosystem models, and the potential use of otolith allometric variation as a cost-effective tool for untangling important species traits.

4.1. Fine-scale variation in life-history explained by otolith allometry, age and growth

Our results indicate that the fastest-growing species (redeye mullet) changes its allometric growth patterns earlier (around 0.8 years), followed by the white mullet (at roughly 0.95 years) and the lebranche mullet, the slowest-growing, at 1.3 years of age. The second change in allometry for the three species highly overlapped with ages at maturity (Figure 6). Such results can be considered evidence that polyphasic allometric growth in fish otoliths can be a suitable indirect indicator of crucial life cycle events such as sexual maturation and ontogenetic habitat shifts. The same has been observed in protrandic hermaphroditic fish, where sex changes are reflected in allometric shifts (Bervian et al., 2006.; Carvalho et al., 2015; Hashiguti et al., 2019; Medeiros et al., 2021). We also show that sympatric *Mugil* species may have temporally asynchronous life cycles to allow coexistence and, more generally, show how life-history traits can vary among congeneric, sympatric species. This asynchrony is likely to be an evolutionary response that increases fitness of ecologically similar co-occurring species exposed to roughly the same environmental conditions (Chang and Iizuka, 2012; Scott and Johnson, 2010).

As mullets exhibit complex, estuarine-dependent life cycles that are largely constrained by local factors (da Silva et al., 2018), it is to be expected that their growth pattern shows a substantial amount of geographical variation (Hegarty et al., 2022). We verified that otolith allometric growth patterns of the studied species appear to show disparities that possibly reflect time-sensitive dynamics of their first year in estuarine nursery habitats. The fastest-growing species (redeye mullet) showed the first allometric growth stanza (SCP1) earlier, followed by the white mullet and the lebranche mullet, the slowest-growing. Understanding which cyclic biological process would cause changes in allometric growth in the juvenile phase is warranted.

Santana et al. (2018), when analyzing otolith microchemistry for the white mullet, suggests that this species appears to remain in the estuary after recruitment, until reaching around one year of age. Avigliano et al. (2020) evaluated the estuarine dependence of white mullet in the Santo Antônio River and found that 81.5% of individuals have an otolith microchemical profile that corresponds to marine-estuarine opportunistic habits. In explanation, these authors highlight the high mobility of juveniles between coastal habitats such as mangroves and lagoons. Therefore, it is worth speculating that

the SCPs showed in our results register the first migration from the estuary to the sea. Such movements between the different seascape habitats in the first year of life are also potentially recorded in otoliths as non-annual macrostructures. These are discarded in age estimates (see materials and methods and Figure 2) and might be related to physiological stress. Similar conclusions were reached by Hsu and Tzeng (2009) and Chang et al., (2000), who found multiple concentric rings around the core region of the otolith before the first annulus in *Mugil cephalus*. They suggest that the possible causes of these 'false rings' could be ontogenetic events, such as metamorphosis from larval to juvenile stage and abrupt changes in environmental factors (Chang et al. 2000).

The life cycle of tropical estuarine-dependent fish species is heavily influenced by the marked seasonality in rainfall of these regions (da Silva et al., 2021, 2022; Macedo et al., 2021). The tropical rainy season is a crucial driver of increased biological productivity (de Barros et al., 2022), which may affect key physiological processes such as seasonally varying growth rates and deposition of calcium carbonate in otoliths (Efitre et al., 2016; Gabriela et al., 2021). Relationships between biological metrics and rainfall were also observed in this study, where ring formation of the lebranche and white mullets appeared to be strongly influenced by the monthly precipitation. Similarly, Basilone et al. (2020) also detected an association of the marginal relative increment in fish otoliths with body condition index, which was true in this study for the white and redeye mullets. Such relationship could indicate an indirect effect of seasonal spawning activity on annuli formation, which can be associated with the physiological stress and intense energy during spawning activity, momentarily reducing the fish condition (Andrade et al., 2013). Other than rainfall and spawning, other factors such as temperature can also influence annuli deposition even in tropical fish (Cappo et al., 2000; Caldow and Wellington, 2003). In this sense, asynchronism in ring formation between some of the studied species may be a result niche partitioning to reduce interspecific competition related to reproduction or resource acquisition, as has been observed in other sympatric fish (Fakoya and Anetekha, 2019; Simon et al., 2012). Also, considering that the redeye and white mullets are phylogenetically closer (Neves et al., 2020), it is to be expected that they should also

exhibit higher degrees of niche overlap and therefore need to evolve temporally decoupled life cycles.

The second change point in allometry (SCP2) highly overlaps with ages at maturity in the three studied species. For the lebranche and white mullets, several studies have shown that sexual maturity is reached at sea, where spawning events take place (Moore, 1974, Santana *et al.*, 2018, Mai, 2019, Ibáñez *et al*., 2012, 2016; Ibañez and Gallardo-Cabello, 1996). In our study, the three species exhibited the second stanza around the third year of life. In addition, they coincided with the change in annual growth rate as shown by switching annuli patterns in the otoliths (wider rings for thinner rings) and the occurrence of double marking (false double ring). Ibañez (2016) described similar age patterns in mugilids to those found in our work.

4.2. Age and growth

The estimated growth parameters for the lebranche and white mullets all lie well within the expected range observed by other similar studies (Table 7). Generally, the literature shows that the lebranche mullet is consistently slower-growing and attains larger maximum sizes, as well as a higher longevity (Alvarez-Lajonchere, 1981; Garbin et al., 2014). However, it should be stated that larger, older individuals were possibly missed by our sampling gears, with the maximum observed age for the lebranche mullet in our study being of only 7 years. As such, despite being considerably similar to other studies (Table 7), the growth parameters for this species, especially the asymptotic length, should be considered with caution. Thus, further work in the region might be needed to advance biological knowledge and address possible uncertainties on population parameters of lebranche mullet. Parameters for the white mullet show that this species grows faster, but still attains considerably old ages (maximum observed age of up to 11 years in Santana et al., 2009), with a reasonably good fit to the data (Figure 6). Despite being an important component of many regional fisheries (*in situ* observations) previous studies on the redeye mullet are only limited to genetics (Nirchio et al., 2007; Neves et al., 2020), parasitism (Cardim et al, 2018), and length-weight relationships (da Silva et al., 2017). Accordingly, this is the first study to report age-length relationships and growth parameters

according to the von Bertalanffy equation for this species. Our results demonstrate that the redeye mullet is fast-growing relative to the other mullet species in this study, which is sustained even until after maturation. The VBGF model also provided a satisfactory fit, with the curve clearly reaching an asymptote (Figure 6).

Although the parameters in this study are considerably similar to estimations in previous studies, there is still a notable amount of variation (Table 7). This may be because mullets exhibit complex, estuarine-dependent life cycles that are largely constrained by local factors. Therefore, it is reasonable to expect that their growth patterns show a substantial amount of geographical variation in response to local environmental variability (Hegarty et al., 2022).

Table 3. von Bertalanffy growth parameters for each studied species gathered from the literature

Study	Location	Species	L_∞	k	Size range (cm)	Maximum observed age
Present study	Tropical Southwestern Atlantic	Lebranche mullet	70.37	0.21	7 -75	8
Alvarez-Lajonchere (1981)	Cuba	Lebranche mullet	88.8	0.11	25 - 37	4
Castro (2009)	Temperate Southwestern Atlantic	Lebranche mullet	56.8	0.30	13 – 54	9
Garbin et al. (2014)	Temperate Southwestern Atlantic	Lebranche mullet	66.2	0.168	24 – 65	12
Giombelli-da-Silva et al (2021)	Subtropical Southwstern Atlantic	Lebranche mullet	50.4	1.10	28–81	5
Present study	Tropical Southwestern Atlantic	White mullet	39.45	0.25	4.9 – 45	9
Santana et al. (2009)	Tropical Southwestern Atlantic	White mullet	34.4	0.36	1.3-39.5*	11
Ibáñez-Aguirre	Southwestern	White	40.3	0.161	18-41	5

& Gallardo-Cabello, (1996)	Gulf of Mexico	mullet				
Gallardo-Cabelo et al (2005)	Subtropical Pacific, Mexico	White mullet	36.4	0.21	7-32	5
Giombelli-da Silva & Vaz-dos-Santos (2019)	Tropical Southeastern Atlantic	White mullet	47.3	0.34	0.2-42.2	4

4.3. Implications for fisheries management

Mugilids are important fisheries resources along the Southwestern Atlantic, being usually exploited by large artisanal and semi-artisanal fleets for local commercialization (González-Castro et al., 2009; Garbin et al., 2014). However, coordinated efforts for assessing and managing such fisheries are considerably scarce, being only available for the Southern and Southeastern regions of Brazil (Miranda et al., 2006; MPA and MMA, 2015). Still, formal reports on mullet fisheries remain largely inconclusive regarding their exploitation status, as well as on the most appropriate management strategy that should take place. In great part, this is due to the lack of appropriate data concerning population structure and dynamics, which prevents the use of established models to inform suitable, evidence-based management targets (ICMBIO, 2007; Garbin et al., 2014). However, such information must be considered of urgent priority to acquire for all exploited stocks, as mullets in the tropical Southwestern Atlantic have showed signs of overexploitation (Mendonça and Bonfante, 2011; Aguirre-Pabon et al., 2022), and their estuarine-dependent life cycles makes them considerably exposed to anthropogenic-related changes in environmental health (Whitfield and Cowley, 2010).

Despite being able to inform patterns of relative vulnerability to exploitation, information on age and growth is only the first step for conducting evidence-based fisheries management (Goethel et al., 2022). Next steps on assessing mullet stocks in the tropical Southwestern Atlantic must include acquisitions of catch and effort time-series, as well as estimates of mortality using the parameters estimated in this study as input. Importantly, any management advice and its implementation should follow bottom-up,

participatory guidelines to ensure compliance and that local needs of communities are met (Mendonça and Bonfante, 2011; Batista et al., 2014). We also demonstrate in this study that examining allometric variation in fish otoliths can give important insights into crucial life cycle events, such as age at migration to the sea and sexual maturation for the studied species. Consequently, such methods can be utilized as potential indicators for life stages and size classes that are important for population persistence and stock maintenance and should be protected.

5 Conclusion

This study provided important insights about crucial life-history traits and their relationships with allometric growth patterns and life cycle of the widespread, sympatric, and congeneric mullets *M. liza, M. curema* and *M. rubrioculus*. More specifically, through crossing information on otolith allometric variation, age and growth, and reproduction, we added evidence that otolith allometric growth patterns traits may be important predictors of major life cycle events, as well as providing insights into ecological consequences of coexistence. Importantly, this study also provided important parameters for future assessment of stock status and ecological modelling, which may be needed in face of potential threats of overexploitation for such crucial fisheries.

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5. INDIVIDUAL AND INTERSPECIFIC PLASTICITY IN THE LIFE HISTORY OF THREE SYMPATRIC *MUGIL* SPECIES IN TROPICAL ENVIRONMENTS: IMPLICATIONS FOR MANAGEMENT AND CONSERVATION.

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Abstract

Understanding the causes and consequences of plasticity is crucial for studies of animal behavior and physiology, especially in exploited populations affected by size-selective fishing. Estuaries, with their fluctuating abiotic conditions, challenge fish to exhibit flexible behavioral responses. This study focuses on the Mugilidae family, exploring individual and intraspecific plasticity in estuarine dependence among *Mugil curema*, *Mugil liza*, and *Mugil rubrioculus*. We hypothesize that greater estuarine dependence corresponds to reduced individual variability in habitat use strategies. Using otolith microchemistry to assess fish migration patterns and connectivity among coastal, marine, and estuarine environments, we sampled across four tropical estuaries along 170 kilometers of the Atlantic coast. Our analyses of Sr and Ba ratios revealed significant differences in habitat use among species. *Mugil liza* demonstrated a strong preference for estuarine habitats, while *M. curema* exhibited higher plasticity across habitats, occupying both marine and freshwater environments. *M. rubrioculus* preferred saltier waters but showed variability in habitat use. Our findings indicate that individual plasticity correlates with lower estuarine dependence, reflecting evolutionary habitat selection processes. This mechanism may be contributing to the coexistence of the three species in sympatry. These results underscore the importance of recognizing individual and species-specific habitat use in fisheries management and conservation, particularly in the context of partial migration and the impacts of global warming.

Keywords: sympatry, estuarine-dependent, life cycle, partial migration, microchemistry.

1 Introduction

Plasticity in terms of ecology is the ability of an individual to adjust their behavior in response to changes in the environment in which they are inserted (Dingemanse *et al.*, 2010). Variation in individual plasticity can have different causes, such as overfishing and sexual maturity size, and when it is persistent over time it can have important evolutionary implications for the persistence of populations in environments that are undergoing change (Nussey *et al.*, 2007; Stamps, 2016). Understanding the causes and consequences of plasticity is fundamental in studies of animal behavior and physiology and it is urgent for exploited populations, where size-selective fishing can induce changes in life history traits (Wilson, et al. al 2019). This need is due to the fact that an organism's ability to respond adaptively to environmental changes is a strategy to mitigate the effects of variations in the environment, maximizing its fitness (Fawcett & Frankenhuis, 2015; Polverino *et al.*, 2019, Urszan *et al.*, 2018). Another way to maximize the fitness of individuals, increasing foraging opportunities, is migration. This behavior establishes connectivity between habitats that are used throughout the life cycle and can occur at different spatial scales (Bauer & Hoye, 2014).

The concept of migratory species has evolved from the traditional view of obligatory long-distance movements to a more flexible one that includes a gradient of behaviors ranging from complete residence to full migration, depending on various habitats and spatial scales (McDowall, 2001, Chapman et al., 2012). This intraspecific variation, known as partial migration, is widespread across the animal kingdom, particularly in fish, where individuals adapt their migratory behavior based on ecological factors and phenotypic differences (Jonsson & Jonsson 1993, Newton 2008; Chapman et al. 2011). Partial migration has significant ecological and evolutionary implications. Ecologically, it contributes to variations in organism abundance, nutrient flows, and ecosystem dynamics, while also influencing the stability of ecosystems (Swanson et al., 2010, Swanson & Kidd, 2010). Evolutionarily, partial migration creates different adaptive landscapes for migrants and residents, leading to varying selection pressures (Chapman et al. 2012). In fish, tropical coastal habitats are ideal for promoting this type of migration, as they offer a

diverse range of resources and favorable conditions at different periods of the life cycle (da Silva et al. 2018, 2021).

For estuarine-dependent fish behavioral plasticity plays a crucial role in the survival and ecological success of these organisms in highly dynamic environments (Mery & Burns, 2010; Ray, 2005). Mainly for juveniles, this behavioral plasticity is essential, as by moving between different coastal environments and micro-habitats within estuaries, juveniles are able to exploit temporarily abundant food resources, avoiding unfavorable areas due to seasonal events or sudden changes in water conditions. tides. This adaptability not only increases their chances of survival, optimizing the use of temporary habitats, but also directly influences their growth and development, impacting the rate of recruitment into the adult population (Bowen, & Allanson, 1982; Blewett et al. 2022). (Bowen, & Allanson, 1982; Blewett *et al.* 2022). Thus, the behavioral adaptation of fish in estuarine environments reflects the complex interaction between ecological and evolutionary factors that shape their life ecology (Mery & Burns, 2010).

In that regard, the Mugilidae are a good example to verify individual and intraspecific plasticity as they are very morphologically similar species, which co-occur in estuarine and tropical coastal marine environments (Rangely et al. 2023, Rangely et al. 2024,). However, despite being obligatory estuarine dependent (Able 2005), since they spend at least one phase of their life cycle in this environment, they occupy the estuary differently, with abiotic variables such as salinity and dissolved oxygen playing an important role in this habitat segregation (Rangely et al. 2024). Recent research has demonstrated high intraspecific and interspecific variability in migration patterns between distinct *Mugil* species (Chang *et al.*, 2004; Chang & Iizuka, 2012; Ibáñez-Aguirre *et al.*, 2012; Avigliano *et al.*, 2015, Fowler *et al.*, 2015; Fowler *et al.*, 2016). This variation in estuarine habitat use indicates a more complex migratory behavior than initially predicted for mullets (Fowler *et al.*, 2016; Mai *et al.*, 2018).

In the first year of life, a change in growth variation occurs in *Mugil* species and the reason for this is still unknown (Rangely et al. 2023). Like this, we want to understand the dynamics of habitat occupancy between different species during the first year of life, a period in which individuals are more restricted to the estuarine habitat. In this sense, we

raise the following question: is there individual variability in estuarine dependence for the species *M. curema*, *M. liza and M. rubrioculus* related to the first phase of the life cycle? Our hypothesis is that: greater estuarine dependence in *Mugil* species (interspecific variation) implies less individual variability (intraspecific variation) in the strategies for using tropical estuarine and coastal habitats. To test this hypothesis we used otolith microchemistry, a powerful tool that allows high resolution to define migration and habitat occupancy and consequently individual plasticity (Walther, 2019, Mai et al. 2018, Santana 2018, de Almeida et al. 2024).

2 Materials and methods

2.1 Study area and sample collection

Sampling activities were carried out in four tropical estuaries of the Atlantic, totaling 170 kilometers, three of which are within the Costa dos Corais Marine Protection Area, namely: Várzea do Una (08°51'39.8"S 035°07'49.6"W), estuary of the Manguaba river (09°09'29.39"S 035°17'35.45"W), estuary of the Santo Antônio river (09º24'50”S and 035º30'24”W) and Estuarine Complex Lagunar Mundaú-Manguaba - CELMM (09°42'52.0" S 035°48'13.1"W) Brazil (Figure 1). These areas exhibit a semi-humid tropical climate, with two well-marked periods, the rainy and the dry. Rainy periods from March to August (rainfall 242.9 - 94.2 mm) and dry periods between September and February (100.7 - 63.9 mm) (Calado & Souza, 2003). Rainfall (in mm) was recorded monthly based on data from the Brazilian National Weather Institute. The average water temperature of 28.3°C. Várzea do Una is characterized by an estuary with an entrance approximately 300 meters wide. While the Mangua ba River estuary is approximately 500 meters at the entrance. The Santo Antônio River estuary has an estuary entrance that is 300 meters wide. These estuaries have mangrove vegetation on their banks dominated by *Rhizophora mangle*, *Avicennia schaueriana* and *Laguncularia racemosa*. In relation to CELMM, sampling was carried out in Lagoa Mundaú, which has a permanent connection with the sea, and an area of 36 km². (Calado & Souza, 2003, Rangely, 2011).

Between 2017 and 2020, the fish were captured during periodic collections conducted by researchers from the Fish and Fisheries Ecology Laboratory at the Federal

University of Alagoas. Using two canoes, the individuals were captured with gillnets forming a semi-siege. The fishermen approach, join the ends of their nets, and then launch the nets into the sea. They hit the water with their oars to direct the school of mullet into the net. Soon after, they retrieve the nets.

2.2 Otolith macrostructure

The sagittae otoliths of the three studied species, *M. curema* (66), *M. liza* (21) and *M. rubrioculus* (55), were extracted, cleaned with NAOH (2%), rinsed in distilled water to remove any remaining contaminants, and stored in bottles. The otoliths, on the right side, of each individual collected were embedded in epox resin, which became solid within 48 hours. The blocks were then cut at the height of the otolith nucleus, each cut with a thickness of 1 mm, carried out on a Metalographic saw (ISOMET 1000). The sections were fixed on microscope slides (10 sections per slide). Each section was photographed and then cleaned in deionized water, in which it was submerged for 10 minutes and simultaneously an anti-static brush was rubbed.

2.3 Microchemistry of otoliths

Elemental concentrations of *Mugil* otolith transects were quantified using an Elemental Scientific NWR193 excimer laser system coupled to an Agilent 7500ce inductively coupled mass spectrometer at the University of Texas at Austin. The laser system is equipped with a large format two-volume laser cell with fast washout (<1s), that accommodated all otolith samples and standards in two separate loadings. Laser ablation parameters were optimized for sensitivity and signal stability from test scan ablations on representative unknowns (Table 1). Prior to analysis, otoliths and standards were pre-ablated (4.5 J cm^{-2} fluence, 20Hz, 75µm spot, 75µm/s scan rate) to remove potential surface contamination (note that some otoliths were coated with epoxy or were unexposed in epoxy below the plane of the surface). All otolith transects ran from cores to edges. Otolith transects were bracketed hourly by standard measurements (MACS-3 and NIST 612, measured in triplicate for 60-s). Oxide production, as monitored during daily tuning on NIST 612,

averaged 0.38±0.03%. Laser energy densities over the analytical sessions averaged 3.23± 0.03 J cm^{-2}. The quadrupole time-resolved method measured 13 masses using integration times of 10 ms ($^{43-44}Ca$, ^{88}Sr), 20 ms (^{24}Mg, ^{85}Rb), and 50 ms (^{7}Li, ^{63}Cu, ^{66}Zn, $^{137-138}Ba$). The sampling period of 0.4552 s corresponds to 94.5 % quadrupole measurement time, and 11 duty cycles per 25µm spot. Time-resolved intensities were converted to concentration (ppm) equivalents using Iolite software (Univ. Melbourne, Hellstrom et al., 2008), with ^{43}Ca as the internal standard and a Ca index value of 38.3 weight %. Baselines were determined from 30-s gas blank intervals measured while the laser was off and all masses were scanned by the quadrupole. USGS MACS-3 was used as the primary reference standard and accuracy and precision were proxied from replicates of NIST 612 analyzed as an unknown. Iron (^{57}Fe) analyses in high-Ca materials are susceptible to Ca- and plasma-related interferences ($^{40}Ca^{17}O^{+}$, $^{40}Ca^{16}OH^{+}$, $^{40}Ar^{17}O^{+}$, $^{40}Ar^{16}OH^{+}$, $^{38}Ar^{18}OH^{+}$), as indicated by high over-recoveries on NIST 612. Excluding Fe, NIST 612 analyte recoveries (N=48) were typically within 6% of GeoREM preferred values (http://georem.mpch-mainz.gwdg.de).

Table 1. LA-ICP-MS Operating Conditions

Laser: ESL NWR193UC

- Wavelength: 193nm
- Pulse width: <4 ns
- Ablation cell: Large format 2-volume
- He flow: 850 ml/min
- Ar flow: 900 mL/min
- Fluence: 3.23±0.03 J/cm^2
- Repetition Rate: 20 Hz
- Spot size: 25 µm
- Scan rate: 5µm/s

ICP-MS: Agilent 7500ce

- RF power: 1600W
- Cones: Nickel
- Sampling depth: 6mm
- Quadrupole parameters
  - Points per mass: 1
  - Integration times for masses:
    - 10ms – 43, 44, 88
    - 20ms – 24, 85
    - 30ms – 55, 57
    - 50ms – 7, 25, 63, 66, 137, 138
  - Sampling period: 0.45

Therefore, the habitat use and specific movement patterns of each individual of the three *Mugil* species were investigated by ablation along the growth axis of the limestone structure starting from the transect of the otolith nucleus, passing through annual growth increments towards to the edge of the otolith (figure 2). Currently there are some studies that validate relationships between ambient salinity and concentrations of elements in otoliths for *Mugil* fish species. So, each individual was classified based on movements between different salinity environments after the early larval/juvenile stage and before capture (the edge of the otolith), following Santana and colleagues (2018), work carried out close to the study area of this research:

Lower limit of the estuarine zone Sr:Ca = $5,0x10^{-3}$

Upper limit of the estuarine zone Sr:Ca = $7,4x10^{-3}$

2.4 Fish ageing

Growth rings were first evaluated and read in the entire otolith, following Rangely *et al.* (2023). After that, the otoliths were sectioned and the growth rings were visualized along the laser ablation raster with the aid of an under transmitted light magnifying glass, coupled to a computer with the imaJ program. To this end, each cut was polished with 1.200 and 2.400 sandpaper and aluminum pruning. They were subsequently stained by leaving them in ethylenediamine tetraacetic acid, (EDTA) 5%, for five minutes, washed in water and left in toluedine blue 1%, for seven minutes, to facilitate the visualization of the growth rings. Aging was done along the laser ablation transects, then the age was linked to otolith chemistry data to visualize variation of elemental concentrations against age.

2.5 Data analysis

To eliminate noise for LA-ICPMS data, Sr:Ca and Ba:Ca ratios were smoothed using a 9-point moving average. Profiles of these ratios were plotted from the core to the edge of the otolith together with thresholds of environments (estuary and marine waters) to interpret migratory strategies. Additionally, the regime shift technique (Rodionov, 2004)

was used to distinguish zones along a transect profile that are chemically different between adjacent zones. A new regime shift or otolith zone was created if the mean values of the two adjacent zones were significantly different using a two-tailed Student t-test ($p < 0.01$). These zones can be referred to environments or habitats because elemental concentrations (e.g. Sr and Ba) between environments are significantly different (Vu *et al.*, 2021a). Kruskal Wallis tests were used to compare means of two independent groups because Sr:Ca data were not normally distributed.

To understand the intraspecific plasticity in the use of coastal esutarine environments in the first phase of growth (described by Rangely and collaborators, 2024), a Generalized Additive Models (GAM) was carried out using the months of the year and the amount of strontium throughout the first year of growth as variables. life, using R. We use the residual analysis of the adjusted model and was used as a proxy for individual plasticity.

3 Results

Mean strontium and barium concentrations varied significantly among the three species (figure 1). Strontium concentrations were lowest for *M. liza* and highest for *M. rubrioculus*, with this species presenting higher amplitude values. *Mugil curema* presented intermediate values and the lowest amplitude.

Analysis of residuals from the adjusted model from GAM analyzes provides insights into data variability, being used as a proxy for *Mugil* individual plasticity over time. Individuals of *M. curema* were those that showed greater plasticity of use within environments. And the individuals of *M. liza* were those that showed less plasticity of use in the first stage of the life cycle.

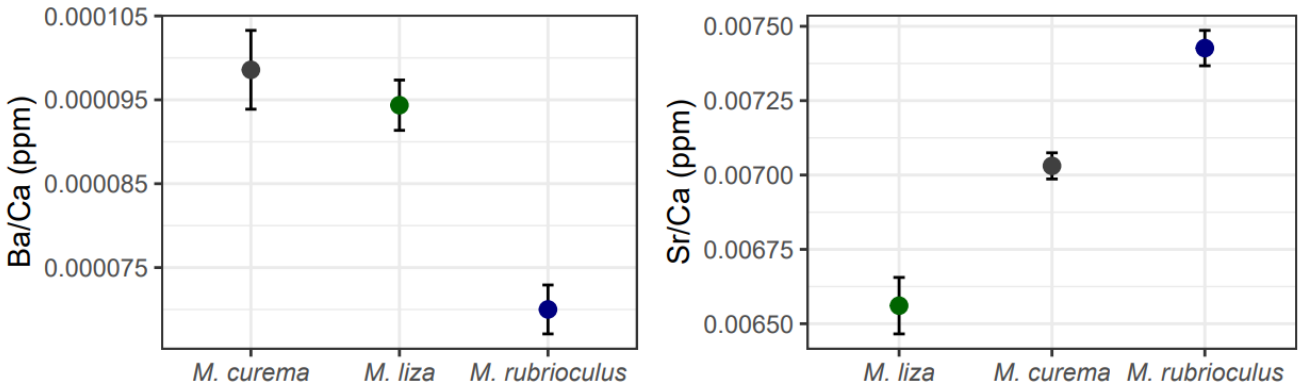

Figure 1. Means and standard deviations (SD) of Ba/Ca and Sr:Ca (mmol.mol-1); in otoliths of *Mugil liza*, *M. curema* and *M. rubrioculus* caught in estuaries of northeastern Brazil. See Appendix for Sr:Ca ratios at the core vs whole transect profile.

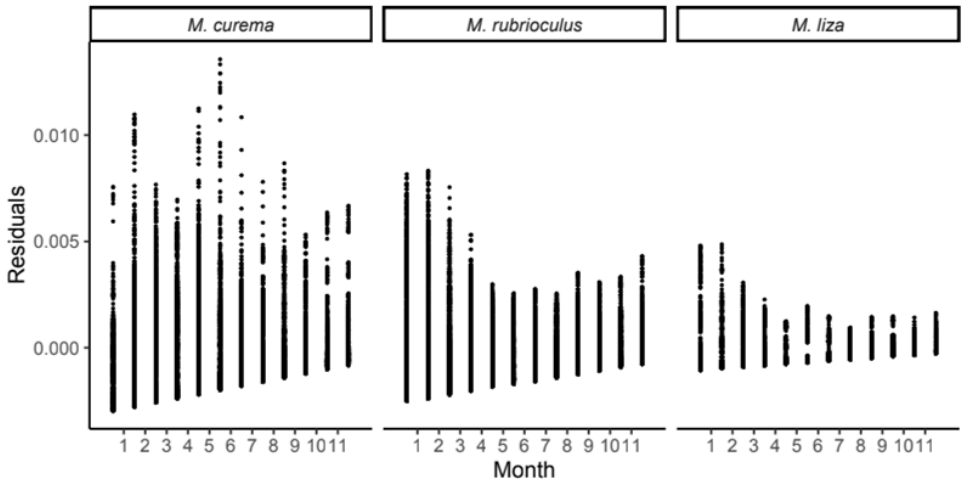

Fig 2. interspecific plasticity in relation to the use of coastal environments, in the first phase of the life cycle (Rangely et al. 2023) GAM residues from the strontium ratio during the first year of life.

The life profiles among otoliths derived from Sr:Ca proportions showed differences in habitat use within *M. liza, M. curema* and *M. rubrioculus* individually, demonstrating individual variability regardless of species (Appendix 1). Lifetime transects of Sr:Ca indicate at least six distinct habitat use patterns, In this way, it was possible to group these profiles into six different categories of habitat use (figure 3). Consecutive migrations:

individuals who carry out repeated migrations between different environments throughout their life cycle. Estuarine resident: individuals who spend all or most of their lives in estuarine environments. They do not make significant migrations to the sea or freshwater rivers. Estuary-sea: individuals that begin their life cycle in the estuarine region but migrate to the sea. Freshwater-sea: These are fish that are born or are in freshwater in their first days of life, after an initial period in these environments, they migrate to the sea. Sea resident: individuals who spend their entire lives exclusively in the marine environment, without making significant migrations to continental or estuarine waters. Sea-estuary: fish that are born in the marine environment but migrate to the estuary before their first year of life.

Mugil liza has only three patterns of habitat use, with a preference for estuarine habitat, making occasional incursions into the marine environment, as in “consecutive migrations” and “estuary-sea” pattern. It is possible to observe greater variability for the beginning of life (large amplitude of the confidence interval) in *M. liza*, mainly for the estuary-sea category.

Mugil curema has greater plasticity between habitats, with individuals occupying both marine, freshwater and estuarine environments, being represented in the six categories of habitat use. In the “freshwater-sea” category it is possible to observe individuals that were in a freshwater environment at the beginning of their lives, while in the “sea residents” category the individuals were in marine waters. Within each category of habitat use, individual variability (amplitude of the confidence interval) was smaller for this species compared to the other two.

Mugil rubrioculus was represented in five categories, with a preference for saltier waters. During the beginning of its life, it is almost always in marine environments. As the individual has more time to live, their choice is always for marine environments, with individuals up to four years old being present in this environment.

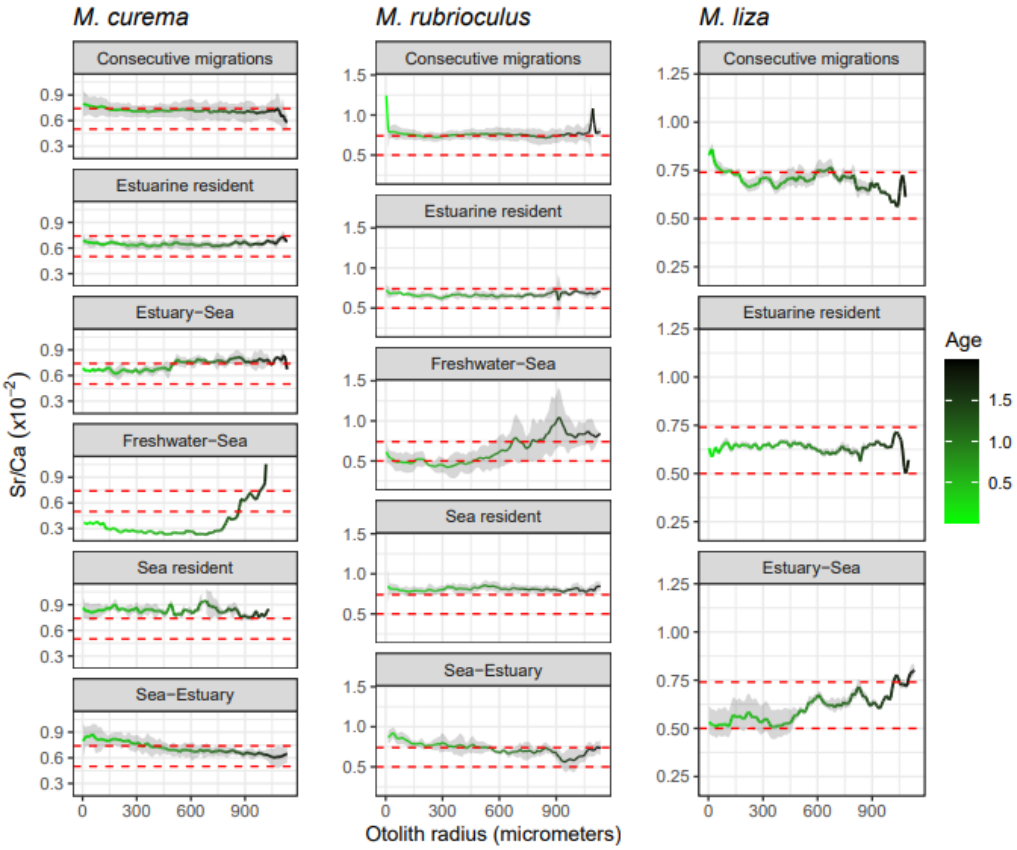

Figure 3. Variations in Sr:Ca ratios from core to edge of otoliths (birth-to-capture) of *M. curema*, *M. rubrioculus* and *M. liza*, with colour representing corresponding age along the ablation path. Red dotted lines are lower (5.0 × 10−3) and upper (7.4 × 10−3) bounds of the estuarine zone. See Appendix A for individual plots of Sr:Ca ratios Data from LA-ICPMS.

The three species had the highest number of individuals in the “consecutive migrations” category, with around 50% of individuals in this category (figure 3). *M. liza* is the species with the largest number of individuals in the “estuarine resident” and also “estuary-sea” categories. *M. curema* has the most divided individuals between the categories, with the “sea-estuary” standing out, after the “consecutive migrations”. *M. rubrioculus* is the species that presents the most individuals in the “sea resident” category.

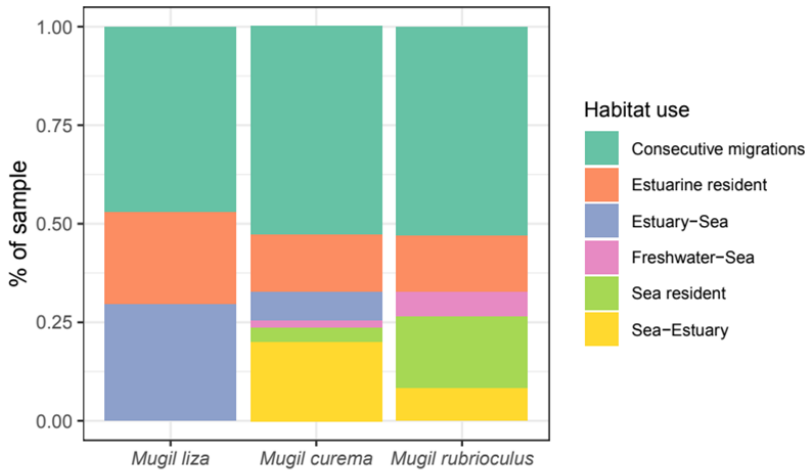

Figure 4. Relative frequency of individuals of each species (*M. liza, M. curema* and *M. rubrioculus*) in each of the six habitat use categories.

4 Discussion

Our results indicate that there is intraspecific and interspecific variability in habitat occupation strategies throughout the first phase of the mullet life cycle, which may be a reflection of evolutionary processes of habitat selection. Greater individual plasticity – greater mobility between estuarine and coastal habitats – related with lower estuarine dependence. In addition to the spatial differentiation between *Mugil* species, there is a temporal differentiation in intraspecific plasticity, the younger the individuals, the greater the movement between habitats ($p < 0.5$).

Mugil curema is the species with the greatest diversity in habitat use, being present in freshwater environments, estuaries and the ocean, in addition to high individual plasticity, as the same individual can frequently migrate between these habitats. *Mugil rubrioculus* also occupies the 3 environments, but this species has a high preference for saltier waters and individuals migrate less between these environments. *M. liza*, on the other hand, prefers to use the estuary, and has low individual plasticity between habitats, remaining more restricted to the estuarine environment. In this sense, a specific inter and intra gradient of estuarine-dependence can be described, between the 3 species that co-

occur in the tropical estuaries of the region. Which may be important for the fitness and growth of individuals.

M. liza is the species with the lowest plasticity of use between estuarine and coastal marine habitats, confirming our hypothesis. However, when observing the large amplitude in the confidence interval close to the first year of life (figure 3), where the change in growth speed occurs (Rangely et al. 2023), it can be seen that individuals are migrating within the same environment demonstrating the adaptation of the species to occupy microhabitats. *Mugil liza*, spends more time in its breeding area, reaching greater total length (Rangely, 2023). At the other extreme, *M. rubrioculus* is the smallest estuarine-dependent species and also the one with the smallest total length (Rangely et al., 2023). *M. curema* is capable of occupying marine, estuarine and even freshwater environments in the first phase of its life cycle.

Avigliano *et al.* (2021), the present work demonstrated that *M. curema* has high plasticity in the use of habitats, which may be related to the species' greater genetic diversity and its evolutionary time. *Mugil liza*, on the other hand, has low plasticity and a preference for the estuarine environment. This species is one of the lineages of the M. cephalus complex and has diversified more recently (Neves et al., 2020), perhaps for this reason it presents low habitat use plasticity. *M. rubrioculus* shows some plasticity but prefers the marine environment. The phylogenetic status of this species is a little more complicated, as although some cryptic lineages have been described (Durand & Borsa, 2015; Neves et al. 2020), the monophyly of the species cannot be rejected (Neves et al., 2020). However, their preference for more saline environments may explain the low genetic diversity, since Poulin & Leon (2017) argue that freshwater environments generate more diversity than marine or terrestrial environments since the fragmentation of habitats promotes greater genetic differentiation.

The capacity for individual plasticity for habitat use and migration patterns appears to have a genetic and phylogenetic character. It has been demonstrated that *Mugil cephalus* presents different migratory patterns according to the microchemistry of the otoliths (Fortunato et al 2017) and it is already known that the species is composed of several cryptic lineages (Durand & Borsa, 2015; Neves et al 2020). Avigliano et al (2021)

also analyzed the microchemistry of otoliths from individuals from different M. curema localities and found different patterns of habitat use and migration. Furthermore, it is also known that *M. curema* is a species complex composed of several cryptic lineages (Durand & Borsa, 2015; Neves et al 2020).

Hanahara et al (2023) demonstrated that within the genus *Eviota* (Gobidae), several cryptic lineages exhibit spatial segregation and the authors suggest that the lineages speciated by spatial segregation on a fine scale. Therefore, there appears to be a correlation between genetic diversity and plasticity in habitat use.

This plasticity in habitat use and estuarine dependence has already been demonstrated through otolith microchemistry (Albuquerque, et al. 2010, 2012, Condini et al., 2016, Mai et al. 2019). Chemical heterogeneity within estuaries, due to riverine and anthropogenic discharges, creates spatial variability between adjacent estuarine and coastal environments. This heterogeneity affects, spatially and temporally, the biological, physical and chemical processes of fish, which can be chemically identified in otoliths (Elsdon & Gillanders, 2005; Elsdon et al., 2008; Walther & Thorrold, 2009). Several researchers have already demonstrated connectivity between the coastal marine region and the estuary, indicating a direct relationship between the amount of Sr:Ca in otoliths and salinity (Santana et al, 2018, Ibáñez et al. 2012, Callicó Fortunato et al. 2017 , Secor et al. 2001, Zimmerman 2005, Labonne et al. 2009). And it is precisely this heterogeneity of habitats that allows the coexistence of *Mugil* species, favoring decoupled in relation to the pattern of habitat use, with *M. curema* being influenced by factors such as temperature and dissolved oxygen, chlorophyll and turbidity, while *M. rubrioculus* is driven by variations in salinity (Rangely et al. 2024) and M. liza is mainly influenced by rainfall (Sousa et al. 2015).

It is possible that intraspecific competition, interspecific competition (in the case of similar species such as *Mugil*) and predation act in synergy to shape partial migration patterns (Ward et al., 2004), thus allowing coexistence. Therefore, partial migration is the temporary reduction of competition with non-migratory species, that is, it can affect the structure of the community, reducing competition and, therefore, allowing coexistence (Johnson, 1980).

4.1 Management and conservation of species

Our research made it possible to classify these three species that co-occur in tropical estuaries, in relation to the time of use of the estuaries, throughout the first phase of the life cycle. And so, it was possible to indicate the priority species for management and conservation for the estuaries studied as *M. liza*, as it is the species that spends almost the entire first phase of its life cycle in this environment. Considering that the longer the stay in this habitat, the more vulnerable the species becomes. This way, we have a measure of vulnerability to habitat loss. This is particularly relevant if we consider the speed of degradation of tropical coastal environments, for the construction of real estate projects and tourism (Miranda et al., 2002). Therefore, the species with the least plasticity in habitat use, which migrates least between environments, will have the greatest damage in relation to the preservation of stocks. Evolutionarily, greater migratory plasticity between habitats can generate greater adaptability of the species and consequently greater resilience (Tamario et al. 2019). This is particularly critical for the estuaries studied, as in 2019 there was one of the largest oil spills in the country's history, one of the most significant global events in terms of contamination and environmental impact in recent years, with concentrations of mercury, cadmium, lead and copper above what is foreseen in Brazilian legislation (Soares et al. 2021).

An important question to consider is how human activities have affected the dynamics of partial migration and the promotion of the evolution of plasticity (Crispo et al., 2010). This can be observed both in relation to fishing and in relation to climate change. For example, the diversity of phenotypes in migratory behaviors that exists within the same population and among the three *Mugil* species studied can also lead to differential survival of individuals due to resilience to fishing pressure. When partial migration occurs, the stock as a whole, to a certain extent, becomes less vulnerable to fishing activity, for example, having greater chances of survival, as they have multiple contingents of fish that use different habitats within the same population (Folwer et al. 2016). And even the reduction in migratory numbers can have negative consequences for resident fish of the same species, as was the case with *S. confluentus*, where remaining populations of this

species persisted as small residents isolated in streams, increasing the risk of extinction. (Nelson et al., 2002, Ryman et al., 1995).

Therefore, understanding partial migration becomes relevant when making decisions related to stock management (Chapman, 2012). Since, population sustainability and resistance to disturbance and potentially the recovery capacity of the stock can be negatively affected by widespread fisheries management, not considering partial migration and different categories of habitat use (Ruzzante et al. 2006). In the present work, although the individuals were grouped into six categories of habitat use, all species present the largest number of individuals in “consecutive migrations”, demonstrating that partial migration is always a strategy of the Mugilidae.

This understanding is also critical for predicting the effects of climate change and informing effective conservation strategies in these scenarios (Chessman, 2013; Comte, Murienne, & Grenouillet, 2014; Sunday, Bates, & Dulvy, 2012). Since global warming can lead to changes in individual growth rate, which can be important in individual migration decisions (Skov et al. 2010). Furthermore, temperature influences habitat preference for species (Matis et al. 2018), and may be an immediate driver that drives partial migration, which is phenotypically plastic (Skov et al. 2010). As ocean temperatures continue to rise we expect increasing pressure on species that depend on a particular habitat to survive while those that utilize a variety of habitats may be considered less vulnerable (Munday, 2004; Pratchett, 2005).

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Appendix 1

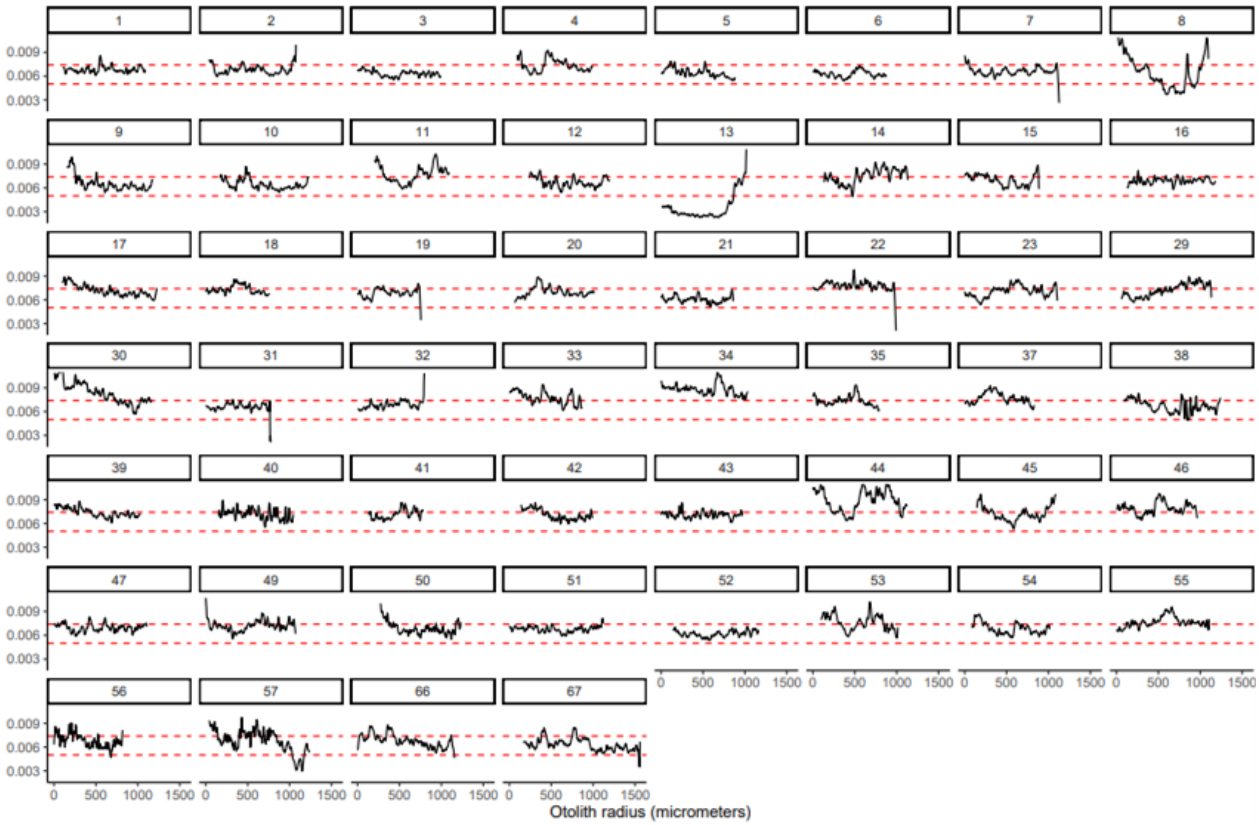

Figure 1 – Microchemical profiles of otoliths of 52 *Mugil curema* from the Northeast coast of Brazil. Red dotted lines are lower (5.0 × 10−3) and upper (7.4 × 10−3) bounds of the estuarine zone. Data from LA-ICPMS.

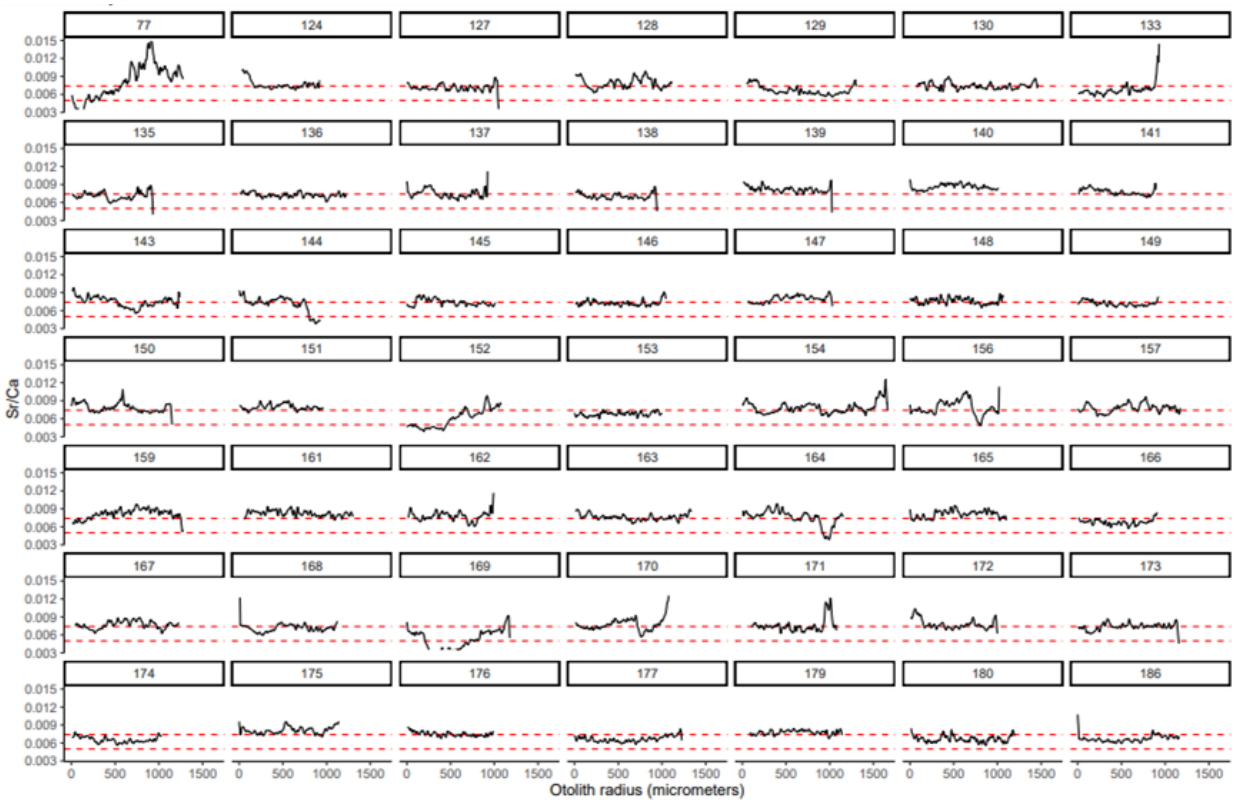

Figure 2 – Microchemical profiles of otoliths of 49 *Mugil rubrioculus* from the Northeast coast of Brazil. Red dotted lines are lower (5.0 × 10−3) and upper (7.4 × 10−3) bounds of the estuarine zone. Data from LA-ICPMS.

Figure 3. Microchemical profiles of otoliths of 12 *Mugil liza* from the Northeast coast of Brazil. Red dotted lines are lower (5.0 × 10−3) and upper (7.4 × 10−3) bounds of the estuarine zone. Data from LA-ICPMS.

6. JOINING DATA-LIMITED STOCK ASSESSMENT AND TRADITIONAL ECOLOGICAL KNOWLEDGE TO INFORM TROPICAL MULLET MANAGEMENT

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Abstract

Small-scale fisheries (SSF) constitute more than half of global fisheries. SSF fishers can offer vital insights into the life history characteristics of target species. Upholding the principles of good governance, the combination of conventional scientific knowledge (CSK) with local ecological knowledge (LEK) is pivotal to ensure the success of SSF management. In this study, we used CSK and LEK to holistically assess the stocks of three commercially important mullet species in three estuaries in the Tropical Southwestern Atlantic, examining how both information sources can contribute to conservation and management efforts. For CSK, we employed a Bayesian size-based model to conduct a stock assessment grounded in prior information on life history parameters. For LEK, we conducted interviews with fishermen, aiming to understand how they perceive stock status, and which factors affect these resources. Both knowledge streams indicated significant fishing pressure, suggesting that two of the stocks are overexploited while one is operating at its maximum sustainable yield. We demonstrate that LEK and CSK largely agree on mullet stock status but not on the causes of declines, highlighting the importance of LEK to provide auxiliary information to fisheries management. Horizontal collaboration is essential in artisanal fisheries, allowing fishers, managers, and scientists an active voice in decision-making. We also identified strengths, weaknesses, opportunities, and potential threats to the mullet stocks in the region, allowing enhanced governance through collaboration among stakeholders and the scientific community.

Keywords: Artisanal fisheries, Mugil, Co-management, Traditional Ecological Knowledge

1. Introduction

Small-scale fisheries (SSF) play a significant role in global fish landings, contributing approximately 40% of the world's total marine fisheries catch and employing a substantial amount of people directly involved in fisheries. According to FAO (2022) and Kelleher et al. (2012), almost half a billion people worldwide depend at least partially on SSF. However, due to their dispersed nature and limited funding allocated to agencies responsible for their management, stocks targeted by SSF are often poorly managed, and their statuses are frequently unknown (Castello et al. 2009). Consequently, many SSF are believed to be overexploited and unproductive (Kurien and Willmann, 2009). These issues highlight the critical need to properly manage SSF to ensure local food security and conservation. Current approaches to fisheries management incentivize understanding human interactions with the environment and promoting fishers' participation in data collection and decision-making processes (Castello et al. 2009).

As opposed to the traditional exclusive reliance on Conventional Scientific Knowledge (CSK), incorporating Local Ecological Knowledge (LEK) into the management process is an alternative to transition to a bottom-up management process that aids in resolving potential disputes between local communities and management needs (Jones et al., 2010). With their extensive empirical experience, fishers can provide valuable information on the life history of target species, including size at first maturity, maximum sizes, habitat use, reproductive seasons, and optimum sizes for capture (Silvano and Valbo-Jørgensen, 2008, Pereira et al., 2021). Obtaining this data solely through CSK would require greater sampling efforts and financial resources. Therefore, the inclusion of LEK not only fosters trust in management measures by incorporating traditional communities on SSF management but also offers useful and costless information than assessments by CSK, aiding in identifying historical baselines and establishing restoration and sustainability for target species (Thornton and Scheer 2012). The integration of CSK and LEK has proven effective in managing SSF, promoting higher compliance with management rules, facilitating data collection, and helping understand the social

dynamics involved in the system (Pita et al., 2009; Mikalsen and Jentoft, 2008, Lorenzen et al., 2010).

In the Tropical Southwestern Atlantic, many SSF target estuarine-dependent fishes of the Mugilidae family, particularly mullets of the genus Mugil. Almost entirely small-scale, mullet fisheries account for about 20% of all commercial fishing catches in Brazil and support numerous traditional communities (Garbin et al. 2014; MPA 2011). Despite their importance, mullets are considered data-deficient by the IUCN. Most mullet fisheries in Brazil remain unassessed and are consequently unregulated due to the chronic lack of fisheries statistics and long-term monitoring programs in the country (Santos et al. 2023). In fact, some stocks are reportedly overfished due to unregulated fishing effort (Mendonça and Bonfante, 2011, Lan et al., 2017). Current management rules, when in place, are often ineffective and fail to meet conservation or fishers' needs (Mendonça and Bonfante, 2011). Without intervention, mullet fishing faces a threat in the near future.

Our study aimed to showcase the integration of Conventional Scientific Knowledge (CSK) and Local Ecological Knowledge (LEK) as a means to foster promote bottom-up management on tropical multispecies mullet fisheries in a tropical Southwestern estuary system in Northeast Brazil. Specifically, we evaluated the stock status of three mullet species (white mullet Mugil curema, lebranche mullet Mugil liza, and redeye mullet Mugil rubrioculus) utilizing length-based methods adapted for data-limited stocks. Additionally, we employed LEK as a complementary method to gather important life-history and fishery information, as well as to identify the strengths, weaknesses, opportunities, and threats associated with the studied fisheries.

2. Materials and methods

2.1 Sample collection

Sampling was conducted in three estuaries and adjacent marine areas in the Tropical Southwestern Atlantic: the estuary of the Santo Antônio River (9º24’50” S and 35º30’24” W), the Mundaú Lagoon (9°38’15” S and 35°46’20” W), and the Manguaba Lagoon in Alagoas, Brazil (Figure 1). These regions experience rainy periods from April to August (with an average rainfall rate of 165.6 mm) and dry periods between September to March (with an average rainfall rate of 85.8 mm), characterized by a semi-arid tropical climate (Nery et al., 1998; Paredes-Trejo et al., 2018).

Monthly length samples (Total Length, cm) were collected over one-year periods for each species: *Mugil curema* and *Mugil rubrioculus* in 2022–2023, and *Mugil liza* in 2011–2012. We used past length frequency data for M. liza because not enough individuals were caught in 2022-2023. We therefore caveat that M. liza stock status reflects the years 2011-2012. Connections of LBB outputs with the fisher’s perceptions should therefore be made with caution for M. liza. Gillnets made of monofilament nylon with mesh sizes of 30 and 40 mm (for *M. rubriculus* and *M. curema*) and 50 and 60 mm (for *M. liza*) were used. These nets were deployed from two canoes, each manned by two crew members. As the canoes approached each other to close the ends of their nets, the fishermen launched them into the sea. To direct the school of mullet into the net, fishers used their oars to strike the water. Following this, the nets were inspected for captured fish. Interviews with fishers were conducted from December 2022 to March 2023 at the landing ports for traditional mullet fishing in the Santo Antônio River, Mundaú Lagoon, and Manguaba Lagoon (Figure 1). Length frequency distributions from these different estuarine systems were pooled to reflect the assumption that there is a single stock for the three species

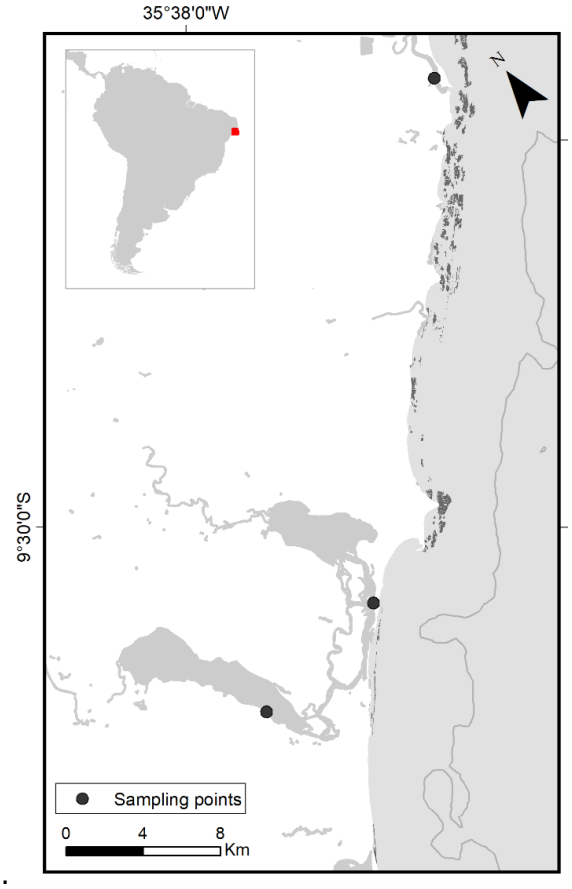

Figure 1. Sampling locations of mullet in the Tropical Southwestern Atlantic: Santo Antonio River (upper point) and Mundaú Lagoon (middle point) and Manguaba Lagoon (lower point), Alagoas state, Brazil.

2.2 Conventional Scientific Knowledge (CSK)

In the field, we measured fish Total Lengths (TL) to the nearest centimenter after the individuals were identified to the species level using a dichotomous key (Menezes et al., 2015). A random subsample was then transported to the laboratory, where individual female gonad development stages were determined through visual examination using a stereoscopic microscope. The stages were classified as immature (stage I), developing (stage II), mature (stage III), post-spawning (stage IV), and spent or resting (stage V) following Vazzoler (1996). To estimate the size at first maturation (L50), the proportion of young and adult female individuals (gonadal development stages I, II, and III) was

calculated based on Vazzoler's (1996) gonadal development stages. All females were included in the analysis, with stages I and II considered immature and stages III, IV, and V considered mature. Subsequently, a logistic curve (King, 2007), was fitted to determine the L50, denoting the length at which 50% of the fish can reproduce.

2.2.1 The length-based Bayesian biomass (LBB) assessment model

The LBB method is grounded in a conceptual model that correlates life-history traits with length-dependent gear selectivity, illustrating how they interact to generate a specific length-frequency distribution (Froese et al., 2018; Wang et al., 2020). Trends in size over time denote elapsed time and are thus utilized to deduce population dynamics, enabling the model to project relative catch, mortality rates, and reference points for management. The model relies on life-history ratios rather than absolute values to reduce parameter demands. Initially, total mortality/growth rates (Z/K) are estimated by estimating the curvature of the predicted catch for fully selected fish in the numbers-at-age curve, formulated as follows:

$$N_L = N_{L_{start}}(\frac{L_\infty - L}{L_\infty - L_{start}})$$

In this equation, NL represents the number of fish surviving at length L, NLstart denotes the number of fish at the starting length (Lstart), where full selection occurs. The following set of equations is utilized to estimate L∞, selectivity parameters, M/K, F/K, and proportions-at-length (PLi) as follows:

$$N_{L_i} = N_{L_{i-1}}(\frac{L_\infty - L_i}{L_\infty - L_{i-1}})^{(\frac{M}{K}+\frac{F}{K}S_{L_i})}$$

$$C_{L_i} = N_{L_i}S_{L_i}$$

$$S_L = \frac{1}{1 + e^{-\alpha(L-L_c)}}$$

$$P_{L_i=\frac{N_{L_i}}{\sum N_{L_i}}}$$

$$N_{L_i} Multinomial(P_{L_i}, n)$$

$$P_{L_i} Dirichlet(\pi)$$

$$\pi uniform(0.5)$$

In these equations, NLi represents the number of individuals in length class Li, and NLi-1 denotes the number of individuals in the previous length class. CLi signifies the expected catch when selectivity (SLi) is taken into account. Selectivity parameters encompass α, the slope of the logistic selectivity curve, and Lc, the length at which 50% of individuals are retained by the gear. Proportions-at-length (PLi) are presumed to adhere to a Dirichlet-Multinomial distribution, where NLi conforms to a multinomial distribution delineating the predicted catch at each size class L with proportions PLi. The Dirichlet rate parameter π follows a uniform distribution as an uninformative prior.

Reference points for management are estimated from the preceding parameters as follows:

$$L_{opt} = L_\infty(\frac{3}{3+\frac{M}{K}})$$

$$L_{copt} = \frac{L_\infty(2+3\frac{F}{M})}{(1+\frac{F}{K})(3+\frac{M}{K})}$$

$$\frac{Y'}{R} = \frac{\frac{F}{M}}{1+\frac{F}{M}}(1-\frac{L_c}{L_\infty})^{\frac{M}{K}}(1-\frac{3(1-\frac{L_c}{L_\infty})}{1+\frac{1}{(\frac{M}{K}+\frac{F}{K})}}+\frac{3(1-\frac{L_c}{L_\infty})^2}{1+\frac{2}{(\frac{M}{K}+\frac{F}{K})}}-\frac{(1-\frac{L_c}{L_\infty})^3}{1+\frac{3}{(\frac{M}{K}+\frac{F}{K})}})$$

$$CPUE' = \frac{\frac{Y'}{R}}{\frac{F}{M}}$$

$$B'_0 = (1 - \frac{L_c}{L_\infty})^{\frac{M}{K}}(1 - \frac{3(1 - \frac{L_c}{L_\infty})}{1 + \frac{1}{(\frac{M}{K})}} + \frac{3(1 - \frac{L_c}{L_\infty})^2}{1 + \frac{2}{(\frac{M}{K})}} - \frac{(1 - \frac{L_c}{L_\infty})^3}{1 + \frac{3}{(\frac{M}{K})}})$$

$$\frac{B}{B_0} = CPU\ E'/B'_0$$

In these equations, Y'/R represents the yield per recruit, CPUE' denotes an index of relative catch per unit of effort, calculated by dividing Y'/R by F/M, and B/B0 denotes the exploitable fraction of the total virgin biomass (B0). The relative biomass to achieve maximum sustainable yield (BMSY/B0) is estimated by setting F/M to 1 and Lc = Lc_opt (Froese et al., 2018). We also employed three indicators to evaluate the structuring of the captured stock and identify population status (Medeiros-Leal et al., 2023).

Stocks were classified into different exploitation statuses based on B/BMSY values (a proxy for current biomass relative to the biomass at maximum sustainable yield) as follows: overexploited status was assigned when B/BMSY < 0.8, fully exploited status when 0.8 ≤ B/BMSY ≤ 1.2, and non-fully exploited status when B/BMSY > 1.2 (Amorim et al., 2019; Froese et al., 2015).

Between-chain convergence was assessed by visually examining MCMC traceplots for each parameter and the potential scale reduction factor (Kruschke, 2021). Model results were considered acceptable if simulated parameter values were consistent across chains and exhibited a potential scale reduction factor close to unity.

2.3 Local Ecological Knowledge (LEK)

2.3.1 Data collection

Fisheries in the coast of Alagoas state, Brazil, are entirely artisanal and yield a few hundred tonnes of catch every year . Mullets are amongst the most important exploited species, contributing up to 20% of the total yearly yield (Torres et al. 2007). Other fished species include various Sciaenids, penaeid shrimp, Carangids, Lutjanids, and spiny lobster (Torres et al. 2007, Rangely et al. 2010, de Barros et al. 2021, 2022). Mullets are mostly targeted with the use of cast nets and gillnets (Torres et al. 2007). Each municipality often houses hundreds of fishers, with thousands alongside the state's coast.

Interviews were conducted with 34 artisanal fishers from December to March 2023. These fishers were all commercial fishers specializing in mullet fisheries along the coast of Alagoas State. Among them, 12 were from the municipality of Barra de Santo Antônio (North coast), 20 were from Pontal da Barra in Maceió City (Central Coast), and 2 were from the municipality of Marechal Deodoro (Central Coast). The initial interviewees were local leaders who then recommended other fishers for the survey, following the snowball method (Gabor, 2007). A questionnaire consisting of semi-structured interviews with open-ended, single-choice, and multiple-choice questions was utilized to gather information on their Local Ecological Knowledge (LEK) regarding mullet species and their fishing practices (see Appendix).

2.3.2 Data analysis

First, normality and homoscedasticity tests were conducted on fishing production data reported by the fishermen. To assess if there is a significant perception of a decrease in mullet stock, we conducted a paired t-test, comparing the weight values (in kg) reported by each fisher for captures per fishing trip in the past and captures per fishing trip nowadays (Appendix, question 10).

During interviews the LEK of fishers were assessed by questions (See, question 2 in questionnaire) related to aspects of life history traits used for stock assessments, such as L50 and Lopt (Table 1). During interviews the LEK of fishers were assessed by questions (See, question 2 in questionnaire) related to aspects of life history traits used for stock assessments, such as L_{50} and L_{opt} (Table 1).

Table 1. Life history traits of stock assessments and respective questions used to assess LEK.

Life history trait	Meaning	Question used to assess life history trait by LEK
L_{opt}	The length at which the product of the number of survivors and their average weight is at its maximum	Which is the best size to capture?
L_{50}	The length at which 50% of the cohort of a fish species reached the sexual maturity.	Which was the smaller size of ovate female you captured?

Additionally, we performed binary tests to evaluate differences in:

I. perceptions of mullet taste by development stage (questions 3 and 4);

II. the practice of selling ovate lebranche mullet at a higher price (question 5).

To evaluate their perception of accountability and attitude toward stock recovery, we categorized their responses regarding the cause behind the alteration (question 11: “Why do you think they are decreasing?”) and the actions needed for stock recovery (question 12: “In your opinion, what must be done in order to recover the mullet stock?”). The perception of accountability of the fisheries sector regarding mullet stock was classified into the following options:

I. Feels that fishers are partially responsible for the mullet stock decreasing;

II. Does NOT feel that fishers are partially responsible for the mullet stock decreasing.

Their attitudes regarding the shared responsibility of fisheries sector to mullet stock recovery was classified in the following options:

I. Recognizes that fisheries sector must share the burden of actions to recover the stock;

II. Does NOT recognize that fisheries sector must share the burden of actions to recover the stock.

To identify points of divergence and convergence between LEK and CSK, information from various sources was compared. Divergences were examined to explore gaps that require further investigation, while convergences were analysed to assess both positive and negative findings, whether they were internal or external to fishery activities.2.5 Similarity between LEK and CSK.

The distributions of fishers' responses regarding Lopt and L50 values for the three species was estimated using the kernel density function of the "ggplot2" R package (Wickham, 2011). To test for overlaps between CSK and LEK, we employed one-sample Wilcoxon signed-rank tests to compare fishers perceptions of Lopt and L50 with CSK model results. Fisher’s responses regarding Lopt and L50 were considered samples to be tested against the median CSK outputs. This non-parametric test was chosen after verifying that the data does not meet parametric assumptions of normality with a Shapiro-Wilk test ($p < 0.05$). We used a significance level of 0.05.

To summarize good and bad practices among mullet fishers, we developed a SWOT matrix (Humphrey, 1960) from the fisher’s interviews, which comprises positive and negative observations pertaining to mullet fisheries, categorized as internal and external factors:

- Strengths (Positive + Internal): Factors within the fishery that are advantageous or beneficial.

- Weaknesses (Negative + Internal): Factors within the fishery that are disadvantageous or problematic.
- Opportunities (Positive + External): External factors outside the fishery that present opportunities for improvement or growth.
- Threats (Negative + External): External factors outside the fishery that pose risks or challenges to the fishery.

3. Results

3.1 Conventional Scientific Knowledge (CSK)

A total of 1,166 specimens were analyzed, comprising 430 individuals of *M. rubrioculus*, 376 of *M. curema*, and 360 of *M. liza*. *Mugil rubrioculus* exhibited the lowest mean size (30.31 ± 2.62 cm) and maximum total length (44 cm), followed by *M. curema* (31.97 ± 4.17 cm and 46 cm) and *M. liza* (48.61 ± 9.87 cm and 78 cm) (Fig. 2).

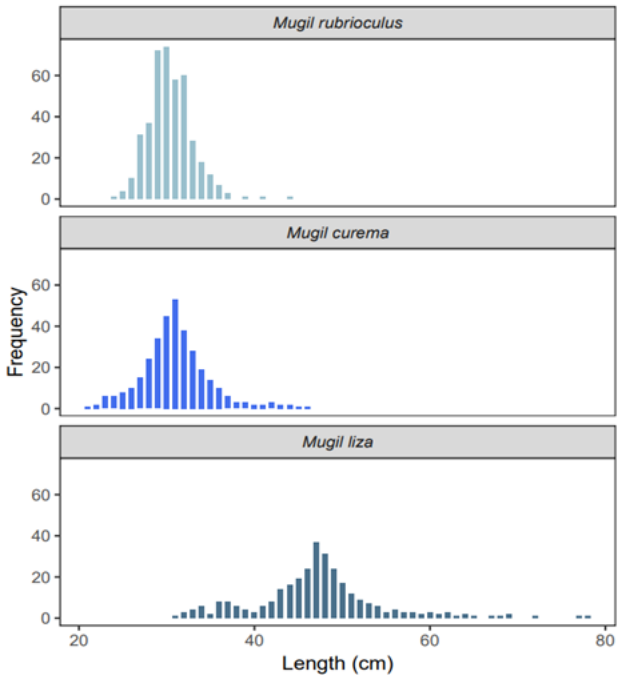

Figure 2. Length frequency data of populations of three mullet species: *Mugil rubrioculus*, *M. curema* and *M. liza*.

Lc/Lc_opt ratios were above unity (1) for all stocks, indicating that length distributions are not truncated and thus providing no evidence of inadequate catch of small, undersized individuals. However, other indicators suggest potential overfishing situations (Figure 3). For instance, despite the infrequent capture of small individuals, *L95/L∞* ratios indicate very low abundances of larger and older individuals. Additionally, mortality/growth (Z/K) ratios were considerably high for all species (see Figure 3). Similarly, the estimated current biomass values relative to the virgin stock biomass (B/B0) were low, and posterior distributions for *B/BMSY* allowed us to classify *M. rubrioculus* and *M. liza* as overexploited, and *M. curema* as fully exploited. Total mortality rates (Z) were 0.45, 0.39, and 0.37 year-1 for *M. rubrioculus*, *M. curema*, and *M. liza*, respectively (see Table 2).

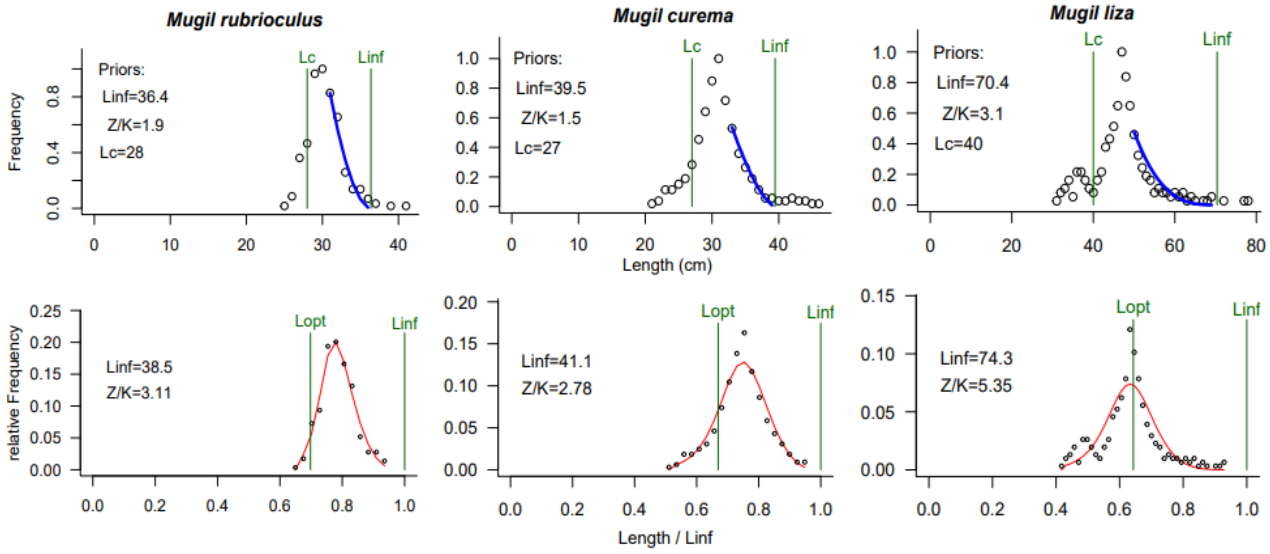

Figure 3. The top curves depict the LBB model's fit to the length data, and the bottom curves depict the LBB method's prediction, where L_c denotes the length of 50% of the individuals caught, L_∞ is the asymptotic length, and L_{opt} is the length when the maximum sustainable yield is achieved.

Table 2. Outputs of the Length-Based Bayesian Biomass (LBB) for *Mugil rubrioculus*, *M. curema* and *M. liza*. Quantities are displayed as medians and 95% credible intervals of Bayesian posterior distributions. *Z* stands for total mortality rates (year^{-1}), L_c stands for the length at first capture, L_{c_opt} stands for the optimal length at first capture, *K* and L_∞ are von Bertalanffy growth parameters, *B* stands for current biomass, B_0 stands for the virgin or unexploited biomass, B_{MSY} stands for the biomass at the maximum sustainable yield, and simple capture structuring indicators.

Species	***M. rubrioculus***	***M. curema***	***M. liza***
L_{50} (cm)	27.7 (25.9 – 29.9)	29.3 (28.6 – 30.0)	51.0 (50.4 – 54.0)
Z (year^{-1})	0.45 (0.38 - 0.55)	0.39 (0.175 - 0.617)	0.37 (0.201 - 0.632)
L_c (cm)	28	27	40
L_c/L_{c_opt}	1.2	1.3	1.1
Z/K	3.11 (2.81 – 3.37)	2.78 (2.53 – 3.05)	5.35 (4.87 – 5.34)
L_∞ (cm)	38.5 (37.81 – 39.26)	41.1 (39.64 – 42.89)	74.3 (71.01 – 78.23)
B/B_0	0.35 (0.24 – 0.47)	0.43 (0.28 – 0.65)	0.21 (0.17 – 0.27)
B/B_{MSY}	0.78 (0.58 – 1.04)	1.13 (0.76 – 1.4)	0.59 (0.47 – 0.74)
Lc/Lmat (>1)	1.01	0.92	0.78
Lmax/Linf (>0.8)	1.14	1.12	1.05
Lmean/Lopt (>0.9)	1.29	1.53	1.28
Stock Status	Overexploited	Fully exploited	Overexploited

3.2 Local Ecological Knowledge (LEK)

On average, fishers have 35.44 (±18.19) years of experience. All the interviewed fishers reported a drastic perceived decrease in the mullet stocks, regardless of age. The

current reported captures are 15.22% (±8.5) less than in past years, reflecting their perception of a decline in the mullet stocks.

Of the 34 fishers interviewed, 70.5% stated that they prefer to consume mullet based on its stage of development ($p < 0.05$), while the remaining fishers asserted that the taste of mullets is not influenced by the stage of development. Among those fishers who expressed a preference for taste based on the stage of development, 70.8% favoured adult mullets ($p > 0.05$), while the remainder preferred juveniles.

When asked if they sell the ovate lebranche mullet (female *Mugil liza* with full gonads), only 23.53% of the fishers reported this practice (binomial test – $p < 0.01$). These fishers mentioned identifying the ovate lebranche mullet by the volume and shape of the belly and selling the entire fish to clients. All fishers reported that they do not sell the gonads separately, and the majority prefers to sell the fish body while keeping the gonads for consumption at home, either fried or stewed as a culinary delicacy.

All fishers reported declining stocks for the three species studied over the years. When analyzing the fishers' responses regarding the perception of the reasons for the depletion in mullet stocks and what should be done to reverse this depletion, 41% of fishers did not cite fishing as a causal factor for the depletion, nor did they point to regulation of fishing as an action for improvement. Only six (~ 17%) fishers cited fishing as a causal factor and regulation of fishing among the actions needed to recover the stock. Nine fishers (~ 26%) cited fishing as responsible for the depletion but did not cite regulation of fishing as an action to promote stock recovery, while three (~ 9%) did not attribute fishing as responsible but cited regulation of fishing as an action to recover mullet stock. The remaining 7% chose not to respond. The Chi-squared test indicates that fishers who feel that increased fishing pressure is responsible for the perceived stock decline are more likely to suggest regulatory measures to promote recovery ($p < 0.05$).

According to the fishers, *M. liza* is called "curimã" and the average value declared for L50 is 59.32 cm with ±11.27 cm of Standard Deviation (S.D.). *M. rubrioculus* is known as "negrão" or "tainha olho de fogo" and has an L50 of 29.68 cm (±5.31 cm S.D.). *Mugil*

curema is called "tainha" and reaches its L50 at 28.95 cm (±4.58 cm S.D.). The species found most frequently in the marine environment was *M. curema*, and in the estuarine environment, it was *M. liza*. The average Lopt for *M. liza* declared by fishers was 73,03 cm (±9.1 cm S.D.), while for M. rubrioculus was 37.83 (±4.97 cm S.D.) and for *M. curema* was 40.06 cm (±5.55 cm S.D.).

3.3 Overlap between CSK and LEK

We found that the L_{opt} sizes indicated by fishers significantly differ (p-value > 0.05) from the L_{opt} of the LBB model, with the model's L_{opt} consistently smaller than those indicated by the fishers. Regarding maturation size (L_{50}), there was no difference between LEK and CSK for *M. curema* (p-value = 0.52), *M. rubrioculos* (p-value = 0.35), and *M. liza* (p-value = 0.11) (see Figure 4).

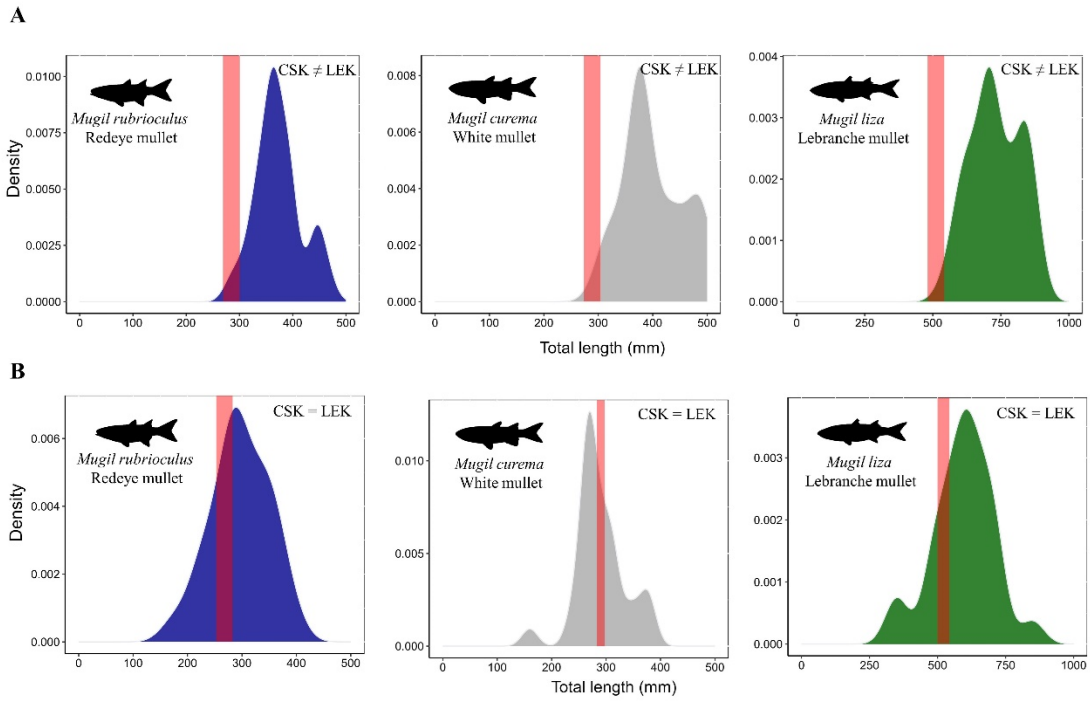

Figure 4. Density distribution of fishers' responses on L_{opt} (A) and L_{50} (B) values for the three *Mugil* species. The red bars indicate the values estimated CSK (the LBB model) of

L_{opt} (A) and L_{50} (B). The distribution of responses given by fishermen for *M. rubrioculus*, *M. curema*, and *M. liza* is represented by the colours blue, gray and green respectively.

4. Discussion

Our study applied the LBB method for the first time to mugilid stocks in conjunction with LEK data in the Tropical Southwestern Atlantic. Overall, results suggest that *Mugil liza* and *M. rubrioculus* stocks are overexploited. Notably, the *Mugil liza* stock appears to be in the most critical situation, with current biomass close to only 20% of virgin biomass (Table 2). This may be closely related to the species' slower growth and late maturity relative to the other species, which is generally associated with lower resilience to exploitation (Rangely et al., 2023; Tanner et al., 2019). This species also reaches the largest size and is therefore highly sought after by fishers due to its high sales value. Nevertheless, our results demonstrate that the three mullet stocks analysed here are impacted by high fishing pressure and therefore need more comprehensive management plans in place to ensure long-term sustainability in resource use and yield maximization. Although artisanal fishing has been considered less impactful on the environment due to a substantial subsistence component compared to industrial fishing (FAO, 2005; Teh and Sumaila, 2018), this practice can also affect biomass levels and cause suboptimal yields (Goetze et al., 2011; Hawkins; Roberts, 2004).

Data with appropriate spatial-temporal resolution such as several years of spatially-explicit monitoring are pivotal to obtain detailed information about population dynamics, as well as biological responses to fishing pressure and environmental changes, a growing scientific concern nowadays (Tanner et al., 2019). However, these long-term datasets are scarce for artisanal fisheries due to their patchy, unregulated nature and poor resource allocation to monitoring efforts. This creates a considerable mismatch between management needs and resource availability, since only ~ 20% of the global catch comes

from regularly assessed industrial stocks (Worm et al., 2006; Costello et al., 2012). In this context, LEK has great relevance to help manage artisanal, small-scale fisheries, as it provides additional information that helps guiding potential strategies to ensure long-term resource use. In this study, we underscore the usefulness of LEK data in monitoring efforts aiming to understand the status of exploited, economically and socially important fish stocks by demonstrating its close agreement with statistical assessment models.

We specifically found that the fisher's perception of stock declines for the three mullet species over the years agree with LBB model results indicating very low relative biomass levels, especially for *M. liza* (Figure 3, Table 1). Our results are strikingly similar to research conducted in the Southwestern Atlantic reporting close agreement between fisher's perception and long-term ecological data on the decline in catches and abundance of important fishery species (Bender et al. 2014). Despite close agreements on stock declines between CSK and LEK, these two sources diverge on the causes of these declines. While LBB model results point to overfishing as the potential cause, most fishers actually point out to environmental degradation. We argue that these results show the potential of LEK not only to inform the management of data-limited fisheries by providing past data on resource trends through structured interviews, but also to provide more comprehensive and holistic views on management problems. We also demonstrated that LEK data closely agrees with CSK on the L50 parameter, but not for Lopt. This is because life-history traits such as growth/size and reproduction are more meaningful and tangible to fishers when compared to Lopt (Herbst and Hanazaki, 2014; Nunes et al., 2019). In fact, the "optimal" size for fishers would simply denote bigger fish that sell for higher prices, while Lopt for LBB denotes the mean length of capture at which yield is maximized. This demonstrates that information on life-history traits and stock status derived from LEK will not always reflect the true underlying population dynamics, and highlights that extensive validation might be needed before using LEK data on its own.

It is paramount to account for potential biases in LEK data such as the Shifting Baseline Syndrome (SBS), where younger fishers are more likely to underestimate potential population declines (e.g. Bender et al., 2014). This phenomenon can happen

because, with the ongoing and widespread environmental degradation that started a long time ago, fisher's acceptable conditions for what resembles a healthy fishery tends to decrease over time (Soga and Gaston, 2018). To tackle this issue, we recommend the inclusion of diverse age groups when conducting interviews to ensure enough contrast in the data, as well as the inclusion of age as a covariate should an effect of this variable be uncovered.

4.1 Good (and Bad) Management Practices

A strong indication that the mullet stocks analysed here are not being appropriately managed is the widespread perception of decline over the past decades, possibly due to historic negative fisher behaviours or external factors such as pollution and habitat degradation (Silva et al., 2010; Silva et al., 2009). An example of good management practices already adopted by local fishers is the preference for consuming adult mullets, which allows at least one or more reproductive cycles to take place before capture (Soares et al., 2020). Moreover, reports of more frequent sizes of mullets ranging around the optimal weight or above the L_{50} are also beneficial for stock management for the same reason (Soares et al., 2020).

However, the practice of consuming *M. liza* (lebranche mullet) roe is potentially negative for stock management since it involves capturing the fish during their reproductive period, specifically before spawning. Historically, during the ascension Thursday, a tradition known as "Dia-da-hora" in Alagoas State, locals consumed lebranche roe without necessarily utilizing the entire fish for consumption (Cascudo, 1984). This led to large quantities of captured lebranche being discarded, which ultimately contributes increased fishing pressure due to the high demand. Nowadays, the practice of consuming lebranche roe has significantly decreased due to the stock decline, and also possibly due to environmental education initiatives (Marques et al., 2005; Santos and Sampaio, 2013; Siemer and Knuth, 2001; Patterson et al., 2009). While the practice of consuming gonads still exists, fishers now also utilize the whole fish for consumption or

selling as opposed to consuming gonads only, which is a positive factor for stock restoration.

The low sense of responsibility among fishers for stock management presents a challenging scenario for management (Table 2). A significant challenge in the recovery of mullet stock in the Mundaú Lagoon and Santo Antônio River is the historical lack of accountability among fishers and their low sense of guilt or responsibility due to unsustainable fishing practices. The magnitude of impacts from pollution and mining in both estuaries may lead fishers to perceive fishing pressure as less impactful, resulting in a reluctance to implement fisheries regulations (Silva and Sousa, 2009; Almeida et al., 2009; Drymon and Scyphers, 2017; Cardona et al., 2013). Historically, global fisheries have been managed through centralized models with limited social participation, leading to a lack of recognition of stakeholders' roles in decision-making (Cochrane, 2000). Efforts to change fisher's perceptions regarding causes of stock declines will improve collective behaviour in the future (Gelcich et al., 2005; Thompson, 2008), and initiatives engaging fishers in decision-making have shown promising outcomes by increasing their sense of participation and promoting accountability in stock management (Pita et al., 2009; Mikalsen and Jentoft, 2008; Lorenzen et al., 2010).

Among positive factors that might contribute to stock recovery in the future, the increased interest of environmental agencies in integrating fishers in the management process is an important factor (Table 2). Local environmental agencies and academic entities are increasingly approaching traditional fisher communities to offer them opportunities to engage in discussions regarding potential management strategies. In addition to building more trust between governmental agencies and traditional communities, these initiatives also help foster a sense of inclusion amongst these communities, which might contribute to increased compliance with eventual management procedures put in place (Castillo et al. 2024).

Table 2. SWOT matrix composed of Positive vs negative points and internal vs. external factors associated with overexploitation according to fishers.

	POSITIVE	NEGATIVE
INTERNAL	**Strengths**: • Consumption of fishes with size/weight ranging within the Optimum Yield per recruit; • Higher preference for consumption of adult mullet individuals; • Low rate of selling of ovate lebranche mullet; • High sense of perception of mullet stock decreasing.	**Weaknesses**: • Strong practices of consumption of mullet roe among fisher; • Low sense of association between stock decreasing and fishing pressure; • Low sense of accountability in management actions needed for mullet stock recovery; • Use of gillnets with mesh size below 35mm between knots among some fisher.
EXTERNAL	**Opportunities**: • Increasing interest of environmental agencies to integrate fishers in co-management initiatives; • Academia is interested in collaborating with the fisheries sector using LEK.	**Threats**: • High levels of estuarine pollution caused by the sugar-cane industry; • Estuarine silting up caused by pollution and mining activities.

Integrating ecological systems with environmental managers, the scientific community, and users of the system, such as fishers, who have different perspectives on the same problem, is a significant challenge. Socio-environmental conflicts and tensions among these actors underscore the need for co-management to achieve genuine socio-ecological connectivity and effective management of this crucial fishing resource. Co-management, as defined by Berkes et al. (1998), involves sharing responsibility and power between resource users and the government. Therefore, management plans must integrate both Local Ecological Knowledge (LEK) and Conventional Scientific Knowledge (CSK) through robust and reliable co-management strategies (Carlsson and Berkes, 2005). Horizontal collaboration is essential, allowing fishers, managers, and scientists to have an active voice in the decision-making process while acknowledging the experiences of actors and stakeholders from traditional communities. The construction of the SWOT matrix (Table 2) serves as an initial step in identifying Strengths, Weaknesses, Opportunities, and Threats. In the case of the mullet stocks, co-management is urgently needed due to the overexploitation of these stocks.

5. Conclusion

Our findings reveal that two of the studied stocks, M. liza and M. rubrioculus, are overexploited, while one is at its maximum sustainable yield and therefore fully exploited (M. curema). The overlap between Conventional Scientific Knowledge (CSK) and Local Ecological Knowledge (LEK) on stock declines underscores the potential of LEK as an accessory tool to inform the management of data-limited fisheries, while differences in perceived causes of declines reflect the need to adopt increasingly holistic approaches to solve broader environmental problems that might contribute to stock declines. This highlights the importance of participatory management (horizontality) among various stakeholders, including government managers, fishers, and the scientific community, to address challenges, promote responsible resource management, and ensure the well-being of ecosystems and fishing communities. The SWOT matrix derived from LEK interviews serves as an initial step in this process, offering insights into the perceptions, attitudes, and behaviours of mullet fishers. Stock assessment outputs emphasize the need for ecological conservation of the species in the face of overexploitation and other anthropogenic effects.

Declaration of interest

We have no conflicts of interest to disclose.

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7. Discussão geral

Os resultados aqui apresentados demonstram a alta complexidade nos mecanismos de coexistência de espécies congenéricas e morfologicamente semelhantes, que podem ser evidenciados por uso de habitat, crescimento e plasticidade individual e interespecífica. Sedo esses mecanismos importantes para compreensão da dinâmica e das interações dentro e entre as populações e que influenciam até mesmo para a avaliação dos estoques pesqueiros.

No primeiro capítulo a diferenciação em relação ao padrão de uso de habitat nos permite compreender os mecanismos de coexistência de duas espécies de *Mugil*. Sendo que *M. curema* é influenciado por fatores como temperatura e oxigênio dissolvido, clorofila e turbidez, enquanto que *M. rubrioculus* é influenciado por variações na salinidade. Considerando que o *M. rubrioculus* e *M. curema* são filogeneticamente mais próximos (Neves *et al.*, 2020), já previámos que exibiriam graus mais elevados de sobreposição de nicho e, portanto, precisam realizar ciclos de vida temporariamente desacoplados. Especificamente, *M. rubrioculus*, ocupa a parte externa do estuário e o mar, já *M. curema* é capaz de ocupar os três ambientes na primeira fase do seu ciclo de vida.

Portanto, um dos mecanismos que poderia ter levado a tais histórias de vida dissociadas em tainhas tropicais é o deslocamento de caráter, reconhecido como um processo comum quando se descobre que espécies simpátricas diferem no uso de recursos (Goldberg & Lande, 2006). Que pode ser explicado como diferenças induzidas pela competição nas características da história de vida através da plasticidade fenotípica, causando a ocorrência de seleção diferencial (Slatkin, 1980). Além das interações complexas entre variáveis bióticas e abióticas podem explicar variações no uso do habitat dos peixes ao longo do tempo e do espaço (da Silva *et al.,* 2021, 2022).

No segundo capítulo nós demostramos que o crescimento polifásico alométrico em otólitos de peixes pode ser um indicador adequado de eventos cruciais do ciclo de vida, como maturação sexual e mudanças ontogenética de habitat. Já que a espécie de crescimento mais rápido (*M. rubrioculus*) atingiu os menores tamanhos assintóticos e

exibiu mudanças mais precoces na alometria e maturação, e a espécie de crescimento mais lento (*M. liza*) mostrou tamanhos maiores e mudanças posteriores nos padrões alométricos e maturidade. Sendo *M. curema* a espécie intermediária, tanto em comprimento, quanto em velocidade de crescimento. Então, as diferentes idades na maturidade e mudanças na alometria mostram que espécies simpátricas de *Mugil* podem ter uma assincronia de tempo e espaço nos ciclos de vida para permitir a coexistência. Essa assincronia é provavelmente uma resposta evolutiva que aumenta a aptidão de espécies coocorrentes ecologicamente semelhantes expostas aproximadamente às mesmas condições ambientais (Chang e Iizuka, 2012; Scott & Johnson, 2010).

Partindo do pressuposto de que a estuarino dependência gera um ponto de inflexão no ciclo de vida, mudando a velocidade de crescimento, ou seja, quanto mais tempo eles passam no estuário, maior é o pré ponto de inflexão, que é a etapa do ciclo de vida de maior investimento em crescimento (Sousa *et al.* 2015) e isso poderá se traduzir em maiores tamanhos. Então, no terceiro capítulo da tese, foi utilizado a temporalização da microquímica expressa pelas diferentes quantidades do elemento traço estrôncio ao longo do *raster* do núcleo a borda do otólito, percebemos que, das três espécies, a que passa mais tempo da sua primeira fase do ciclo de vida no estuário é *M. liza.* Que é justamente a espécie com menor velocidade de crescimento, que possui maior longevidade, com menor plasticidade individual em relação ao uso de habitats. No outro extremo encontramos *M. rubrioculus,* que possui uma menor estuarino dependência, estando adaptado a salinidades mais altas, maior velocidade de crescimento, chega a um tamanho máximo menor entre as espécies estudadas e possui grande plasticidade no uso de habitat. Já os indivíduos de *M. curema* apresentaram a maior plasticidade individual no uso dos habitats, apresentando maior migração parcial.

A migração parcial gera uma redução temporária da concorrência com espécies não migratórias, ou seja, afeta a estrutura da comunidade, reduzindo a concorrência e, portanto, permitindo a coexistência (Johnson, 1980; Peller *et al*., 2023). Evolutivamente, a maior plasticidade migratória entre habitats pode gerar uma maior adaptabilidade da espécie e consequentemente maior resiliência (Tamario *et al.,* 2019). Quando ocorre a migração parcial o estoque como um todo, até certo ponto, fica menos vulnerável a

atividade pesqueira, por exemplo, tendo maiores chances de sobrevivência, já que eles têm múltiplos contingentes de peixes que usam diferentes habitats dentro da mesma população (Fowler *et al.,* 2016). Dessa forma, essa menor plasticidade no uso de habitats, assim como menor taxa de crescimento pode estar afetando diretamente a resiliência em relação a pesca para a população de *M. liza*.

Então, no quarto capítulo dessa tese, constatamos que o estoque de *M. liza* é o mais afetada por essa atividade na região estudada, apresentando o maior declínio, tendo hoje apenas 20% do estoque original. Nesse sentido, é possível indicar essa espécie como prioritária para o manejo e conservação de Mugilidae nos estuários estudados, considerando que quanto maior a permanência no habitat a espécie se torna mais vulnerável a perda desse habitat e a pressão por pesca. Dessa forma, temos uma medida da vulnerabilidade à perda de habitat, às mudanças climáticas e à pesca. Isso é particularmente relevante ao considerarmos a acelerada degradação dos ambientes costeiros tropicais, impulsionada pela especulação imobiliária e pela expansão de empreendimentos voltados ao turismo, frequentemente acompanhados de ocupação desordenada e destruição de áreas essenciais, como manguezais e estuários (Miranda et al., 2002). Adicionalmente, a descarga de esgoto doméstico e industrial não tratado, bem como o despejo de resíduos da tiborna de cana-de-açúcar diretamente nos rios, agravam a poluição e comprometem ainda mais esses ecossistemas frágeis. Esses fatores são agravados pelo aumento da pressão da pesca decorrente do crescimento populacional na região (Blaber & Barletta, 2016) e pelos registros de sobrepesca (Mendonça & Bonfante, 2011). Diante desse cenário, a necessidade de preservar os estuários torna-se crucial, uma vez que eles desempenham um papel indispensável como áreas de berçário para diversas espécies marinhas e como reguladores naturais da qualidade da água. A conservação desses habitats é vital para garantir não apenas a sustentabilidade dos recursos pesqueiros, mas também a manutenção da biodiversidade e o equilíbrio ecológico.

Nesse sentido, para fazer a gestão adequada desse recurso também é relevante considerar o conhecimento Conhecimento Ecológico Local (LEK), já que ressaltamos a compreensão dos pescadores sobre os traços da história de vida. Como já visto por

Karnad (2022), o uso da gestão participativa pode aumentar a conservação dos ambientes. E Sultana e Abeyasekera (2008) trouxe evidências estatísticas de que o apoio à gestão de recursos foi mais eficaz quando iniciado através de um processo envolveram a participação da comunidade e o estabelecimento de instituições locais de gestão das pescas. Destacamos então a importância da gestão participativa (horizontalidade) com os atores da pesca, incluindo gestores governamentais, pescadores e a comunidade científica, para promover a gestão responsável dos recursos e garantir o bem-estar dos ecossistemas e que as necessidades locais das comunidades sejam atendidas.

Constatamos que a coexistência entre espécies congenéricas de *Mugil* é facilitada por uma complexidade de mecanismos, nos quais fatores como uso do habitat, padrões de crescimento e plasticidade desempenham papéis fundamentais para a compreensão das dinâmicas populacionais e das interações ecológicas. A segregação espacial observada entre as espécies parece resultar de adaptações divergentes às condições ambientais, refletidas nos padrões de crescimento alométrico dos otólitos, que se mostram preditores significativos de eventos críticos do ciclo de vida.

Dada a plasticidade de uso do habitat, é razoável concluir que *M. curema* é mais capaz de sobreviver e manter populações em uma variedade de salinidades. Essa característica aumenta suas chances de sobrevivência ao otimizar o uso de habitats temporariamente favoráveis o que a beneficia em relação a manutenção dos estoques pesqueiros. Por outro lado, a menor plasticidade de *M. liza* em relação ao uso do habitat a torna mais dependente de ambientes específicos e estáveis para completar seu ciclo de vida. Essa dependência, aliada ao seu crescimento mais lento, aumenta a vulnerabilidade da espécie à degradação dos habitats costeiros, como estuários e áreas de manguezais, que são frequentemente impactados por atividades humanas, como poluição e ocupação desordenada. Esses fatores, somados à intensa pressão de pesca, resultaram na redução de seus estoques para apenas 20% do nível original. Concluímos que a gestão adequada dos recursos pesqueiros de Mugilidae exige uma abordagem abrangente, que leve em conta a variabilidade ambiental e as peculiaridades de cada espécie, além de integrar o Conhecimento Ecológico Local (LEK) das comunidades pesqueiras para promover uma gestão sustentável dos recursos.

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