Universidade do Estado do Rio de Janeiro
Centro Biomédico
Instituto de Biologia Roberto Alcântara Gomes

Joice Silva de Souza

Mecanismos associados à vulnerabilidade da ictiofauna estuarina às alterações climáticas globais

Rio de Janeiro
2023

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Tese apresentada, como requisito parcial para obtenção do título de Doutor, ao Programa de Pós-Graduação em Ecologia e Evolução, da Universidade do Estado do Rio de Janeiro.

Orientador: Prof. Dr. Luciano Neves dos Santos

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DEDICATÓRIA

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remember the body
of your community
breathe in the people
who sewed you whole
it is you who became yourself
but those before you
are a part of your fabric
- honor the roots

Rupi kaur

RESUMO

SOUZA, Joice Silva de. *Mecanismos associados à vulnerabilidade da ictiofauna estuarina às alterações climáticas globais.* 2023. 210 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2023.

A conservação da biodiversidade frente às mudanças climáticas depende da identificação de mecanismos associados com a persistência das espécies no habitat original, a fim de prevenir impactos em níveis ecológicos mais elevados (i.e. comunidade, ecossistema). Na presente tese avaliou-se (I) a importância relativa de mudanças na dominância e ocupação das espécies para a reorganização de comunidades sob influência do aquecimento global (Capítulo 1); (II) a influência da heterogeneidade local na temperatura e salinidade sobre a vulnerabilidade térmica de *Atherinella brasiliensis* (Quoy & Gaimard, 1825), espécie de peixe residente em estuários tropicais (Capítulo 2); e (III) a relação entre o nicho térmico realizado de espécies não-nativas e sua área geográfica de introdução (Capítulo 3), além de outros fatores preditores da riqueza não-nativa. Uma meta-análise de estudos com série temporal igual ou superior a 20 anos foi realizada para avaliar padrões na beta-diversidade e perfil térmico da ictiofauna estuarina, a fim de atingir o 1º objetivo proposto (Capítulo 1). Para a realização do 2º capítulo, juvenis de *A. brasiliensis* capturados na Baía de Guanabara, RJ, foram aclimatados em diferentes condições de temperatura e salinidade, e expostos à uma rampa térmica de +1ºC a cada 15 minutos, a fim de determinar sua tolerância máxima. Para atingir o 3º objetivo proposto, realizou-se uma seleção de modelo para detectar os principais fatores antropogênicos e ambientais associados com a riqueza de espécies não-nativas em estuários, que foi compilada a partir de uma revisão na literatura científica. A relação entre os limites térmicos das espécies não-nativas e a latitude do estuário invadido também foi investigada. Os resultados revelaram que mudanças na dominância das espécies residentes contribuíram majoritariamente para a tropicalização da ictiofauna em região temperada, contrariando expectativas de um papel primário da imigração. A persistência detectada para as espécies estuarinas pode estar associada à diversos mecanismos, incluindo a tolerância térmica. Os testes experimentais revelaram tolerância de *A. brasiliensis* à temperaturas até 40,6ºC, e plasticidade nos limites térmicos em função da temperatura e salinidade de aclimatação. Estes resultados indicam uma potencial persistência da espécie durante ondas de calor e cenários intermediários de aquecimento à longo-prazo. No entanto, os limites máximos de *A. brasiliensis* não sofreram alteração após aumento exclusivo na temperatura de aclimatação, revelando que a espécie pode estar próxima de atingir seus limites térmicos absolutos. Os limites térmicos também apresentaram relação com a área de introdução de espécies não-nativas ao redor do globo, indicando conservação de nicho climático durante invasões. O tráfego de navios e flutuações na salinidade também foram associados com a riqueza de peixes não-nativos, revelando um papel primário da pressão de colonização e o filtro ambiental para sua ocorrência em estuários. Os dados gerados pela presente tese contribuíram para avançar o conhecimento acerca de respostas da biodiversidade às mudanças climáticas, e fornecem importantes subsídios para o desenvolvimento de planos de manejo e conservação da fauna nativa.

Palavras-chave: Temperatura. Mudanças climáticas. Plasticidade térmica. Ecologia de comunidades. Invasões biológicas. Estuários. Salinidade.

ABSTRACT

SOUZA, Joice Silva de. *Mechanisms underlying estuarine fish assemblages' vulnerability to climate change.* 2023.210 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2023.

Biodiversity conservation in the face of climate change relies on identifying mechanisms associated with species persistence in their original habitat, in order to prevent impacts at higher ecological levels (i.e. community, ecosystem). The present thesis assessed (I) the relative importance of shifts in species dominance and occupancy for reshaping communities under warming (Chapter 1); (II) the influence of local-scale heterogeneity in temperature and salinity on the thermal tolerance of Brazilian silversides *Atherinella brasiliensis* (Quoy & Gaimard, 1825), which is a resident species in tropical estuaries (Chapter 2); and the relationship between non-native species' thermal niche and their geographic area of introduction, and drivers of non-native richness (Chapter 3). In order to achieve the 1^{o} goal, a meta-analysis was performed using studies with a time series equal or greater than 20 years. Trends in beta-diversity and the mean thermal affinity of estuarine fish assemblages were assessed using the compiled database (Chapter 1). For the 2^{o} goal, experiments were performed with *A. brasiliensis*' juveniles captured at Guanabara Bay, RJ. Fish were acclimated under distinct temperature and salinity levels in the laboratory, previous to their exposure to a thermal ramp (+1^{o}C each 15 minutes until specimens' reached endpoint) for detecting their Critical Thermal Maxima (CTMax) (Chapter 2). To achieve the 3^{o} goal, model selection was performed using proxies of anthropogenic activities and environmental filtering, to assess the primary drivers of non-native fish species in estuaries. The relationship between non-native species' thermal limits and latitude of invaded estuary was also investigated. Tropicalization of estuarine fish assemblages in the temperate realm was primarily driven by shifts in abundance of resident species with distinct thermal affinities, disagreeing with previous expectations regarding a central role of immigration. Estuarine species' persistence may be related to several mechanisms, including thermal tolerance. Experimental tests revealed *A. brasiliensis* tolerates temperatures up to 40.6^{o}C. Plasticity on thermal limits in response to acclimation temperature and salinity was also detected. These results indicate *A. brasiliensis*' has potential to persist in the estuary under heatwaves and intermediate warming scenarios. Nonetheless, lack of acclimation in the thermal maxima after exposure to temperatures predicted in "worst-case" scenarios, suggests *A. brasiliensis* heat tolerance is close to reaching a "ceiling". Thermal limits were also related to the geographic area of introduction of non-native fish species, suggesting conservatism of the climatic niche during invasions. Shipping traffic and salinity were also associated with richness of non-native species, revealing a central role of colonization pressure and habitat filtering for non-native occurrence. These represent novel and timely insights for advancing theory and practice on biodiversity change in response to warming.

Keywords: Temperature. Climate change. Thermal plasticity. Community ecology. Biological invasions. Estuaries. Salinity.

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ITC	Índice de Temperatura da Comunidade
MST	Margem de Segurança Térmica

SUMÁRIO

INTRODUÇÃO GERAL

Um dos principais desafios da atual crise da biodiversidade consiste em prever a vulnerabilidade das espécies às mudanças climáticas. A avaliação de mecanismos à nível molecular (e.g. produção de proteínas "*heat-shock*"; MADEIRA et al., 2021), fisiológico (e.g. tolerância térmica; MADEIRA et al., 2014) e comportamental (e.g. termorregulação comportamental; REISER et al., 2017), é o foco de estudos que buscam investigar potenciais impactos do aquecimento sobre uma variedade de organismos. No entanto, as respostas detectadas à nível do indivíduo raramente são analisadas de maneira integrada, dificultando estimativas sobre padrões de diversidade em diferentes escalas. Neste sentido, a análise de dados provenientes de monitoramentos à longo-prazo pode revelar como os impactos sobre o indivíduo se refletem na composição e estrutura de comunidades (MCLEAN et al., 2019; KIMBALL et al., 2020), e potenciais consequências para o funcionamento de ecossistemas (DI PANE et al., 2022).

Mudanças na temperatura foram associadas à reorganização das comunidades marinhas em região temperada, a qual se caracterizou por um aumento temporal na riqueza de espécies (ANTÃO et al., 2020). A imigração de espécies tropicais seria o principal processo subjacente à este resultado, culminando na "tropicalização" de ecossistemas situados em maior latitude (CHEUNG et al., 2013; BRICE et al., 2019; LEHIKOINEN et al., 2021). Este fenômeno é descrito como o aumento em espécies de afinidade térmica quente (MCLEAN et al., 2021), e pode ser mensurado através da decomposição do Índice de Temperatura da Comunidade (ITC). Este índice revela o perfil térmico da comunidade, que é ponderado pela abundância das espécies que a compõem (DEVICTOR et al., 2008). Desta forma, flutuações temporais no ITC refletem alterações na ocupação (i.e. imigração e emigração) e dominância (i.e. abundância) das espécies. A decomposição do ITC proposta por MCLEAN et al. (2021) revelou ainda que aumentos na afinidade térmica média da comunidade, geralmente associados à tropicalização, também podem resultar do declínio em espécies de afinidade fria (i.e. deborealização). Nesse caso, a imigração de espécies teria um papel secundário para a reorganização temporal das comunidades sob influência da mudança do clima, contrariando as expectativas de grande parte da comunidade científica.

O aumento das taxas de colonização em sistemas temperados, acompanhado da potencial substituição de espécies de afinidade térmica fria por quente (CHEUNG et al., 2013; ANTÃO et al., 2020), sugere um papel central da dispersão na formação de novas comunidades. No entanto, uma síntese de dados realizada por DORNELAS et al. (2019) revelou uma alta proporção de populações persistentes em diferentes regiões climáticas do globo. Além disso, tendências de aumento e declínio populacional foram detectadas para poucas espécies, gerando questionamentos sobre a importância relativa de mudanças na ocupação e dominância para a reorganização da biodiversidade local. No entanto, os padrões detectados por DORNELAS et al. (2019) não foram associados à nenhum fator específico como as mudanças climáticas, e/ou outras ameaças à biodiversidade. Embora mudanças na ocupação das espécies sejam frequentemente reportadas em comunidades sob a influência do clima (ANTÃO et al., 2020), sua contribuição relativa para a formação das novas comunidades ainda não foi estimada. Esta análise é crucial para identificar (I) as principais espécies que sustentam a reorganização das comunidades, e (II) a escala adequada (i.e. pool regional x comunidade local) para a implementação de políticas de manejo e conservação da diversidade. Comunidades formadas por alterações na dominância de espécies residentes (i.e. detectadas durante grande parte da série temporal), por exemplo, indicariam a importância de identificar mecanismos em escala local subjacentes à sua persistência (e.g. variação intraespecífica, termorregulação comportamental, entre outros), a fim de investigar seu potencial para continuar amortecendo impactos futuros.

Além do aumento da temperatura média global à longo-prazo, as mudanças climáticas também são caracterizadas pela maior ocorrência de eventos extremos de curta-duração, como as ondas de calor (IPCC, 2021). Este fenômeno corresponde ao aumento de pelo menos 5º Celsius na temperatura máxima do habitat pelo período mínimo de cinco dias (VINAGRE et al., 2018), e pode antecipar a exposição da fauna ectotérmica às temperaturas previstas para meados e final do século 21. A avaliação dos limites térmicos de espécies prioritárias na reorganização das comunidades pode ser utilizada para investigar sua persistência na região de estudo (BENNETT et al., 2019; FOX et al., 2019; MCKENZIE et al., 2021), auxiliando na previsão de trajetórias futuras da biodiversidade local e funcionamento do ecossistema. Essas avaliações são especialmente importantes para a biota em ecossistemas tropicais, em função da (I) menor margem de segurança térmica exibida por estas espécies (TEWKSBURY et al., 2008; VINAGRE et al., 2018), e (II) a baixa detecção de impactos *in situ* das mudanças climáticas, devido à falta de programas de monitoramento contínuo. O limitado potencial para plasticidade de espécies tropicais foi reportado por vários estudos com design experimental unifatorial (i.e. avaliam apenas mudanças na temperatura; MADEIRA et al., 2017; VINAGRE et al., 2018; GERVAIS et al., 2021). No entanto, outros fatores ambientais podem interagir com a temperatura para moldar a tolerância térmica dessas espécies (REISER et al., 2017;

MADEIRA et al., 2021), mas sua associação com a plasticidade na resposta térmica ainda não foi avaliada, o que pode afetar as estimativas de vulnerabilidade à eventos climáticos.

O clima também pode interagir com outras ameaças à biodiversidade, como as espécies invasoras (HELLMAN et al., 2008; RAHEL; OLDEN, 2008). Diversos processos ecológicos foram associados com o sucesso da bioinvasão, como a pressão de propágulos, disponibilidade de recursos e o filtro ambiental (ENDERS et al., 2020). A pré-adaptação às condições ambientais na área recipiente têm sido reportada como um fator importante para a ocorrência de espécies não-nativas (WEIHER; KEDDY, 1995), e evidências sugerem um papel primário do clima. A conservação do nicho climático foi detectada para grande parte das espécies invasoras (LIU et al., 2020), embora um baixo nível de especialização ecológica seja frequentemente reportado para essas espécies (CLAVEL et al., 2011). No entanto, a relação entre o nicho térmico realizado e a área geográfica de introdução das espécies não-nativas ainda não foi avaliada. Limites térmicos mínimos, máximos e a faixa de tolerância, foram correlacionados com a distribuição latitudinal de espécies nativas tropicais e temperadas em ecossistemas marinhos rasos (Stuart-smith et al., 2017), e estão associados com as mudanças projetadas para os padrões de diversidade em escala global (SUNDAY et al., 2011; GARCÍA MOLINOS et al., 2016). A análise do clima como barreira para a ocorrência das espécies é particularmente importante no contexto da bioinvasão, visto que o transporte de organismos não-nativos entre áreas geográficas é mediado por atividades humanas (BLACKBURN et al., 2011). Neste sentido, investigar a relação entre a afinidade térmica das espécies invasoras e sua área de introdução pode auxiliar na identificação de pares "espécie-região" prioritários para monitoramento em condições atuais e futuras, a fim de prevenir a homogeneização biótica (CLAVEL et al., 2011).

Impactos precoces das mudanças climáticas foram observados para comunidades de peixes em estuários (MCLEAN et al., 2019; KIMBALL et al., 2020). Esses sistemas apresentam baixa inércia térmica e rastreiam rapidamente a temperatura do ar, fornecendo, portanto, um modelo adequado para avaliar as respostas da fauna ectotérmica às mudanças climáticas (Roessig et al., 2004; Madeira et al., 2012, McLean et al., 2019). A heterogeneidade nas condições locais de temperatura e salinidade também pode influenciar os limites térmicos das espécies que habitam estes sistemas (MADEIRA et al., 2014), afetando sua vulnerabilidade às ondas de calor e alterações à longo-prazo na temperatura. Além disso, a concentração de vetores relacionados à atividades antropogênicas (e.g. aquacultura, tráfego de navios, pesca) e seus impactos associados (e.g. modificação do habitat em decorrência da urbanização), conferem uma alta invasibilidade aos estuários (WILLIAMS; GROSHOLZ, 2008; PREISLER et al., 2009). Desta forma, estes sistemas permitem uma avaliação do efeito de variáveis climáticas (e.g. temperatura, salinidade) sobre a distribuição, composição e abundância da ictiofauna nativa e não-nativa, e a identificação de mecanismos subjacentes à sua tolerância térmica em escala local.

A presente tese objetivou avaliar a importância relativa de alterações na distribuição e dominância das espécies para a reorganização temporal das comunidades sob influência do aquecimento global, assim como identificar potenciais mecanismos subjacentes à tolerância térmica das espécies em escala local. A influência do clima sobre padrões de riqueza e a distribuição de espécies não-nativas também foi investigada. Para tal, utilizamos a ictiofauna associada à estuários como modelo, devido à sua alta exposição às mudanças na temperatura e salinidade. A Tese é composta por três capítulos redigidos em inglês, apresentados no formato especificado pelo periódico científico de publicação e/ou futura submissão. O primeiro capítulo compreende uma compilação de estudos que identificaram o efeito de mudanças no clima sobre a ictiofauna em estuários, com série temporal igual ou superior a 20 anos. Foram avaliados padrões temporais na beta-diversidade, a fim de detectar (I) a prevalência do ganho ou perda de espécies e indivíduos nos sistemas avaliados; e (II) a contribuição de espécies residentes, imigrantes e emigrantes para mudanças no perfil térmico da comunidade, de forma a quantificar a importância relativa da dominância e dispersão para a formação das novas comunidades. O segundo capítulo consistiu na avaliação experimental dos limites e margens de segurança térmicas (MST) de uma espécie de peixe residente em estuários tropicais, o peixe-rei *Atherinella brasiliensis* (Quoy & Gaimard, 1825). A variação intraespecífica na tolerância térmica desta espécie em decorrência da heterogeneidade local na temperatura e salinidade também foi investigada. O terceiro capítulo realizou uma avaliação global de fatores antropogênicos e ambientais associados com a riqueza de espécies não-nativas em estuários, utilizando dados compilados a partir de uma abrangente revisão da literatura. A existência de uma barreira climática para a ocorrência das espécies não-nativas também foi investigada, através de correlação entre a afinidade térmica das espécies e a latitude do estuário invadido. Os resultados obtidos em cada capítulo foram discutidos de forma integrada, fornecendo direções para a criação de planos de manejo e conservação da fauna nativa e não-nativa frente às mudanças climáticas.

1. RESIDENT SPECIES, NOT IMMIGRANTS, DRIVE REORGANIZATION OF ESTUARINE FISH ASSEMBLAGES IN RESPONSE TO WARMING

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Abstract

Climate change is reshaping biological communities, as species track environmental temperature. Assemblage reorganization is underpinned by shifts in species abundance and distribution, but studies often focus on documenting compositional turnover. As consequence, phenomena such as the tropicalization of temperate communities have been widely associated with increased occupancy of warm-affinity species. Abundance-weighted change in thermal affinity can be tracked with the Community Temperature Index (CTI), and decomposed into four processes: tropicalization (increasing warm-affinity), borealization (increasing cold-affinity), deborealization (decreasing cold-affinity), and detropicalization (decreasing warm-affinity). Further evaluation of these processes according to species persistence (i.e. immigrant, emigrant and resident) may provide insights on whether novel communities emerge primarily from local shifts in species abundance or distribution. Using long-term data on fish assemblages undergoing climate change's effects across 19 temperate estuaries surveyed for at least 20 years, we hypothesized a) deborealization is the main process reshaping communities under climate change, and b) the contribution of resident species to processes reshaping communities surpass the ones from immigrants and emigrants. Community dissimilarity was calculated through the Temporal Beta Index (TBI), which was further decomposed into species and individual losses and gains. These values were then used as effect sizes in the meta-analyses performed to detect systematic trends in assemblage reorganization in response to climate change. We also calculated CTI and the strength of temperature-related processes for resident, immigrant and emigrant species. Species and individual gains outweighed losses in estuaries. Temperature was correlated with changes in species abundance, but not occurrence. Fish abundance decreased with warming, and initially cooler estuaries gained more fish than warmer ones. Novel communities were shaped by a variety of processes, but mainly tropicalization. Assemblage reorganization was primarily driven by shifts in abundance of resident species with distinct thermal affinities, while contributions of arriving and exiting species played a secondary role. These findings reveal that novel communities are drawn primarily from the local species pool, due to changes in climate-related drivers that favor distinct resident species.

Keywords: Assembly rules; Beta-Diversity; Climate change; Community Temperature Index; Deborealization; Long-term; Tropicalization

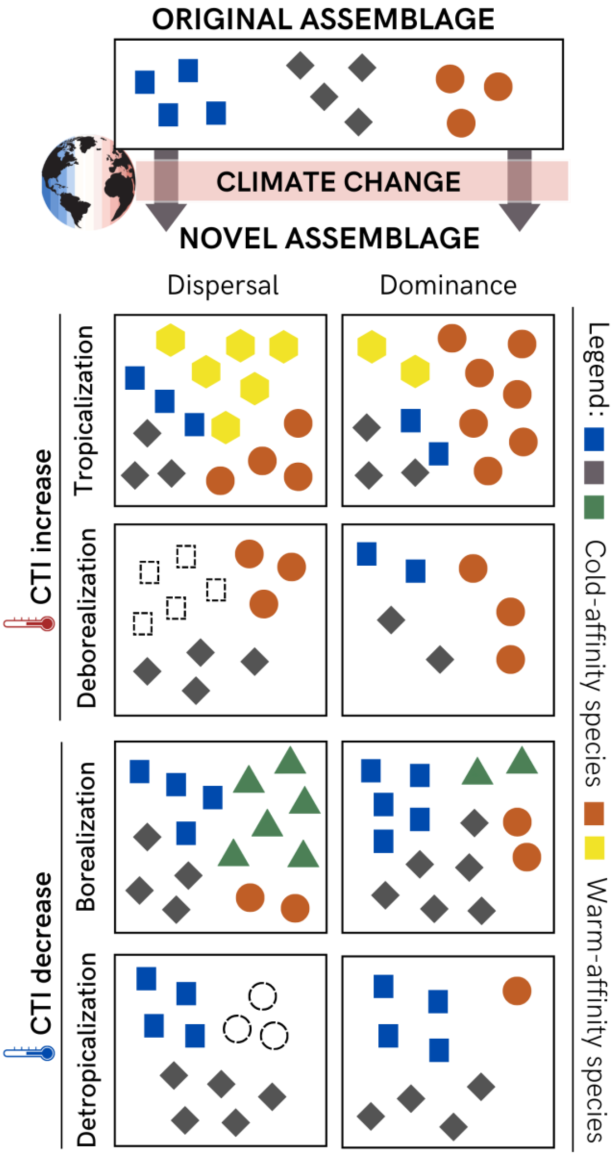
1.1 Introduction

Temporal dynamics in ecological communities have been extensively studied to unveil the mechanisms affected by global change. Assemblage-level regulation has been reported for metrics such as richness and abundance (GOTELLI et al., 2017), but not for species composition (DORNELAS et al., 2014). Change in species identity leads to novel communities, which may remain undetected by alpha diversity (VELLEND et al., 2013; DORNELAS et al., 2014; BLOWES et al., 2019). Nonetheless, comprehensive analyses of assemblage data revealed increasing richness in temperate systems (DORNELAS et al., 2014; ELAHI et al., 2015). The raise in diversity has been associated with warming in the marine realm (ANTÃO et al., 2020), and is underpinned by the influx of species tracking suitable isotherms (PINSKY et al., 2013; LENOIR et al., 2020). Colonization by species with warmer affinities has led to an increase in communities' thermal affinity (CHEUNG et al., 2013; BRICE et al., 2019; LEHIKOINEN et al., 2021), and is considered as the main driver of tropicalization in temperate ecosystems. However, recent work by MCLEAN et al. (2021) revealed this phenomenon may also be related to the loss and/or decline of cold-affinity species.

Four processes underlie assemblage reorganization in response to temperature change. These are non-exclusive (i.e. may occur concurrently in a given community), and are underpinned by temporal shifts in the relative abundance of species with distinct thermal affinities (MCLEAN et al., 2021). For instance, tropicalization and borealization are described as the increase of warm and cold-affinity species, respectively. Conversely, the decline of these respective species is known as detropicalization and deborealization. These processes result from the decomposition of the Community Temperature Index (CTI), which measures the abundance-weighted mean thermal affinity of any given community (DEVICTOR et al., 2008). Quantification of each process strength can provide a mechanistic view of temporal trends in diversity detected by synthesis studies (ANTÃO et al., 2020), and point to ecosystems' resilience (in case of tropicalization or borealization) or vulnerability (in case of deborealization or detropicalization). For instance, increases in CTI may either result from tropicalization or deborealization; however, the first process is associated with a positive balance in community change (i.e. gain outweigh loss), which could maintain productivity under future warming, despite changes in species composition. Conversely, communities wherein loss prevails (i.e. deborealization) are more prone to population crashes and local extinctions in the near future (MCLEAN et al., 2021). Prevalence of one process over the others has been associated with abiotic factors and species traits. Baseline temperature, long-term temperature change, depth and the incidence of species with high maximum thermal limits (among other characteristics) were positively associated with tropicalization. Conversely, deborealization prevails in sites close to human centers, and is positively correlated with the incidence of species with wide thermal ranges (for details on other features and processes, please see MCLEAN et al., 2021). Yet, potential relationships between species occurrence over time and their respective contributions to CTI change have not been assessed, despite their valuable insights into the role of dispersal and dominance for assemblage reorganization.

Novel communities emerge from shifts in species occurrence and abundance over time (DORNELAS et al., 2019), and both of these biodiversity components are temperature-dependent. Species thermal limits have been shown to predict their geographic ranges (SUNDAY et al., 2012; STUART-SMITH et al., 2017), while heating tolerance is tightly coupled with population size (PAYNE al., 2021). Despite their separate contributions to community change, most studies focused primarily on understanding compositional change without further looking into potential shifts in dominance (BATES et al., 2014; ANTÃO et al., 2020). As consequence, ecologists have been associating phenomena such as the tropicalization of temperate systems with increased occupancy of warm-affinity species. Novel communities would then emerge primarily via increased dispersal from the regional species pool to the local community (i.e. immigration). Nonetheless, increases in communities' mean thermal affinity could also result from a) the increased abundance of resident species with warmer affinities or b) deborealization (i.e. decline or exit of cold-affinity species; MCLEAN et al., 2021) (Figure 1). In these cases, novel assemblages would arise either from local shifts in species dominance or via increased dispersal outside the local community (i.e. emigration). Classification of species according to their occurrence across time series (i.e. migrants versus residents) could provide insights into this matter, and either a) support dispersal as the main process shaping the novel communities, in accordance with a growing number of studies reporting distribution shifts (PINSKY et al., 2013; LENOIR et al., 2020); or b) reveal its minor role compared to shifts in abundance of resident species, as persistence over time is positively correlated with species dominance (MAGURRAN; HENDERSON, 2003).

Figure 1 - Conceptual figure combining CTI change, the temperature-related processes and species-level mechanisms underlying assemblage reorganization.



Legend: CTI increase can result from either tropicalization or deborealization, whereas CTI decrease can be attributed to either borealization or detropicalization. Each of these processes may develop primarily from shifts in species dispersal (left column) or dominance (right column). In the first case, migrant species would have the greatest contribution to processes driving change; in the second case, community change would be driven by shifts in abundance of resident species.
Source: The author, 2022.

Here, we assessed the main temperature-related process (i.e. tropicalization, borealization, detropicalization, deborealization) and group of species (i.e. immigrants, emigrants and residents) driving community change, using long-term data on estuarine fish assemblages surveyed for at least 20 years. Our framework combined beta-diversity, meta-analyses, CTI decomposition and the evaluation of process strength at species-level, to examine the importance of shifts in species distribution (i.e. dispersal) and abundance (i.e. dominance) for communities under climate change. To accomplish this goal, we divided the time series into early and late periods, and labeled species according to their occurrence: resident – present during both periods; immigrant – present in the late period; or emigrant – present in the early period. We hypothesized a) deborealization is the primary process reshaping communities, leading the loss of species and individuals in estuaries, and b) the contribution of resident species to the temperature-related processes driving community change surpass the ones from immigrants and emigrants. Our expectations regarding the key role of deborealization over the other processes (including the often-reported tropicalization) were related to estuaries' heat-conservative properties, which may accentuate fish assemblage's exposure to warming, leading to a negative balance between losses and gains. Nonetheless, the great thermal ranges commonly exhibited by resident species inhabiting these dynamic systems (ELLIOTT et al., 2007) may favor their persistence over time, despite declines in abundance.

1.2 Materials and methods

1.2.1 Search strategy

A literature search was conducted using Scopus, Web of Science and Google Scholar online databases, applying the keywords: [Climate Change OR Global Warming OR Warming OR Climate Warming OR Changing Climate] AND [Long-term] AND [Fish assemblage OR Ichthyofauna OR Fish species] AND [Estuar*]. Search string development was an iterative process conducted on the aforementioned platforms, and the chosen combination presented the best balance between comprehensiveness and relevance (see details on Appendix S1). As climate change is a subject of increasing interest in the scientific community, the number of studies on the topic is scaling up, but we found that only a few have assessed the relationship between climate-mediated drivers and fish assemblages in estuaries. Therefore, we added [Long-term] and level of organization (i.e. assemblage, ichthyofauna and species) to our search string, which increased the number of relevant entries for the meta-analysis (Appendix S1). Publications retrieved from the search were screened, and those that met the established criteria (see section 2.2) were compiled into a database. We also screened the references list of all retrieved studies for eligibility and included additional articles in our review whenever they fitted our criteria. Paleoclimatic and fishery-based studies were excluded from our database, as we were interested in current effects of climate change on fish assemblages and not just commercial species.

1.2.2 Article screening and eligibility

The screening process was divided in two parts: first, the title and abstract were examined for the following criteria: 1) Relevant subject, i.e. long-term changes in estuarine fish communities; 2) Relevant exposure, i.e. surveys performed for a minimum of 20 years, whether continuously or not; and 3) Relevant outcome, i.e. availability of ecological data such as species occurrence and abundance. We established 20 years of sampling as the minimum time scale for selecting studies, since estuarine fish assemblages are very dynamic due to the occurrence of species from several guilds of functional use (marine and freshwater stragglers and migrants, anadromous and catadromous, among others; ELLIOTT et al., 2007), which may conceal long-term trends, even with a decade of data (VAN DER VEER et al., 2015; JAMES et al., 2018). Studies with a discontinuous time series were also kept in the screening process, as several authors reported that fish assemblage similarity is higher between closer years and declines over time (COLLIE et al., 2008; HOWELL & AUSTER, 2012; OLSSON et al., 2012); therefore, discontinuous samples far apart in time would still reveal shifts in community structure and composition. Articles that fit these criteria were then forwarded to the second part of the screening process, and had their full-texts reviewed. At this stage, articles were critically appraised in search of the following information: 1) Relevant subject (see description above); 2) Relevant study design, i.e. similar fishing gear must have been employed during all surveys, which must also have been performed in the same areas within the estuary; 3) Relevant exposure (see description above); 4) Relevant results, i.e. studies must have tested and found a statistical association between climate-mediated drivers and community change; and 5) Relevant outcome (see description above). Studies that met all these criteria were then compiled into a database. Statistically significant results were included as eligibility criterion, as we aimed to identify the ecological processes underpinning community reorganization in response to climate change. Therefore, studies must have reported an explicit effect of climate-related drivers on the fish assemblage, rather than just documenting changes in species occurrence and abundance over time (e.g. some studies retrieved by the search presented trends for temperature and assemblage descriptors, but did not test whether these were correlated; Appendix S2: Table 6). We are aware that statistical correlations may be biased by sample size, and thus excluding studies that did not find a relationship between environmental drivers and community change may narrow our results. However, we decided to adopt such conservative approach and retain the statistical test as a criterion, to increase confidence that trends reported herein are climate-driven. We also excluded studies performed with the same dataset, to avoid bias related to duplicated data (Appendix S2: Table 6). Studies with the longest time series were kept in the compiled database.

1.2.3 Data extraction and transformation

Fishing gear type, number of samples, fish position at the water column and life stage, taxonomic richness, species occurrence and abundance, statistical analysis performed in the study and significant explanatory variables, were extracted from the final set of articles. If these data were unavailable, the corresponding author was contacted twice. Failure to respond to these contact attempts or refusal to hand over the data led to study exclusion from the database (Appendix S2: Table 6). Data from each study was provided for a distinct sample unit (i.e. values for each survey replicate, month or year), and grouped in two time periods: early and late. These periods were defined according to the year of community shift described in the original paper. For instance, COLLIE et al. (2008) detected a major shift of the fish assemblage at Whale Rock, Narragansett Bay, between 1980 and 1981; therefore, the early and late periods comprised data before and after 1980, respectively. We adopted this approach for three main reasons: first, midpoint was not available for some studies with a discontinuous time series; second, pooling data into early and late periods reduces the likelihood of overestimating changes in species occurrence and abundance in contrast to adopting a single baseline year (e.g. first year of sampling); and third, most original studies tracked community change over time using ordination methods, which favors the establishment of early and late assemblages based on similarity, rather than as result of randomly splitting the time series. Abundance data were converted to densities (number of individuals per 100 m^2) to avoid bias, as the sampling effort (i.e. number of samples and total area sampled) between the early and late periods was different for some studies included in the review. Conversion of abundance data to density represents a suitable method for standardizing unbalanced sampling efforts in estuaries (NICOLAS et al., 2010; HOLLWEG et al., 2020), and represents an alternative to downsampling procedures, which require data at sample unit level (an information that, unfortunately, was not available for all studies in our database).

Mean temperature values for the early and late periods were also extracted from the screened articles. Geographical coordinates of each estuarine system were obtained from Google Earth (http://www.google.fr/intl/fr/earth/index.html), and marine realm was identified according to SPALDING et al. (2007). Species cited on the retained publications were verified for terminology updates using the Eschmeyer's Catalog of Fishes online database (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp; FRICKE et al, 2020).

1.2.4 Temporal change in fish assemblages

Community change was evaluated through the Temporal Beta Index (TBI; LEGENDRE, 2015). The TBI measures the dissimilarity (*D*) in community composition between the first (i.e. early period) and second (i.e. late period) surveys performed at a particular system, and has been considered a valuable tool for assessing anthropogenic impacts such as climate change (LEGENDRE, 2019). Dissimilarity varies between 0 and 1, and can be further decomposed into losses (B) and gains (C), thus revealing the quantitative importance of each ecological process in shaping the novel assemblage (LEGENDRE, 2015; 2019). TBI values were calculated based on species occurrence and abundance (i.e. density) matrices, using the *TBI.R* function (LEGENDRE, 2015) in the *adespatial* package (DRAY et al., 2020) for the R software (R CORE TEAM, 2020). The percentage difference index ($D_{\%diff}$, also known as the Bray-Curtis index in other computer packages) was chosen for calculating dissimilarity, due to suitability for both occurrence and abundance data (LEGENDRE, 2019). Dissimilarity values were calculated for each estuary separately unless systems were interconnected (i.e. sites at Narragansett Bay and some bays in Texas coast). In the latter case, we also produced B-C plots (i.e. which show the relative importance of loss and gain processes in a study area) to identify whether adjacent sites share similar responses to climate change (e.g. all sites gained species) or not (e.g. some sites gained species while others lost) (LEGENDRE, 2019).

1.2.5 Meta-analysis

Three-level meta-analyses were conducted to identify whether climate change is leading to the loss or gain of fish species and individuals in estuaries. TBI gain and loss values were each used as the observed effect sizes for the meta-analyses performed, while sampling variance was calculated as: *1/Ntotal - |Npre-warming - Npost-warming|*. We adopted this innovative approach for three main reasons: first, solely looking at temporal differences in richness and total abundance may conceal community shifts, since several studies reported little change in these descriptors across years (OLSSON et al., 2012; GOTELLI et al., 2017; CROSBY et al., 2018); second, the risk and odds ratio methods would not detect changes in species abundance (i.e. dominance); and third, community studies often perform multivariate statistical analyses, which returns non-linear coefficients that are inappropriate for conversion to the Fisher's z scale (HUNTER; SCHMIDT, 1990).

We calculated the mean effect sizes for species and individual gains and losses using the random effects model with maximum-likelihood estimation (i.e. “REML”) in the *metafor* package (VIECHTBAUER, 2010). To control for potential non-independence of effect sizes among studies performed in proximate areas (i.e. spatial autocorrelation; e.g. COLLIE et al., 2008; PAWLUK et al., 2021), we nested “estuary” within “ecoregion” (BATES et al., 2015; NAKAGAWA et al., 2017). Model heterogeneity (I^2) was partitioned between two sources: variance explained by I) estuary and II) ecoregion, using the *dmetar* package (HARRER et al., 2019). Additionally, we reran the models using long-term temperature change (i.e. difference between early and late period values) and baseline temperature (i.e. mean value recorded in the early period) as moderators (VIECHTBAUER, 2010), since all studies in our database found an association between temperature and community change. Then, we compared the Corrected Akaike Information Criterion (AICc; BROCKWELL; DAVIES, 1991) and the percentage (%) of reduced variance exhibited by models with moderators, in order to assess the relationship between temperature and fish gain and loss. The model with the lowest AICc value and highest % of reduced variance was retained for analysis; however, if the difference between AICc values of models was lower than 4, these were considered as indistinguishable (MAZEROLLE, 2016) and the retained model was chosen based only on the % of reduced variance. Despite a subset of studies also reported an effect of variables other than temperature (e.g. salinity, sea level; see Table 1) on fish assemblages, these were not included as moderators in the meta-analyses due to lack of adequate sample size (i.e. number of entries per predictor). The number of missing studies (fail-safe N) was calculated to check for bias and outliers in the dataset using the methods proposed by ROSENTHAL (1979) and ROSENBERG (2005), which are available in the *metafor* package for the R software (R CORE TEAM, 2020).

1.2.6 Community Temperature Index (CTI) and process strength

Fish assemblage mean thermal affinity was calculated for the early and late periods, and the entire time series of each estuary, through the Community Temperature Index (CTI; MCLEAN et al., 2021). In CTI, species thermal affinity is weighted by its observed abundance (hereby, density; DEVICTOR et al., 2008); therefore, changes in CTI are related not only to shifts in species occurrence, but also in their dominance. Species thermal affinity (STI) was estimated by overlapping occurrence data and mean sea surface temperature (SST; ^{o}C), which were extracted from the Global Biodiversity Information Facility (GBIF, 2022; http://www.gbif.org/) and BioOracle (https://www.bio-oracle.org/; TYBERGHEIN et al., 2012; ASSIS et al., 2018) databases, respectively. Occurrence records were tested for duplicates, equal coordinates, validity, zeros, capitals, centroids, gbif, institutions and urban areas, using the *clean_coordinates* function in the *CoordinateCleaner* package (ZIZKA et al., 2019). Flagged records were then removed from the dataset. The *sp* (PEBESMA; BIVAND, 2005; BIVAND et al., 2013) and *rgdal* (BIVAND et al., 2021) packages were used to transform species occurrence data from csv to shapefile format, and to create a polygon delimiting each species range of occurrence; then, mean SST values were extracted for each polygon using the *extract* function in the *raster* package (HIJMANS; VAN ETTEN, 2012) for the R software (R CORE TEAM, 2020).

Next, species thermal affinity (STI) was weighted by its density, which was calculated using the total abundance of each period (i.e. single value obtained from pooling samples within each period). The resulting values were then summed up and divided by total density (i.e. combined density of all species recorded in each period), determining CTI. CTI change was calculated as the difference between late and early CTI, whereas CTI based on the full time series was used to sort species as either warm- (i.e. STI > CTI full time series) or cold-

(i.e. STI < CTI full time series) affinity, following the methods proposed by MCLEAN et al. (2021). This classification was applied to assess the strength of each process (i.e. tropicalization, borealization, detropicalization and deborealization) underlying CTI change across periods. First, we calculated the difference in species density between late and early periods. Next, we multiplied this value by the difference between species thermal affinity (STI) and CTI based on the full time series. Process strength was determined by summing up the resulting values for all species within four categories: 1) tropicalization – warm-affinity species which increased in density; 2) detropicalization – warm-affinity species which decreased in density; 3) borealization – cold-affinity species which increased in density; and 4) deborealization – cold-affinity species which decreased in density (for more details see MCLEAN et al., 2021). We further decomposed the strength of each process among resident (i.e. present during the early and late periods), immigrant (i.e. recorded only in the late period) and emigrant (i.e. recorded only in the early period) species, in order to assess the contribution of each group to assemblage reorganization. Permutational Analysis of Variance (PERMANOVA) was applied on the log10 x transformed strength values to detect the main process and group of species assembling the novel communities. We adopted a mixed-model design with "process" and "group of fish species" as fixed-factors, and nested "estuary" within "ecoregion" to control for potential spatial autocorrelation. Euclidean dissimilarity distance (1000 permutations) was used for the PERMANOVA tests, which were performed using the *adonis2* function in the *vegan* package (OKSANEN et al., 2020) for the R software (R CORE TEAM, 2020).

1.3. Results

1.3.1 Review descriptive statistics

The literature search retrieved 4,327 articles, of which 48 were screened at full-text. Details on the screening process and the list of studies screened at full-text with reasons for its inclusion or exclusion from the review can be found in Appendix S2: Figure 15 and Table 6. The final dataset consisted of 10 articles published between years 2008 and 2021, encompassing 19 estuaries (Table 1; Appendix S2: Table 6 and Figure 15). Estuaries were located in temperate realms (covering |23° to 60°| degrees in latitude) mainly in the northern hemisphere, whereas the southern region was poorly represented in the data (Figure 2; Table 1). Fish assemblages were sampled using six types of gear, starting in 1959 (early period in the Narragansett Bay) and ending in 2016 (late period for the North Inlet and the Norwalk Harbor). The compiled articles recorded a total of 380 fish species; CLOERN et al. (2010) captured the lowest number of species (S=11) at the San Francisco Bay, while ARAÚJO et al. (2018) surveyed 117 species at Sepetiba Bay (Appendix S2: Table 7). Fish assemblages were composed of pelagic, benthopelagic and demersal species, excepting at the North Inlet (only pelagic and benthopelagic species), the San Francisco Bay (only demersal species) and the Norwalk Harbor (only demersal species). Also, communities assessed by PAWLUK et al. (2021) in bays of Texas were composed exclusively of adult fishes.

Studies reported major community shifts between the mid 80's and the end 90's, excepting for the Norwalk Harbor at the Long Island Sound (Table 1). These shifts were primarily associated with temperature and regional climate such as the North Atlantic Oscillation (NAO) and the North Pacific Gyre Oscillation (NPGO), but also to changes in salinity, sea level, dissolved oxygen and proportion of hypoxic days, chlorophyll-a concentration, presence of top predators, habitat degradation and pollution. Long-term temperature change ranged from 0.50°C at Narragansett Bay to 1.71°C at the North Inlet, while baseline temperature varied from 5.56°C at Kattegat to 27.24°C at the Lower Laguna Madre, in the Northern Gulf of Mexico (Table 1).

Table 1 - Estuary (decimal coordinates), survey years (early and late periods), explanatory variables, long-term temperature change (^{o}C) and baseline temperature (^{o}C), extracted from each study included in the present review.

Study	Estuary	Survey years	Explanatory variables	Temperature	
				Change	Baseline
Kimball et al., 2020	North Inlet (33.327011, -79.167301)	Early: 1981 to 1984 Late: 2013 to 2016	Mean temperature (annual)	1.7	18.4
Araújo et al., 2018	Sepetiba Bay (-23.000671, -43.914823)	Early: 1983 to 1985 and 1993 to 1999 Late: **2000** to 2006 and 2011 to 2015	Mean temperature (annual)	0.9	26
Howell & Auster, 2012	Long Island Sound (41.101207, -72.871826)	Early: 1984 to 1998 Late: **1999** to 2008	Mean temperature (spring; autumn)	0.55	9.29
Henderson et al., 2011	Bridgewater Bay (51.213902, -3.142063)	Early: 1981 to 1985 Late: **1986** to 2009	Mean temperature (annual), salinity, NAO	1.36	12.08
Olsson et al., 2012	Kattegat (Vendelsö) (57.30475, 12.158173)	Early: 1976 to 1986 Late: **1987** to 2008	Mean temperature (annual), NAOw	0.68	5.56
	Baltic Proper (Kvädöfjärden) (58.050266, 16.774174)		Mean temperature (annual), salinity, NAOw	0.52	8
	Bothnian Sea (Forsmark) (60.399444, 18.18875)		Mean temperature (annual; spring), salinity, NAOw	1.23	16.33
Pawluk et al., 2021	Sabine Lake (29.877478, -93.851353)	Early: 1986 to 1994 Late: **1995** to 2008	Mean temperature (spring, autumn), salinity, sea level, dissolved oxygen	1.19	25.28
	Galveston Bay (29.510513, -94.847889)			0.61	26.32
	Matagorda Bay (28.564323, -96.312273)			0.99	26.2
	San Antonio Bay (28.300768, -96.72836)			1	26.25

	Aransas Bay (28.072052, -97.001494)			0.8	26.97
	Corpus Christi Bay (27.771875, -97.262627)			0.95	26.45
	Upper Laguna Madre (27.281196, -97.442972)			0.59	27.12
	Lower Laguna Madre (26.400829, -97.315607)			0.6	27.24
Crosby et al., 2018	Norwalk Harbor at Long Island Sound (41.09265, -73.407723)	Early: 1990 to 2005 Late: **2006** to 2016	Mean temperature (annual), salinity, dissolved oxygen, proportion of hypoxic days	1.26	20.45
Cloern et al., 2010	San Francisco Bay (37.806234, -122.351122)	Early: 1980 to 1998 Late: **1999** to 2008	NPGO	-	-
Collie et al., 2008	Narragansett Bay: Fox Island (FI) and Whale Rock (WR) (41.554167, -71.41752)	FI - Early: 1959 to 1984 Late: **1985** to 2005 WR - Early: 1959 to 1979 Late: **1980** to 2005	Mean temperature (annual, spring, summer), chlorophyll-a concentration, NAOw	0.5	11.1
Van der Veer et al., 2015	Mokbaai (53.004041, 4.764133)	Early: 1960 to 1984 Late: **1985** to 2011	Mean temperature (summer), chlorophyll-a concentration, NAOw, nitrogen and phosphorus loadings, sand mining and beach nourishment, top predator	0.8	16.5

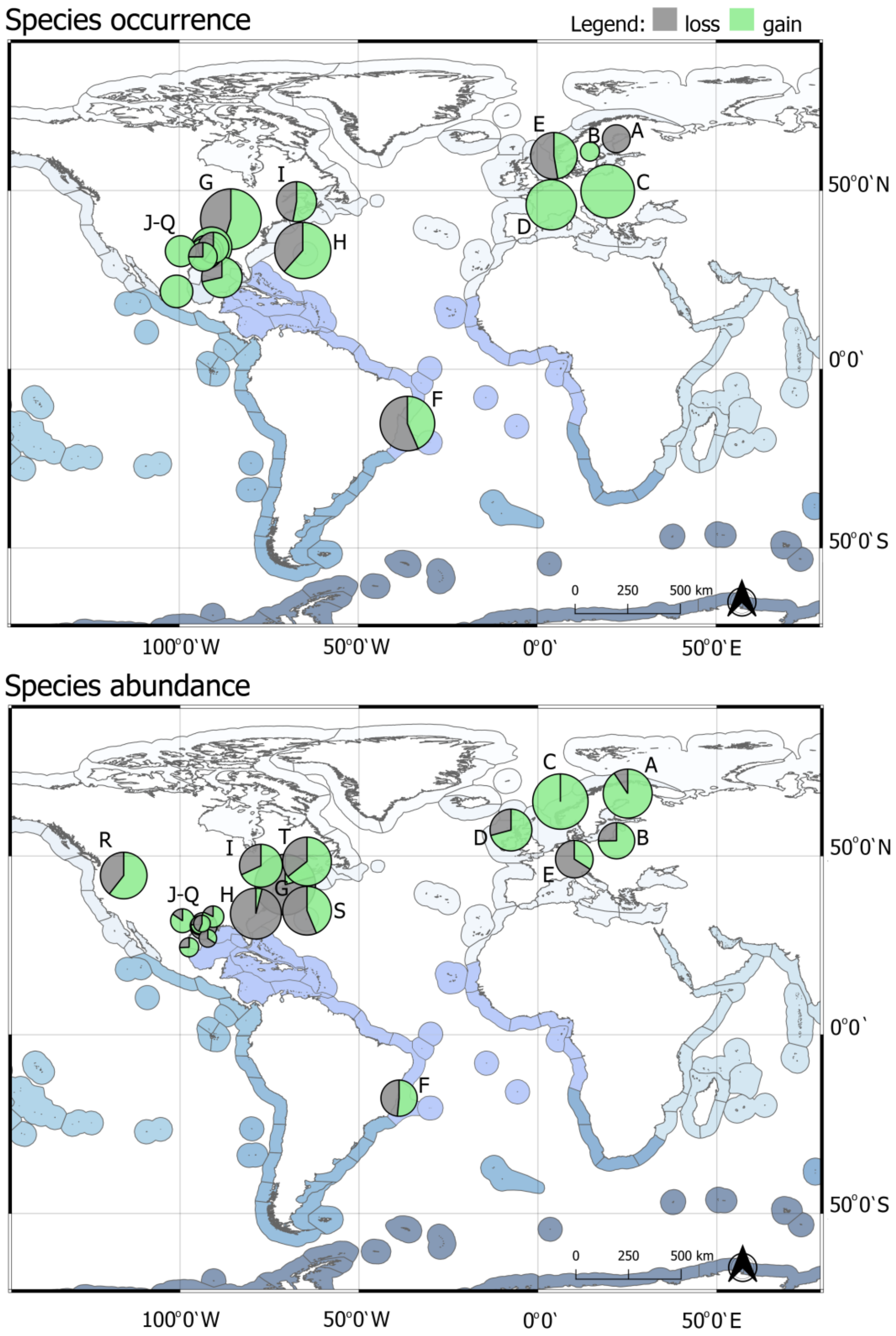
Legend: The year of community shift described in each paper is indicated in bold. NAO = North Atlantic Oscillation Index, NAOw = North Atlantic Oscillation Index (winter), NPGO = North Pacific Gyre Oscillation.

1.3.2 Temporal change in fish community

Temporal Beta-Index (TBI) values were higher for fish abundance (i.e. density; ranging from *D* = 0.06 to 0.77) than for occurrence (ranging from *D* = 0.02 to 0.25), revealing a greater shift in species dominance rather than composition (Fig. 2; Appendix S2: Table 8). The highest TBI values were recorded at the North Inlet, for both occurrence (*D* = 0.25) and abundance (*D* = 0.77) data. Dissimilarity in species abundance was also high at Kattegat (*D* = 0.64), and for species occurrence at the Norwalk Harbor (*D* = 0.21) and Sepetiba Bay (*D* = 0.2). Systems with the lowest values were located in southern North America, between 26°N and 29°N latitude (Fig. 2). The Baltic Proper (58°N latitude) also showed little dissimilarity in species occurrence (0.02) across the early and late periods (Appendix S2: Table 8).

Gains were higher than losses for most estuaries evaluated, excepting for Mokbaai (species occurrence and abundance data); the North Inlet, Norwalk Harbor, Fox Island at the Narragansett Bay, Lower Laguna Madre and Galveston Bay (species abundance data); and the Bothnian Sea and Sepetiba Bay (species occurrence data; Fig. 2; Appendix S2: Table 8). Species turnover was also quite balanced at the Long Island Sound and Corpus Christi Bay, as these systems showed nearly equal values between gain and loss components. Adjacent bays in the coast of Texas (Fig. 2, letters J-Q) shared similar responses to climate change, excepting for species abundance data at Galveston Bay. Overall, sites gained more species and individuals than lost. Adjacent sites in Narragansett Bay showed distinct responses to climate change; loss of individuals prevailed at Fox Island, whereas gain was observed at Whale Rock (Appendix S2: Figure 16).

Figure 2 - Map of Temporal Beta-Index (TBI) values, showing the loss (gray) and gain (green) components for each site evaluated in the present review, using species occurrence and abundance data.



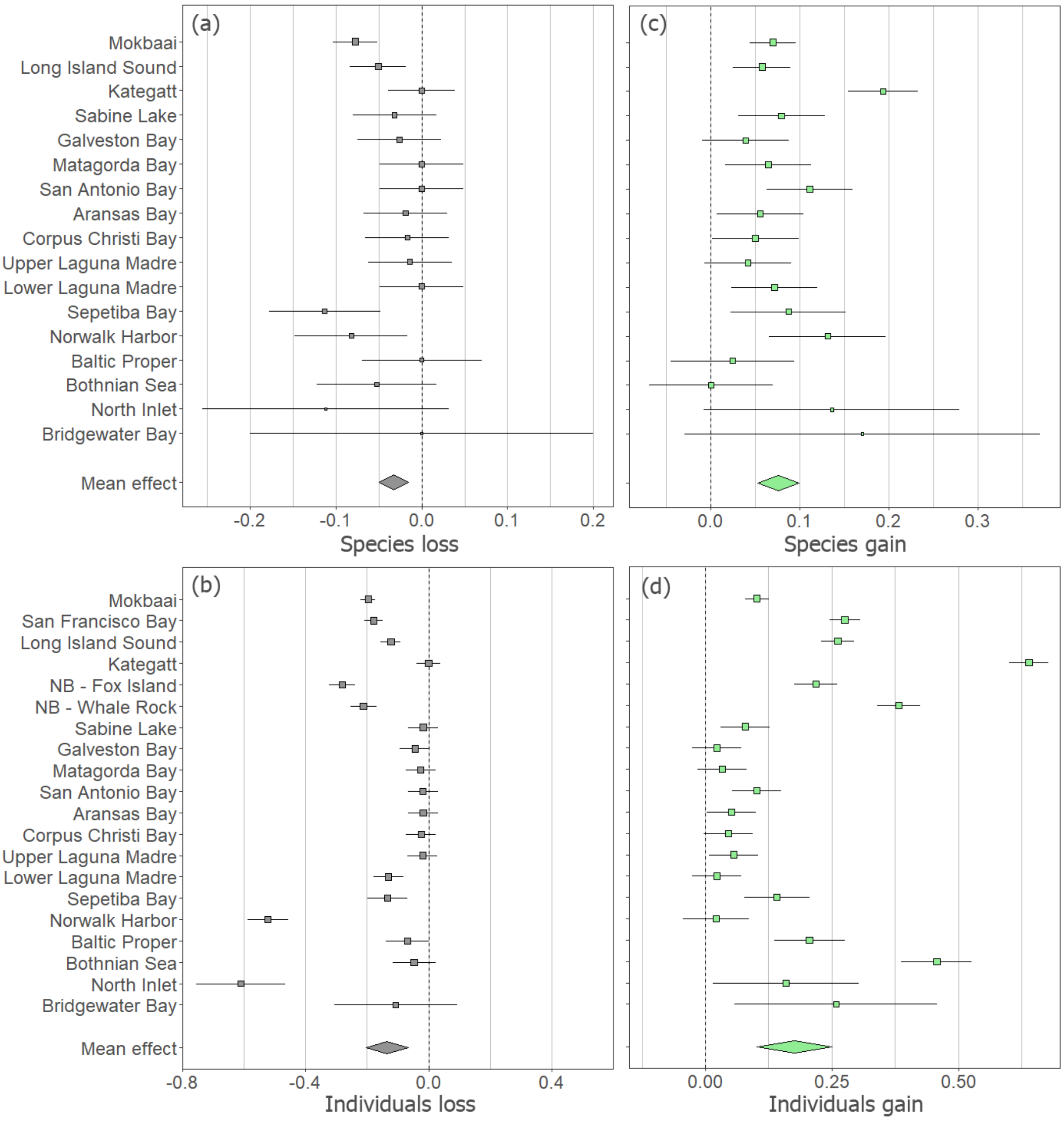
Legend: Gray = loss; green = gain. Circles are scaled according to TBI values. Blue shaded areas represent the marine realms established by SPALDING et al. 2007. Letters indicate estuarine systems evaluated in the present review: A – Bothnian Sea; B – Baltic Proper; C – Kattegat; D – Bridgewater Bay; E – Mokbaai; F – Sepetiba Bay; G – North Inlet; H – Norwalk Harbor; I – Long Island Sound; J to Q - bays in the coast of Texas; R - San Francisco Bay; S – Narragansett Bay (Fox Island); T – Narragansett Bay (Whale Rock). Notice that TBI values based on fish species occurrence at Narragansett Bay and São Francisco Bay are not shown, since these studies only reported the occurrence of the most frequent fish species (FO%>95%).
Source: The author, 2022.

1.3.3 Meta-analysis

Mean effect sizes differed significantly from zero for species (loss: mean effect size=-0.04, p=0.001; gain: mean effect size=0.08, p<0.001) and individual (loss: mean effect size=-0.17, p=0.003; gain: mean effect size=0.21, p<0.001) meta-analyses (Figure 3). Estimates were higher for gains rather than losses (Figure 4), revealing a long-term increase in the number of fish species and individuals in temperate estuaries. The Q-test detected significant heterogeneity for species (loss: I^2=56.42%, Q(df=16)=32.09, p=0.01; gain: I^2=74.82%, Q(df=16)=55.52, p<0.0001) and individual (loss: I^2=98.21%, Q(df=19)=463.08, p<0.0001; gain: I^2=98%, Q(df=19)=1032.5268, p<0.0001) meta-analyses. Variance between estuaries within an ecoregion (I^2=45.88% - 65.44%) was higher than between ecoregions (I^2=28.95% - 32.56%) for species and individual gain meta-analyses, whereas the opposite pattern was observed for species and individual loss meta-analyses (I^2=20.35% - 30.64% within ecoregions; I^2= 36.06% - 67.57% between ecoregions).

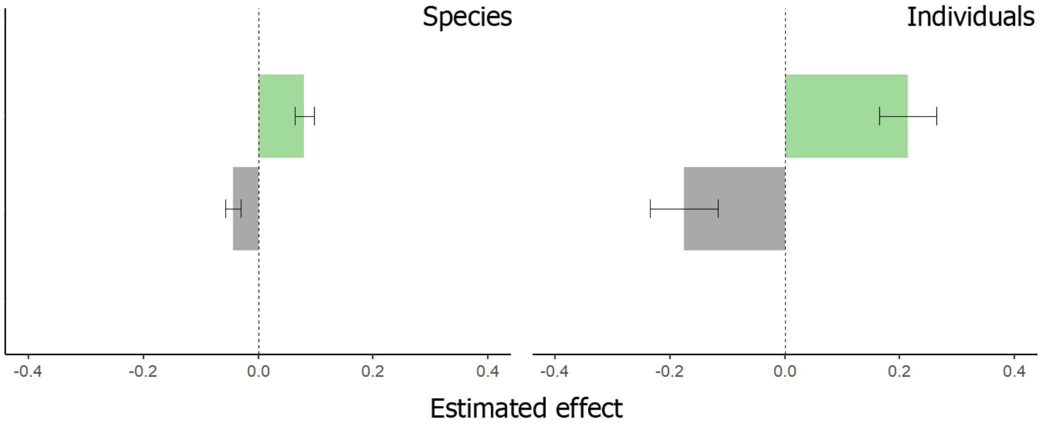
Heterogeneity was partially explained by long-term temperature change (mean effect size=-0.18, p=0.04) and baseline temperature (mean effect size=-0.02, p<0.0001) in the individual loss (QM(df=1)=4.03, p=0.04) and gain (QM(df=1)=15.96, p<0.0001) meta-analyses, respectively. Inclusion of these covariates in the models reduced variance by 15.80% and 42.23% (Table 2). Individual loss was positively correlated with warming (Figure 5), and prevailed as the main driver of community change in estuaries such as the North Inlet and Norwalk Harbor (Fig. 3). Further, increases in fish species abundance were more pronounced in initially cooler estuaries, such as the Baltic Proper and the Long Island Sound (Fig. 3, 5). Residual heterogeneity was detected for both loss (I^2=82.42%, QE(df=17)=450.7237, p<0.0001) and gain (I^2=55.77%, QE(df=17)=540.9812, p<0.0001) meta-analyses even after accounting for the temperature-related covariates. Variance between estuaries within an ecoregion (I^2=55.76%) was higher than between ecoregions (I^2==0%) in the individuals gain meta-analyses; the opposite pattern was detected for the individuals loss test (I^2=29.48% - 52.94% within and between ecoregion, respectively). Regarding occurrence data, neither the loss nor gain of species were significantly correlated with long-term temperature change (QM(df=1) = 1.1090 - 1.8416, $p \geq 0.1748$) and/or baseline temperature (QM(df=1)= 2.4886 - 0.3007, $p \geq 0.1147$), and therefore initial models (i.e. without covariates) were retained for analysis (Table 2). These results were robust to publication bias, since Rosenthal's (species loss=165; species gain=903; individual loss=3,857; individual gain=7,950) and Rosenberg's fail-safe N (species loss=152; species gain=724; individual loss=3,254; individual gain=6,868), revealed a high number of studies would be necessary to reduce the significance level of mean effect sizes to >0.05.

Figure 3 - Species and individual losses (a-b) and gains (c-d) in response to climate change, as revealed by a three-level mixed-effects meta-analysis.



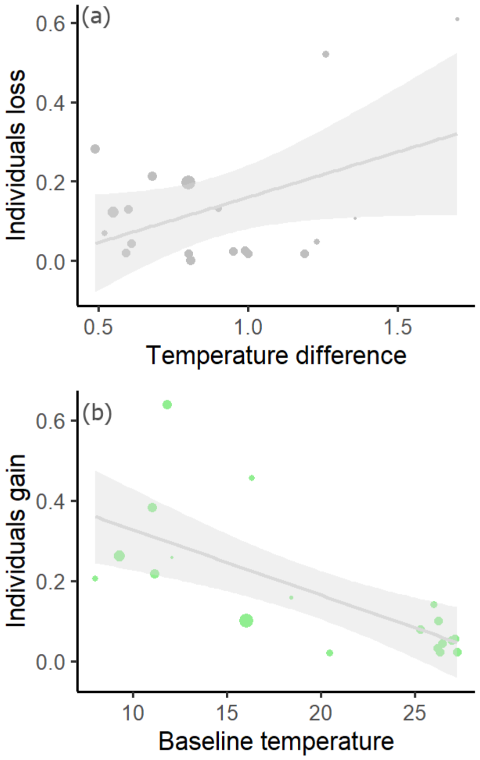
Legend: Losses = a and b panels; Gains = d and e panels. Studies are ordered by sampling variance. Squares represent the estimated effect size and black lines represent the 95% confidence interval within each study. Polygons at the bottom of each graph indicate the mean effect sizes. Notice that data from the Narragansett Bay (i.e. NB – Fox Island and NB – Whale Rock) and São Francisco Bay are not shown in the species gain and loss meta-analyses, since these studies only reported the occurrence of the most frequent fish species (FO%>95%). Source: The author, 2022.

Figure 4 - Species and individual gains (green) and losses (gray) in response to climate change, as revealed by three-level mixed-effects meta-analyses.



Legend: Gains = green; losses = gray. Bars represent the mean effect sizes and whiskers indicate the standard errors. Polygon at the bottom of each figure represents the mean effect size, and polygon width represents the standard errors.
Source: The author, 2022.

Figure 5 - Observed effect sizes of individuals loss (gray) and gain (green) meta-analyses in response to long-term temperature change (a) and baseline temperature (b).



Legend: Loss = gray; Gain = green. Point size is scaled according to study weight and light gray-shaded areas represent the 95% confidence interval.
Source: The author, 2022.

Table 2 - Corrected Akaike Information Criterion (AICc) and percentage of reduced variance for species and individual gain and loss meta-analyses.

Model		**Without moderators**	**Long-term temperature change**	**Baseline temperature**	**Long-term temperature change and baseline temperature**
Species loss	**AICc**	**-53**	-45.9787	-46.8426	-45.9787
	% of reduced variance	**-**	0	0	0
Species gain	**AICc**	**-42.0671**	-38.6226	-38.8904	-30.6101
	% of reduced variance	**-**	0	0	0
Individuals loss	**AICc**	-11.5991	**-10.4151**	-12.5782	-5.8428
	% of reduced variance	-	**15.80%**	0	0
Individuals gain	**AICc**	-10.6048	-3.4523	**-10.8292**	-4.9486
	% of reduced variance	-	0	**42.23%**	41.89%

Legend: The model retained for analysis is indicated in bold.

1.3.4 Community Temperature Index and process strength

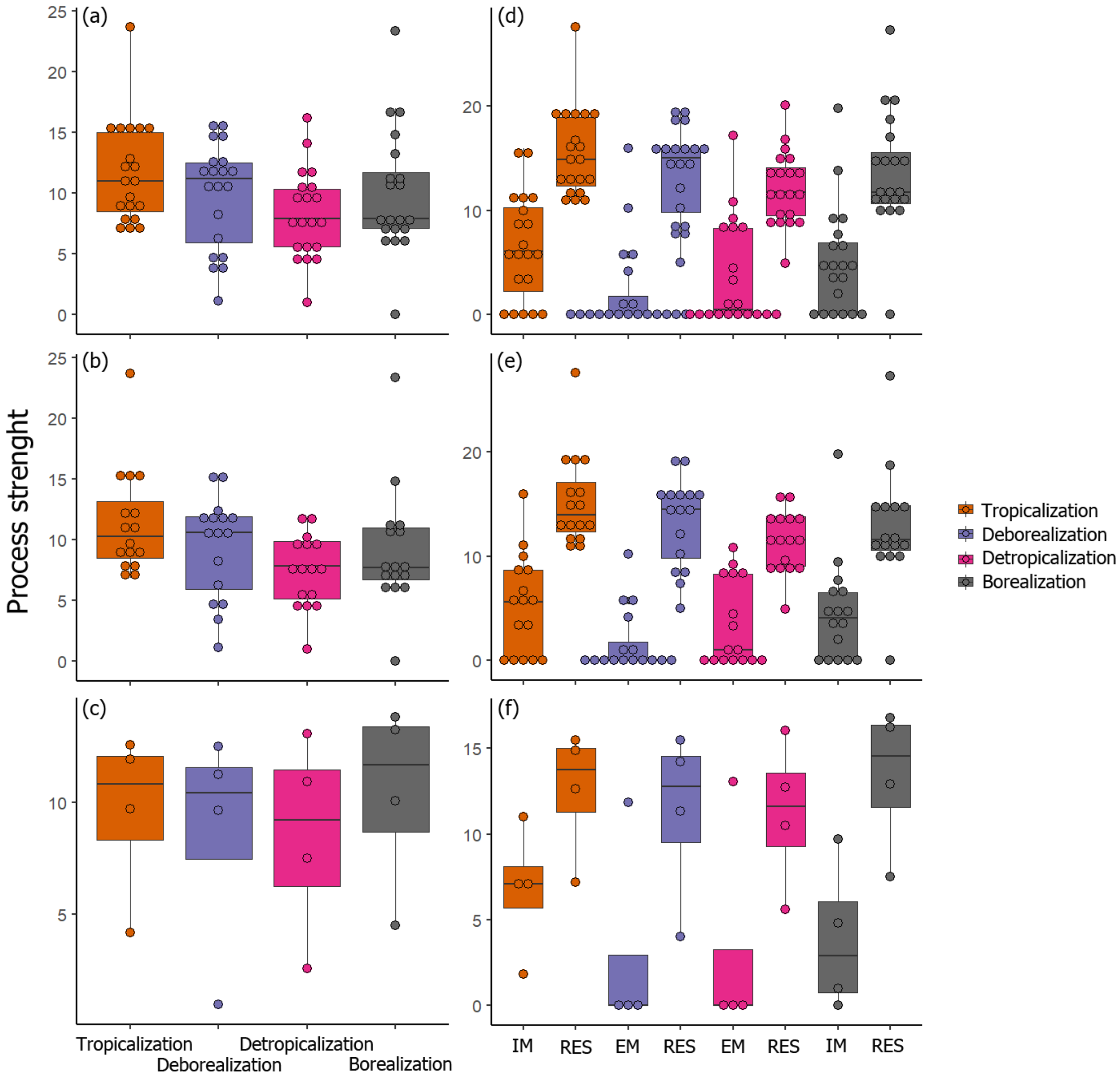
Fish assemblages' mean thermal affinity (CTI) changed across time periods in the 19 estuaries evaluated (Table 3). Increases in CTI were noticed for 16 systems, and ranged from 0.004 to 1.65. However, half of these communities showed a subtle increase in CTI of less than 0.1°C. Fish assemblages at three estuaries located in eastern North America exhibited the largest increases in CTI, reaching over 1°C. Tropicalization was the main process underlying community change in ten sites where CTI increased (F(3,54)=2.33, p=0.01; Figure 6), including two out of the four estuaries that warmed the most, i.e. Long Island Sound and Whale Rock at Narragansett Bay. Nonetheless, deborealization prevailed in the remaining six fish assemblages with increased CTI, namely at the Norwalk Harbor, Fox Island at Narragansett Bay, North Inlet, Galveston Bay, Lower Laguna Madre and Mokbaai. Decreases in community mean thermal affinity (CTI) were observed at three locations, and values ranged from -0.19 to -0.004. Borealization was the main process shaping the novel communities in all sites, with exception for the Sepetiba Bay (Table 3), but this pattern was not statistically significant (F(3,16)=0.16, p=0.32; Fig. 6). Differences in CTI and the processes shaping the novel fish assemblages were also noticed for adjacent bays in Texas coast, but Galveston Bay was the only estuary among them where deborealization and loss of individuals prevailed (Appendix S2: Figure 16).

Tropicalization was also the strongest process underlying community change across all sites (i.e. estuaries with increased and decreased CTI; F(3,76)=1.96, p=0.01). Resident species contributed most to each and every one of the four temperature-related processes (Fig. 6), while immigrants and emigrants played a secondary role (all estuaries: F(7,152)=25.09, p=0.0009; increased CTI: F(7,112)=22.92, p=0.0009; decreased CTI: F(7,32)=3.30, p=0.0009). Tropicalization was also the strongest process underlying community change across all sites (F(3, 68)=1.34, p=0.04), and sites with increased CTI (F(3,52)=1.60, p=0.05), when we reran analyses excluding data from the San Francisco and Narragansett bays (Appendix S2: Figure 17), which only comprised the most frequent species in the assemblage (FO>95%). These tests also revealed resident species had the greatest contribution to the four temperature-related processes underlying CTI change (F(7,136)=16.6, p<0.001 for all sites; F(7,104)=13.45, p<0.001, for sites with increased CTI).

Table 3 - Temperature-related process and fish group that contributed the most to changes in the Community Temperature Index (CTI) per estuary.

Estuary	**CTI change**	**Process**	**Fish group**
Bridgewater Bay	-0.192	Borealization	Residents
Sepetiba Bay	-0.153	Detropicalization	Emigrants
Matagorda Bay	-0.01	Borealization	Residents
Baltic Proper	-0.004	Borealization	Residents
Sabine Lake	0.004	Tropicalization	Residents
Upper Laguna Madre	0.013	Tropicalization	Residents
Galveston Bay	0.014	Deborealization	Residents
Bothnian Sea	0.019	Tropicalization	Residents
Lower Laguna Madre	0.036	Deborealization	Residents
Aransas Bay	0.057	Tropicalization	Residents
San Antonio Bay	0.068	Tropicalization	Residents
Corpus Christi	0.091	Tropicalization	Residents
Mokbaai	0.149	Deborealization	Residents
Kattegat	0.273	Tropicalization	Residents
San Francisco Bay	0.463	Tropicalization	Residents
North Inlet	0.822	Deborealization	Residents
Norwalk Harbor	1.165	Deborealization	Residents
Long Island Sound	1.262	Tropicalization	Residents
Narragansett Bay (Whale Rock)	1.452	Tropicalization	Residents
Narragansett Bay (Fox Island)	1.652	Deborealization	Residents

Figure. 6 - Strength of each process underlying CTI change for all sites pooled (a-d), sites where CTI increased over time (b-e), and sites where CTI decreased over time (c-f).



Legend: The left panels show the value for each process regarding all species combined; the right panels show the value of each process per species groups. IM – immigrants, EM – emigrants, RES – residents.
Source: The author, 2022.

1.4 Discussion

Our work summarized evidence of long-term fish assemblage reorganization in response to warming, and explored the underlying mechanisms at assemblage (i.e. CTI change and processes) and species-level (i.e. persistence-related groups). Analysis of data did not support our first hypothesis that deborealization is the main temperature-related process underlying community change. Instead, we found tropicalization is the strongest process driving CTI change for most assemblages evaluated in the present review, agreeing with the formerly reported rise of warm-affinity species in temperate systems (CHEUNG et al., 2013; ANTÃO et al., 2020; MCLEAN et al., 2021). However, this process (and the three others) was primarily underpinned by changes in resident species abundance, while immigrants and emigrants had minor contributions. These results demonstrate that novel communities emerge primarily from local shifts in dominance of persistent species with distinct thermal affinities, despite the high turnover in occupancy rates reported for the marine realm (DORNELAS et al., 2014; BLOWES et al., 2019). Our study provides novel and timely insights on climate-driven biodiversity change, and revealed warming reshapes communities by favoring thermally distinct species from the local pool (i.e. dominance shift) rather than through increased dispersal.

Temperature has been proposed as one of the main drivers of biodiversity change, as it predicts species distribution and abundance (SUNDAY et al., 2012; STUART-SMITH et al., 2017; PAYNE et al., 2021). Such influence on species dispersal and dominance has been associated, in turn, with assemblage dissimilarity at both local and regional scales (HENRIQUES et al., 2017), and across time (ANTÃO et al., 2020). Nonetheless, most studies have associated the rise of novel communities with the replacement of original species by new settlers (i.e. increased dispersal; DORNELAS et al., 2014; BLOWES et al., 2019), without further looking into potential shifts in dominance. For instance, increases in CTI are frequently associated with the influx of tropical species at temperate areas (CHEUNG et al., 2013; BATES et al, 2014); in such cases, immigrant species would account for the largest proportion of CTI change, surpassing residents. However, our work showed that species that were already present in temperate estuaries during the early period had the biggest contributions for shifts in CTI, irrespective of the dominant process (i.e. tropicalization, borealization and others). These findings provide some unexpected insights on how assemblages are coping with climate change, starting with the uncoupled relationship between the main group of species driving community reorganization and temperature-related processes.

The importance of resident versus immigrant and emigrant species for novel assemblages was predicted to be dependent on the strongest temperature-related process driving CTI change. For instance, resident and emigrant species were expected to have greater contributions to CTI change at systems where the loss of individuals prevailed, either through deborealization or detropicalization. In addition, immigrant species would account for the greatest proportion of CTI change whenever a positive balance in community change was detected (i.e. gains outweigh losses). Disagreeing with these expectations, we found that resident species were more important for CTI change regardless of individual losses and gains, and the prevailing temperature-related process. This pattern may be underpinned by a) the correlation between species abundance and their persistence within a community, with dominant species being the ones present in a system for a large number of years (MAGURRAN; HENDERSON, 2003), and b) the tight relationship between temperature and species abundance (PAYNE et al., 2021), since we did detect a shift in the dominance of residents according to their thermal preference. These results suggest that, under ocean warming, novel fish assemblages are drawn primarily from the local pool rather than via dispersal. Poleward shifts in species distribution have been increasingly documented over the years (CHEUNG et al., 2013; BATES et al., 2014; BATES et al., 2017), and were expected to have a key role in assemblage reorganization. However, recent findings revealed warming also leads to large-scale shifts in species abundance (MCLEAN et al., 2021), which we have found to surpass the contribution of immigrants to the processes underlying community change in temperate estuaries. Secondary contributions of immigrants to CTI change also raises concern on whether temperature-tracking species (range-shifting or not) are prone to a successful establishment at colonizing sites. These species were expected to show increased abundance under the new thermal regime, and ultimately replace the original core species (MAGURRAN; HENDERSON, 2003). However, our findings suggest that other ecological pressures may hinder the growth of immigrant species in novel environments, which can increase their vulnerability to extinction while tracking suitable isotherms.

The largest contribution of residents to processes underlying CTI change could also be related to the greater number of species in this category (Appendix 2: Table 9), as result of splitting the time series into early and late periods. For instance, species sampled twice were labeled as residents, given their capture occurred in each time period. Nonetheless, few species accounted for 75% of CTI change, and these were recorded in estuaries for over half of the time series (Appendix 2: Table 9). These species also experienced large shifts in abundance, but were not necessarily amongst the most abundant ones within the community. Species traits were consistent across all studies with a continuous time series, as we could not assess temporal occurrence at systems with disrupted surveys, such as Sepetiba Bay (where residents and emigrants accounted for 75% of process strength) and the North Inlet. Remaining residents, immigrants and emigrants accounted for only 25% of CTI change. Most of these species popped in and out of the community over years, which may underlie turnover rates reported by previous studies assessing biodiversity change, as these often adopt the first year of sampling as baseline for temporal comparison (DORNELAS et al., 2014; ANTÃO et al., 2020). Nonetheless, low contribution to CTI change suggests these species occurrence is less related to warming's effects. Hence, it is unlikely the number of species in resident, immigrant and emigrant categories biases the trends reported herein, which corroborate with previous reports showing that few species drive assemblage reorganization (GOTELLI et al., 2022).

Evidence supporting the patterns detected in our study were mostly retrieved from temperate systems. However, divergence from the "residents trend" was found for Sepetiba Bay, which is located in a climatic transitional zone between subtropical and warm-temperate waters (22^{o}-23^{o}S latitude; ARAÚJO et al., 2018). Detropicalization was the strongest process underlying assemblage reorganization at this estuary, which was underpinned by emigrant species. Abundance declines and/or retraction are expected for tropical species in response to warming, due to their low thermal safety margins and acclimation capacity (TEWKSBURY et al., 2008; VINAGRE et al., 2019). Unfortunately, the lack of long-term data in the tropical region hinders a comprehensive estimation of beta-diversity components in our and previous studies (ANTÃO et al., 2020), and prevent from further investigating latitude-related variation in the group of species leading community reorganization. Nonetheless, data retrieved from Sepetiba Bay agrees with the high vulnerability reported for the tropical fauna (TEWKSBURY et al., 2008; VINAGRE et al., 2019). Therefore, assessing the upper thermal tolerance of resident, dominant species, in tropical communities may be critical for determining the risk of collapse in future scenarios of change.

Our meta-analyses only covered estuaries that warmed, since the literature search did not retrieve any study performed in cooling areas. Nonetheless, decreases in CTI were detected at four systems (Table 3). Borealization was the strongest process reshaping these communities, excepting for Sepetiba Bay (discussed above). Similar results were reported by MCLEAN et al. (2021), which revealed wider thermal ranges for cold-affinity species driving borealization. Tolerance to distinct temperatures can buffer species against warming impacts, favoring persistence within their original habitat over dispersal (MORAN et al., 2016) – which is aligned with the main findings of our study. Such ecological trait is common to estuarine species, which are subject to continuous shifts in temperature and other environmental conditions (ELLIOTT et al., 2007). However, generalist species often show a trade-off between thermal plasticity and tolerance, and thus are highly vulnerable to subtle increases in maximum temperature (TEWKSBURY et al., 2008; VINAGRE et al., 2019). Hence, tolerance to current warming may not prevent from major species and individuals loss in future scenarios of change (MCLEAN et al., 2021), despite the generalist trait of estuarine species.

Assemblage reorganization was correlated with other climate-mediated drivers besides temperature in the original studies. Sea level and salinity were associated with community change in bays along the coast of Texas, and in the Baltic Proper and the Bothnian Sea, respectively. These systems also showed little change in CTI (Table 3), revealing drivers other than temperature can have a greater influence in assemblage reorganization. The synergistic effect of climate and other anthropogenic threats also represents a topic of interest for further studies in the field, since ecosystems under several human-induced pressures (e.g. high population density and fishing) have been associated with deborealization (MCLEAN et al., 2021). Unfortunately, we did not have enough entries to evaluate the relationship between these factors and community change, as several studies retrieved by the literature search had significant methodological inconsistencies and thus were excluded from our database (e.g. surveyed distinct areas or used distinct sampling methods across time periods; Appendix S2: Table 6). Lack of a significant relationship between climate-related drivers and community change also led to exclusion of 12 studies (out of the 48 screened at full-text) from the compiled database (Appendix S2; Table 6). However, the majority of these studies (N=11) did not test for such relationship, but rather reported on spatial and temporal patterns of the fish assemblage. As consequence, losses and gains estimated from these data could be related to confounding factors, compromising the identification of climate-related processes underpinning assemblage reorganization. We recognize our methodological approach may overestimate meta-analyses mean effects, and thus results should be interpreted with caution. Nonetheless, the ecological patterns reported herein agree with the ones detected by ANTÃO et al. (2020). Moreover, studies with significant results are more likely to get published (i.e. file drawer problem; ROSENTHAL, 1979; ROSENBERG, 2005; BORENSTEIN et al., 2021), leading potential bias in meta-analysis regardless of the criteria we have established. However, Rosenthal’s and Rosenberg’s fail-safe N tests revealed our results were robust to publication bias.

Loss and gain of species and individuals over time may also have been influenced by sampling effort. Number of years and samples were quite balanced across the early and late periods for all but five sites (Appendix S2: Table 10). Nonetheless, studies with higher sampling variance are given less weight when performing a meta-analysis, thus contributing little to the mean effect (BORENSTEIN et al., 2021). For instance, among the five estuaries with unbalanced samples, only Sepetiba Bay and Kattegat had significant effect sizes (Fig. 3), and the first system lost species despite increased sampling in the late period. Meta-analyses estimates based on species abundance data are also unlikely biased, as we corrected the number of individuals per sampled area (i.e. density; Appendix S2: Table 10;). Therefore, mean effect sizes are likely robust and effectively controlled the unbalanced sampling effort detected for some studies in our database.

In summary, our study revealed that novel communities arise primarily via temperature-mediated shifts in resident species dominance, rather than distribution (i.e. immigration and emigration). We also demonstrated this mechanism is uncoupled from a) the final balance between individual losses and gains in a given community, and b) the strongest temperature-related process underlying CTI change (i.e. tropicalization, detropicalization, borealization, deborealization). These results emphasize the importance of management practices for the local species pool, since original species remained the core of novel communities, despite increased colonization rates in response to warming (CHEUNG et al., 2013; ANTÃO et al., 2020). Dispersal to novel environments is particularly important for tropical species, but lack of long-term data prevented from detecting the main processes reshaping these communities. Future synthesis studies combining evidence from distinct taxa and realms may help to elucidate whether the main group of species driving community reorganization change across climatic zones, and further strengthen the results reported herein.

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2. THERMAL PLASTICITY OVER A MARINE-ESTUARINE ECOCLINE CAN BUFFER A TROPICAL FISH FROM WARMING

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Abstract

Intraspecific variation in thermal tolerance can favor species persistence in a warmer ocean, but is often overlooked in fine-scale studies. Nonetheless, local drivers (e.g. salinity) interact with temperature to shape species' thermal response. Here, we acclimated juveniles of Brazilian silversides *Atherinella brasiliensis* captured at the limits of a marine-estuarine ecocline under reciprocal-cross conditions, to test for phenotypic plasticity in heat tolerance. We also tested whether silversides acclimated to temperatures predicted for 2100 (+3-4.5ºC). Fish in warm-brackish waters showed higher CTMax (Critical Thermal Maximum) than those in cold-marine conditions, regardless of their origin. Silversides' CTMax reached up to 40.6ºC, but it did not increase after exposure to temperatures predicted for 2100. Lack of acclimation response suggests that silversides heat tolerance has reached a "ceiling", despite thermal plasticity. Our findings show that fine-scale environmental heterogeneity can promote phenotypic plasticity for tropical species, reducing the risk of short-term extirpation.

Key-words: *Atherinella brasiliensis*, Temperature, Climate change, Indicator species, Common Garden Experiment, Thermal Safety Margin

2.1 Introduction

One of the main challenges regarding the current biodiversity crisis is to predict whether species can keep pace with warming. Global-scale climate change interacts with local drivers, shaping individuals' response to novel environmental conditions (GERVAIS et al., 2021; DUBOIS et al., 2022). Rising temperatures often lead to species dispersal, reshuffling communities (PINSKY et al., 2013; ANTÃO et al., 2020; LENOIR et al., 2020). However, phenotype variation can favor species persistence within its original habitat, a phenomenon known as the “Portfolio effect” (BENNETT et al., 2019; FOX et al., 2019; MCKENZIE et al., 2021). Portfolio refers to a broad range of phenotypes (and genotypes) within and among species’ populations, which would reduce their risk of extirpation under climatic scenarios (BOLNICK et al., 2011; MORAN et al., 2016).

A growing number of studies have estimated species vulnerability to warming via thermal limits and safety margins (MORA; OSPINA, 2001; MADEIRA et al., 2017; VINAGRE et al., 2018). Experimentally obtained values have also been coupled with ecological niche models (ENMs) to improve predictions of species distribution under current and future climate (PEROTTI et al., 2018; PONTES-DA-SILVA et al., 2018). However, most thermal tolerance studies overlook intraspecific variation and risk bias by recognizing species as static, homogeneous units. Intraspecific variation in thermal tolerance has been detected across species life stages, occurrence range, and even seasons (TURKO et al., 2020; MORENTE-LÓPEZ et al., 2022), and is underpinned by plasticity or adaptation (BENNET et al., 2019; GERVAIS et al., 2021; DUBOIS et al., 2022). The first represents a reversible change in a biological trait in response to the environment, whereas local adaptation consists of genetic selection leading a shift in population phenotype toward a local optimum (BENNETT et al., 2019). Environmental heterogeneity has been reported for driving local adaptation in thermal tolerance at regional and local scales (BIBLE; SANFORD, 2016; GERVAIS et al., 2021; DUBOIS et al., 2022), but gene flow amongst populations can reduce adaptive divergence, favoring phenotypic plasticity (SULTAN; SPENCER, 2002; BENNETT et al., 2019). Identifying the source of phenotypic variation is crucial for preventing maladaptation in a management context, since each mechanism has implications at distinct time scales (e.g. plasticity is expected to buffer from immediate impacts of warming such as heatwaves, while adaptation also has potential to dampen against decadal warming; BENNETT et al., 2019). Evidence on the main mechanism underlying intraspecific variation can be retrieved from common garden experiments, which are based on the acclimation of individuals from distinct sites under similar environmental conditions (GERVAIS et al., 2021; DUBOIS et al., 2022).

Thermal history (i.e. the temperature range experienced by an individual in their natural environment) often shapes species' thermal tolerance (GIOMI et al., 2016; OLSEN et al., 2021). Nonetheless, multiple abiotic variables can interact with temperature, creating additive, synergistic or antagonist effects in heat tolerance (i.e. combined effect equal, greater or smaller than the sum of each independent variable, respectively; RE et al., 2012; FONG et al., 2018; REISER et al., 2017; MADEIRA et al., 2021). The interplay between temperature and salinity has been the subject of several studies performed with coastal species, as salinity interacts with temperature to shape species thermal tolerance (REISER et al., 2017; MADEIRA et al., 2021). Local-scale mosaics regarding temperature and salinity can be observed in estuaries, due to overlapping marine-estuarine (i.e. ocean to mid-estuary) and estuarine-freshwater (i.e. mid-estuary to river) ecoclines (ATTRILL; RUNDLE, 2002). The environmental gradient in temperature and salinity drives community turnover between the upper, middle and lower estuary, filtering species from distinct functional-use guilds according to their tolerance, particularly regarding salinity (ATTRILL; RUNDLE, 2002; CHAVES et al., 2018). However, resident species inhabiting these systems often show phenotypic variation to cope with heterogeneity in environmental conditions (GERVAIS et al., 2021). Therefore, these species represent a good model for assessing the combined effects of temperature and salinity in heat tolerance, as well as to unveil potential mechanisms underlying fine-scale intraspecific variation.

Brazilian silversides *Atherinella brasiliensis* (Quoy & Gaimard, 1825) is a resident fish species in estuaries along the southwestern Atlantic, and thrives under varied salinity and temperature conditions within these systems (SOUZA et al., 2018; DAMASCENO, 2020). Despite their wide distribution across the estuary, site-fidelity has been reported for Atherinidae species, particularly during early life stages (GREEN et al., 2012; CLAUDINO et al., 2013). Limited dispersal between estuarine zones and a partially dispersive reproductive strategy (i.e. adhesive bottom eggs followed by a larval stage; FÁVARO et al., 2003; DEL RÍO et al., 2005) may lead to distinct phenotypes between local populations (BENNETT et al., 2019). Intraspecific variation can play an important role in protecting species from warming in heat-conservative systems, since spatial and temporal (i.e. from hours to years) microclimate variation may exceed the thermal limits of individuals distributed across the estuary. These fine-scale assessments are particularly important for determining tropical species vulnerability to rising temperatures, since they have been reported to have low acclimation capacity despite their high Critical Thermal Maximum (CTMax; TEWKSBURY et al., 2008; VINAGRE et al., 2018).

Here, we investigated intraspecific variation in heat tolerance and the potential for phenotypic plasticity and local adaptation over a fine-spatial scale (<20 km), using experimental data from a resident estuarine fish species, *Atherinella brasiliensis*. Experiments were performed exclusively with juveniles in order to avoid confounding effects related to ontogenetic variation; we chose this particular life stage to test our hypotheses due to their lower mobility and high site-fidelity (GREEN et al., 2012; CLAUDINO et al., 2013). Fish were acclimated under the average temperature and salinity of two sites at the opposite limits of a marine-estuarine ecocline, using a reciprocal-cross design (i.e. silversides were acclimated to original and alternate conditions of their capture site). Therefore, experimental treatments mirrored the cold-marine (27.5ºC and 32 ppt) and warm-brackish (29.7ºC and 25 ppt) conditions observed at each site. We expected a higher CTMax for fish in warmer and less saline waters, regardless of specimens' capture site (i.e. phenotypic plasticity). We also predicted CTMax of fish from both treatments would increase after exposure to temperatures predicted under the SSP2-4.5 and SSP5-8.5 scenarios. A second set of experiments was performed to disentangle current temperatures' effect on CTMax of silversides acclimated in marine and brackish salinities. Higher CTMax was expected for fish in warmer waters, irrespective of treatment's salinity. Silversides' life-history traits (i.e. site-fidelity and a partly dispersive reproductive strategy) justify our expectations regarding phenotypic plasticity at local scale. Further, euryhalinity would underlie the lack of a salinity effect on species thermal tolerance, as fish were acclimated under regular habitat conditions (i.e. as opposed to stressful hypo or hypersaline levels, e.g. JÚNIOR et al., 2021). Therefore, we hypothesized that thermal history would be the main factor underlying intraspecific variation in *A. brasiliensis* thermal tolerance.

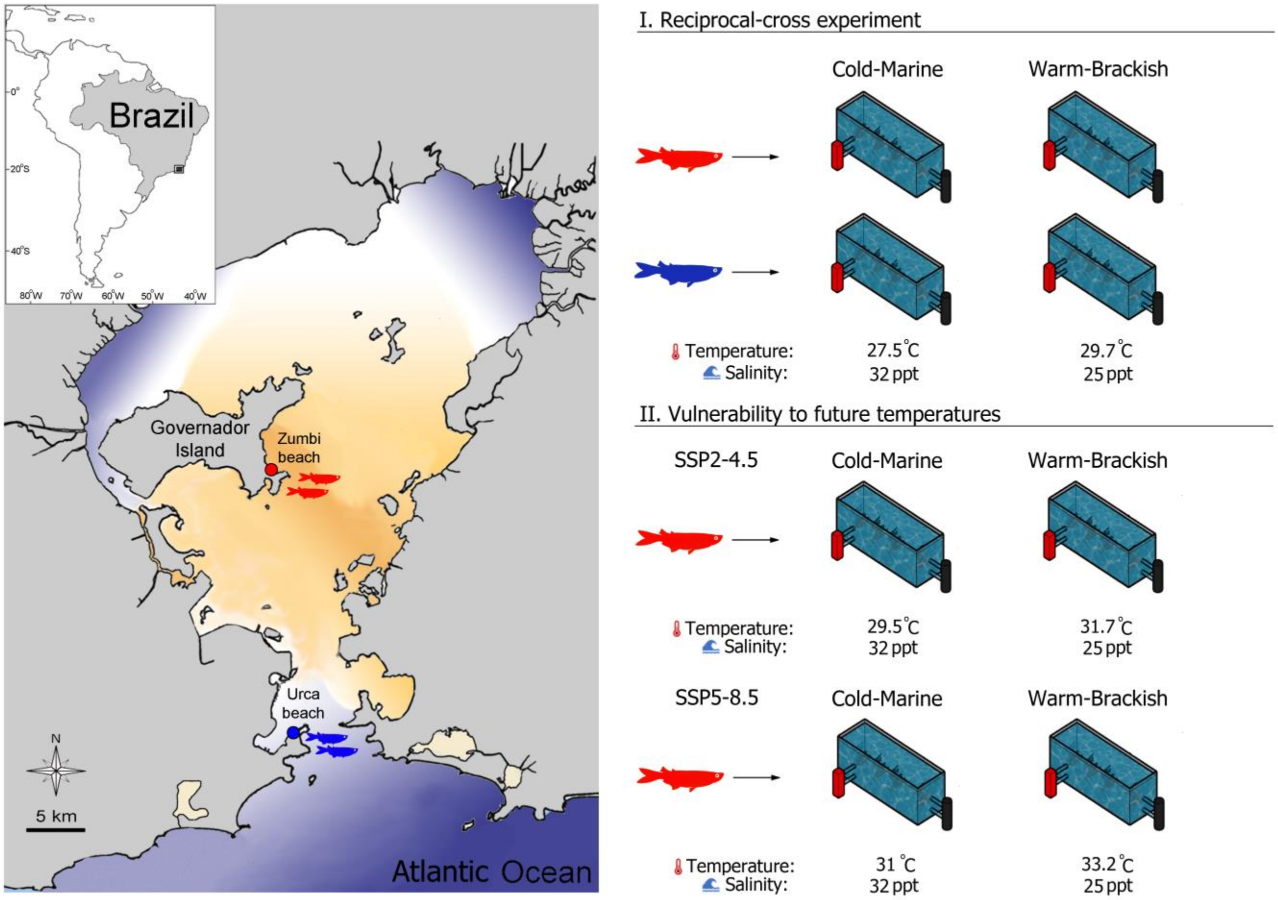
2.2 Materials and Methods

2.2.1. Animal collection and husbandry

Brazilian silversides were caught using a seine net with a codend (20m width x 2m height – 7mm mesh size; 3mm mesh size for codend) in two beaches located at the entrance and northwest zones of Guanabara Bay, Rio de Janeiro, Brazil (Figure 7). These sites are ca. 20 km apart from each other, and were chosen for this study as they represent the opposite boundaries of a marine-estuarine ecocline, particularly regarding temperature (CHAVES et al., 2018). Urca Beach (22º56’52’’S, 43º09’48’’W) is located near Guanabara Bay entrance, where marine conditions prevail (KJERFVE et al., 1997). Mean salinity ranges from 29-32 ppt throughout the year, and mean temperature from 23ºC-28ºC (SOUZA et al., 2018; DAMASCENO, 2020). Zumbi Beach (22º49’13’’S, 43º10’23’’W) is located in the inner western portion of the bay, where hydrodynamic energy is low. As consequence, water residence time is high (FISTAROL et al., 2015), and temperatures reach up to 33ºC during summer - the highest value recorded for the entire bay (ROSMAN et al., 2017; DAMASCENO, 2020). Discharge from polluted rivers and the decreased velocity of tidal currents results in salinities around 25 ppt in the region (CHAVES et al., 2018).

Fish were captured in early 2022 at both Urca and Zumbi beaches. Silversides were placed in coolers and plastic bags filled with in situ seawater, which were continuously aerated using a portable oxygen compressor (Boyu D-200) during transport to the Laboratory of Theoretical and Applied Ichthyology (LICTA) at Federal University of the State of Rio de Janeiro (UNIRIO). Fish were transported within 1 hour, and placed in aerated recipients filled with in situ seawater upon arrival at the laboratory. Then, an equal volume of artificial seawater was gradually added to each recipient to avoid osmotic and thermal stress during fish acclimation to experimental conditions. After this process, 40 fish were randomly placed in each of two individual aquariums of 472 L (68 x 150 x 53 cm, Model Ea-150L.h- - Boyu). Each tank was filled with artificial seawater of temperature and salinity similar to the average levels at Zumbi and Urca beaches (see section 2.2.2 for more details). Temperatures were controlled using thermostats (Kintons Kth-8800, Minjiang MJ-HF500), and experimental salinities were achieved by adding synthetic salt (Ocean Tech Reef Active) to filtered water. Tanks were also equipped with a diffuser stone connected to an air pump (Maxxi Power Pro-2000), ceramic rings (Professional Sera Siporax), fine gravel (i.e. Aragonite Aquarium Sand) and fluorescent white lights. Fish were conditioned for 48 hours prior to the start of experimental trials, under a summer photoperiod of 14h light: 10h dark. Juveniles were fed ad libitum with *Artemia salina* once a day during housing in the laboratory. Water quality parameters were monitored every 24 hours, and kept within the standard range regarding organisms’ welfare (mean±S.E): pH=8.0±0.02, dissolved oxygen=5.88±0.18 ppm, ammonia=0.08±0.01 ppm and nitrite=0.33±0.03 ppm (values were monitored using Labcon tests for the respective variables). Tanks were allowed to stabilize for 6 weeks before housing silversides. Animal collection, husbandry and experimental protocols were authorized by the Brazilian Institute of Environment and Natural Resources (IBAMA, license no 70942).

Figure 7 - Map of Guanabara Bay, Brazil, showing the two sites where Brazilian silversides were collected (i.e. Urca Beach and Zumbi Beach).



Legend: The conceptual color gradient represents cold (blue) and warm (orange) areas within the bay, and is based on hydrodynamic models of water residency time and field data retrieved from previous studies (Rosman et al., 2017; Chaves et al., 2018; Souza et al., 2018; Damasceno, 2020). Experimental design and treatments regarding the reciprocal-cross and future vulnerability tests are also shown. Blue fish = captured at Urca Beach; Red fish = captured at Zumbi Beach.
Source: The author, 2022.

2.2.2 Reciprocal-cross experiment

Fish were acclimated to mean temperature and salinity recorded during summer at Urca (i.e. designed as the cold-marine treatment hereafter) and Zumbi (i.e. designed as the warm-brackish treatment hereafter) beaches. Water temperature was stable at 27.5^{o}C ±0.2 (mean±SE) and salinity at 32 ppt ±0.1 in the cold-marine treatment; these respective variables were maintained at 29.7^{o}C ±0.02 and 25 ppt ±0.1 in the warm-brackish treatment (Figure 7).

Silversides were acclimated under original and alternate (reciprocal-cross) temperature and salinity of their respective capture site. Therefore, we had four groups of acclimated fish: a) cold-marine treatment (original), b) cold-marine treatment (cross), c) warm-brackish treatment (original), and d) warm-brackish treatment (cross) (Figure 7). In the original-labeled treatments, fish were kept under similar conditions of their respective capture site; in the cross-labeled treatments, silversides were exposed to alternate conditions (i.e. fish captured at Urca Beach was acclimated to the temperature and salinity of Zumbi Beach and vice-versa). We adopted this experimental design to detect whether differences in silversides' heat tolerance varied with environmental conditions or not (i.e. home-site advantage). Fish were acclimated for five days, during which we performed a daily check of their health status (i.e. wounds or disease symptoms). Afterwards, a subset of individuals had their upper critical limits assessed (see section 2.2.5. for details). Acclimation duration was defined based on previous literature that reported tropical species fully acclimate to elevated temperatures within 2-5 days (SCHMIDT-NIELSEN, 1997). Moreover, a comprehensive meta-analysis also revealed a short period (i.e. 3 days) is required for CTMax acclimation regarding species with a small body size (ROHR et al., 2018), such as the Brazilian silversides.

2.2.3 Silversides' vulnerability to temperatures predicted for 2100

Subsequent experiments were performed to evaluate *A. brasiliensis*' vulnerability to warming scenarios predicted for 2100. These trials were performed using only fish from the cold-marine (cross) and warm-brackish (original) treatments, as statistical analyses of reciprocal-cross experiments revealed a significant effect of acclimation condition but not specimen's origin on CTMax. Fish in the cold-marine and warm-brackish treatments were acclimated for five more days under temperatures increased by +2ºC (i.e. cold-marine treatment: 29.5ºC ±0.1 temperature, 32 ppt ±0.2 salinity; warm-brackish treatment: 31.7ºC ±0.04 temperature, 25 ppt ±0.2 salinity) (Figure 7). Then, we estimated CTMax for a subset of individuals. The experimental +2ºC rise in temperature, combined with the currently reported +1ºC in the natural environment, amounts to a warming of +3ºC, which is expected by 2100 under the SSP2-4.5 scenario (IPCC, 2021). We adopted temperature values from this "inequality" scenario, since an increase of +2ºC to +3ºC degrees has been proposed as the likely range of warming by the end of the century (BAUER et al., 2017; BURGESS et al., 2022). After the end of this acclimation period, we further exposed the remaining fish in both treatments to an increase of +1.5ºC in temperature, thus achieving the mean value predicted for 2100 under the SSP5-8.5 scenario (IPCC, 2021). Therefore, the cold-marine treatment had 31ºC ±0.4 temperature and 32 ppt ±0.25 salinity, and the warm-brackish treatment had 33.2ºC ±0.1 temperature and 25 ppt ±0.2 salinity (Figure 7). Despite SSP-8.5 has been considered as an unlikely scenario (BURGESS et al., 2022), the temperature values predicted may be reached during extreme events in heat-conservative systems, such as estuaries. Therefore, we used values from this "fossil-fueled development" scenario for conservation and comparative purposes. Fish were acclimated for five days, and then another subset of individuals had their CTMax estimated. No individual was exposed to CTMax trials more than once.

2.2.4 Temperature's isolated effect on CTMax

We performed a second set of experiments to assess temperature change's effect on *A. brasiliensis* CTMax, using values currently observed at each capture site. Silversides were conditioned for 48 hours before the start of acclimation period (see section 2.2.1), and 15 fish were randomly placed in each of two individual aquariums of 472 L (68 x 150 x 53 cm, Model Ea-150L.h^{-} - Boyu). These aquariums were set with salinities from the marine (i.e. 32 ppt) and brackish (i.e. 25 ppt) treatments (see section 2.2.2), and had a starting temperature of 27.5ºC ±0.1. Fish were acclimated for five days, and then a subset of individuals had their upper critical limits (CTMax) assessed. Afterwards, we increased the aquariums' temperature to 29.7ºC ±0.1 for five more days. At the end of this period, CTMax was estimated for another subset of individuals. No fish was exposed to more than one CTMax trial.

2.2.5 Critical Thermal Maxima

Silversides' upper thermal limits were estimated through the CTMax method (MORA; OSPINA, 2001; VINAGRE et al., 2015; MADEIRA et al., 2017). Fish from each trial (see sections 2.2.2, 2.2.3 and 2.2.4) were transferred to two individual aquariums of 40 L (35.2 x

53.5 x 32.3 cm, Model ZJ 401 - Boyu), which were equipped with a digital thermostat (TIC-17RGT - Full Gauge), a diffuser stone connected to an air pump (Maxxi Power Pro-2000), ceramic rings (Professional Sera Siporax), fine gravel (aragonite) and fluorescent white lights. Temperature and salinity were set according to acclimation conditions of each experiment described in the previous sections. For instance, to assess CTMax of fish acclimated to temperatures predicted for SSP5-8.5 (section 2.2.3), we set the cold-marine tank with a stable temperature of 31^{o}C and salinity at 32 ppt, while the warm-brackish tank's temperature and salinity was 33.2^{o}C and 25 ppt, respectively. CTMax was estimated by exposing fish to a constant rate of temperature increase of 1^{o}C per 15 min, and loss of equilibrium was defined as end-point (i.e. specimen turned upside down and failed to return to the original position). Warming rate was chosen based on VINAGRE et al. (2015), and represents an ecologically suitable estimate for coastal ecosystems, such as estuaries. The critical upper temperature (CTMax) of each individual was recorded through the digital thermostat (TIC-17RGT - Full Gauge). Fish were anesthetized with eugenol and euthanized by freezing in ice, before having their total length (mm) and weight (0.00 gr) recorded.

2.2.6 Data analysis

We calculated the arithmetic mean of thermal endpoints (CTMax) obtained for individuals from each treatment (MORA; OSPINA, 2001). Intraspecific variability (%CV) of CTMax was determined by dividing standard deviation by the mean, multiplied by 100 (MADEIRA et al., 2017). Thermal safety margins (TSM) were estimated as the difference between fish CTMax and maximum habitat temperature (i.e. values were retrieved from DAMASCENO, 2020), to investigate specimens' risk of ecological function loss (MADEIRA et al., 2017). We also provided TSM estimates considering heatwave events (i.e. +5^{o}C above the average maximum temperature of a location; VINAGRE et al., 2018) in present-day conditions, and the maximum temperatures predicted for 2100 under SSP2-4.5 e SSP5-8.5 scenarios.

Permutational Analysis of Variance (PERMANOVA) was performed to assess the effect of specimen's origin (i.e. capture site) and acclimation condition (i.e. cold-marine and warm-brackish treatments) on silversides' CTMax and TSM, using $\log_{10}x$ transformed total length (cm) as covariate. The Euclidean distance (1000 permutations; $p \leq 0.05$) was chosen for

PERMANOVA tests, which were performed using the *adonis2* function in the *vegan* package (OKSANEN et al., 2022) for the R software (R CORE TEAM, 2022). We also assessed homogeneity of data variance between levels of each factor (e.g. treatment, species origin) using the *betadisper* function in the *vegan* package (OKSANEN et al., 2022). Linear Mixed Models (LMM) were performed to assess the effect of acclimation temperature on silversides' CTMax and TSM (i.e. experiments described in section 2.2.3). Acclimation temperature (fixed factor; levels=current, SSP2-4.5 and SSP5-8.5 scenarios) was nested within treatment (fixed factor; levels=cold-marine, warm-brackish) for these tests. We also included trial number as a random effect, to account for the lack of temporal independence between acclimation scenarios (e.g. fish from CTMax trial number 2 were exposed to acclimation temperatures of both current and SSP2-4.5 scenarios, and so on). Our mixed-model also tested for an effect of $\log_{10}x$ transformed total length (cm) on silversides' CTMax. The same statistical design was employed to analyze current temperatures' influence on fish CTMax (i.e. experiments described in section 2.4.). Acclimation temperature (fixed factor; levels = 27.5ºC and 29.7ºC) was nested within salinity treatment (fixed factor; levels = 25 ppt and 32 ppt), and a random effect was specified for trial number. Total length ($\log_{10}x$ transformed; cm) was also included in the model. LMMs were performed using the *lme* function from the *nlme* package (PINHEIRO; BATES, 2000; PINHEIRO et al., 2022). Post-hoc pairwise comparisons were calculated using the *lsmeans* package (LENTH, 2016). Prior to performing LMM models, we confirmed the Gaussian distribution of the response variable through the visual inspection of histograms. Model residuals were also checked for normality and homogeneity of variance using qqplots from the *stats* package (R CORE TEAM, 2022).

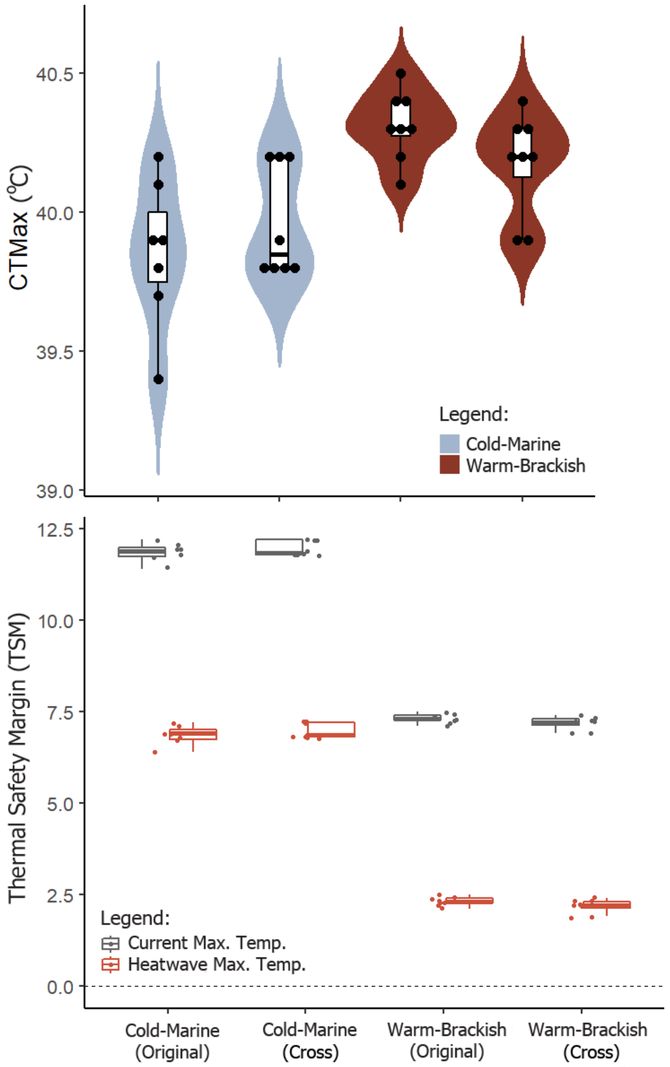
2.3 Results

2.3.1 Reciprocal-cross experiment

Heat tolerance (CTMax) was influenced by acclimation conditions ($F_{1,29}=20.91$, $p=0.001$, $R^2=0.43$), but not silversides' origin ($F_{1,29}=2.30$, $p=0.15$, $R^2=0.05$) or the interaction between these factors ($F_{1,27}=0.03$, $p=0.85$, $R^2=0$). Fish acclimated in warm-brackish conditions showed a higher CTMax than ones from the cold-marine treatment (both original and cross) (Table 4; Figure 8). Fish size did not influence CTMax ($F_{1,30}$=0.01, p=0.91, R^2=0), nor interacted with acclimation conditions ($F_{1,29}$=1.98, p=0.17, R^2=0.04) and specimen's origin ($F_{1,29}$=0.007, p=0.93, R^2=0). We also did not detect a significant interaction between CTMax and acclimation condition, specimen's origin and size ($F_{1,27}$=0.21, p=0.64, R^2=0). Variance regarding CTMax data was homogeneous between acclimation treatments ($F_{1,29}$=1.25, p=0.27) and specimen's origin ($F_{1,29}$=0.31, p=0.58). Intraspecific CTMax variation (%CV) within treatments was low, and ranged from 0.31% to 0.66% (Table 4).

Fish from the cold-marine treatment had higher thermal safety margins (TSM) than ones from the warm-brackish treatment, regarding both regular and heatwave scenarios ($F_{1,29}$=4093.96, p=0.001, R^2=0.99; values for both tests) (Table 4; Figure 8). Specimen's origin ($F_{1,29}$=2.79, p=0.09, R^2=0), size ($F_{1,30}$=0.01, p=0.9, R^2=0), the interaction between these factors ($F_{1,29}$=0.97, p=0.33, R^2=0), and with acclimation condition ($F_{1,27}$=0.21, p=0.65, R^2=0) did not have a significant effect on silversides' TSM (i.e. values given refer to regular temperature and heatwave tests). Acclimation condition also did not interact with specimen's origin ($F_{1,27}$=0.03, p=0.86, R^2=0) nor size ($F_{1,27}$=1.03, p=0.32, R^2=0), regarding regular and heatwave TSMs. Variance of TSM data was homogeneous between acclimation treatments ($F_{1,29}$=1.25, p=0.27) and specimen's origin ($F_{1,29}$=0.05, p=0.82), for both regular and heatwave scenarios. Differences between silversides' upper tolerance and habitat's maximum temperature ranged from 11.96^{o}C (TSM of fish in the cold-marine treatment) to 2.18^{o}C (TSM of fish in the warm-brackish treatment during a heatwave) (Table 4; Fig. 8).

Figure 8 - Critical Thermal Maxima (CTMax, ^{o}C) and Thermal Safety Margin (TSM, ^{o}C) of Brazilian silversides acclimated under cold-marine (27.5^{o}C, 32 ppt) and warm-brackish (29.7 ^{o}C, 25 ppt) waters. Fish were acclimated under original and crossed habitat temperatures and salinities.



Legend: Boxplots represent the first and third quartiles around the median (solid line), and the whiskers (errors) represent the minimum and maximum values of outliers.
Source: The author, 2022.

Table 4 - CTMax (°C) and intraspecific variability (%CV), Thermal Safety Margin (TSM, °C; calculated using maximum habitat and heatwave temperatures), number of individuals tested and their mean size (cm), with respective standard errors (SE), for each treatment and experimental trial.

	CTMax	**SE**	**%CV**	**N**	**Size**	**SE**	**TSM**	**SE**	**TSM (heatwave)**	**SE**
Reciprocal-cross experiment										
Cold-Marine (original)	39.86	0.10	0.66	7	6.50	0.05	11.86	0.10	6.86	0.10
Cold-Marine (cross)*	39.96	0.07	0.50	8	5.38	0.25	11.96	0.07	6.96	0.07
Warm-Brackish (original)*	40.31	0.04	0.31	8	5.56	0.17	7.31	0.04	2.31	0.04
Warm-Brackish (cross)	40.18	0.06	0.46	8	5.25	0.40	7.18	0.06	2.18	0.06

Vulnerability to temperatures predicted for 2100										
*Current**										
SSP2-4.5										
Cold-Marine	39.98	0.09	0.23	6	5.85	0.28	9.48	0.09	4.48	0.09
Warm-Brackish	40.31	0.12	0.80	7	5.59	0.22	4.81	0.12	-0.19	0.12
SSP5-8.5										
Cold-Marine	40.02	0.13	0.74	5	6.02	0.16	7.32	0.13	2.32	0.13
Warm-Brackish	40.36	0.12	0.65	5	6.10	0.11	2.66	0.12	-2.34	0.12
Temperature's isolated effect on CTMax										
Salinity 32										
27.5 ºC	40.12	0.04	0.21	5	4.76	0.26	-	-	-	-
29.7 ºC	40.07	0.09	0.38	3	4.57	0.41	-	-	-	-
Salinity 25										
27.5 ºC	39.94	0.10	0.55	5	4.66	0.09	-	-	-	-
29.7 ºC	40.18	0.10	0.51	4	4.35	0.09	-	-	-	-

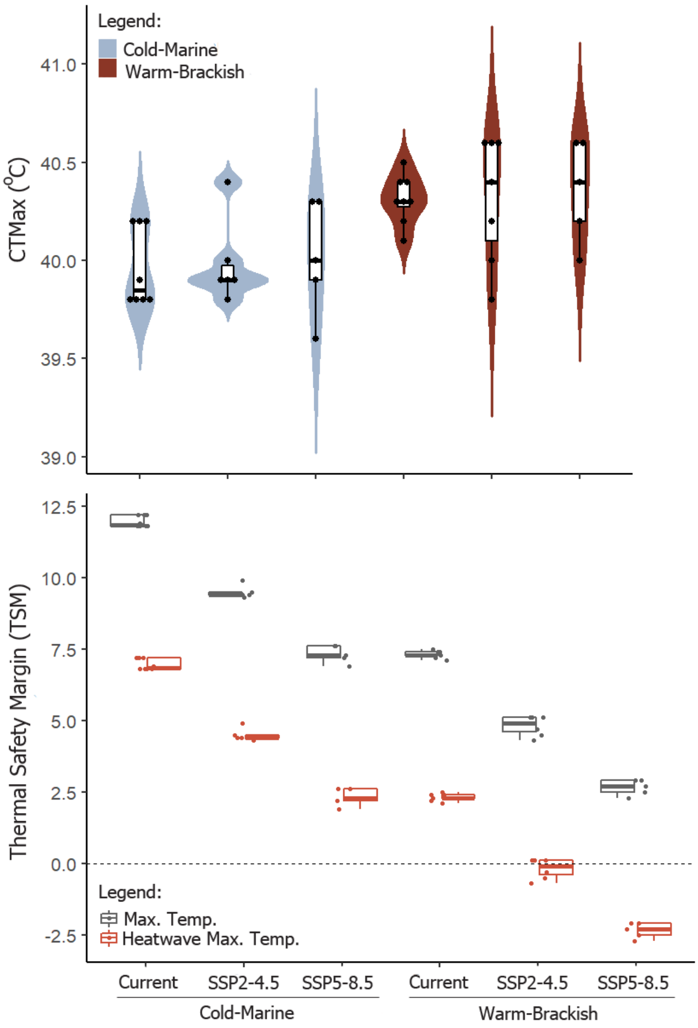
*Experiments to assess silversides' vulnerability to future warming were subsequently performed using fish from these treatments, since PERMANOVA results revealed acclimation conditions had a significant effect on CTMax, but not specimens' origin. Therefore, values from the referred treatments represented the current scenario in subsequent statistical tests concerning silversides' vulnerability to predicted temperatures.

2.3.2 Vulnerability to temperatures predicted for 2100

Acclimation conditions had a significant effect on silversides' upper tolerance (t-value=2.80, p=0.009). Fish acclimated in warm-brackish waters showed higher CTMax than the ones from the cold-marine treatment, regarding both current and predicted temperatures (Table 4; Figure 9). However, silversides' CTMax did not increase after exposure to temperatures predicted under SSP2-4.5 (Cold-marine treatment: t-value=-0.02, p=0.97; Warm-brackish treatment: t-value=0.002, p=0.99) and SSP5-8.5 scenarios (Cold-marine treatment: t-value=0.06, p=0.95; Warm-brackish treatment: t-value=0.06, p=0.96). Fish size also did not influence CTMax (t-value=0.81, p=0.42). Intraspecific CTMax variation (%CV) ranged from 0.23% to 0.80% (Table 4).

Silversides' thermal safety margins (TSMs) were influenced by acclimation condition and warming scenario (Table 4; Fig. 9). Fish from the cold-marine treatment had higher TSM than the ones acclimated in warm-brackish waters (t-value=-38.69, p<0.001, values given refer to regular and heatwave tests). TSMs were also higher in current scenarios, and decreased in SSP2-4.5 (Cold-marine: t-value=-16.68 and -8.85, p<0.001; Warm-brackish: t-value=-17.69 and -8.96, $p<0.001$; t-values are given for regular and heatwave tests, respectively) and SSP5-8.5 (Cold-marine: t-value=-29.22 and -16.21, $p<0.001$; Warm-brackish: t-value=-29.76 and -16.30, $p<0.001$; t-values are given for regular and heatwave tests, respectively). Tukey's post-hoc test revealed TSM values differed between all treatments and scenarios ($p<0.001$), excepting for the TSM of warm-brackish fish in the current scenario and that of cold-marine fish under temperatures predicted for SSP5-8.5 (p=1; Fig. 9). Fish size did not influence TSM values under regular and heatwave conditions (t-value=0.81, p=0.42, values given refer to both tests).

Figure 9 - Critical Thermal Maxima (CTMax, ^{o}C) and Thermal Safety Margin (TSM, ^{o}C) of Brazilian silversides acclimated under cold-marine (27.5^{o}C, 32 ppt) and warm-brackish (29.7 ^{o}C, 25 ppt) waters. CTMax and TSM values are also reported after fish acclimation to temperatures predicted under the SSP2-4.5 (C-M: 29.5^{o}C, W-B: 31.7^{o}C) and SSP5-8.5 (C-M: 31^{o}C, W-B: 33.2^{o}C) scenarios.



Legend: Boxplots represent the first and third quartiles around the median (solid line), and the whiskers (errors) represent the minimum and maximum values of outliers.
Source: The author, 2022.

2.3.3 Temperature's isolated effect on CTMax

Silversides' upper thermal tolerance did not change between salinity treatments (t-value=1.54, p=0.15), nor after exposure to increased temperatures within each treatment (salinity 32: t-value=-0.11, p=0.91; salinity 25: t-value=1.09, p=0.30) (Supplementary Figure 18). We also did not detect any differences in CTMax regarding fish size (t-value=1.53, p=0.15). Intraspecific variability (%CV) of CTMax was also low within each treatment, and ranged from 0.21% to 0.55% (Table 4).

2.4 Discussion

Our work revealed intraspecific variation in heat tolerance of Brazilian silversides over a fine-spatial scale (< 20 km), is best explained by site acclimatization (i.e. phenotypic plasticity) and not local adaptation. Analysis of data revealed fish acclimated in warm, brackish waters had higher CTMax than those in cold, marine conditions. The relationship between acclimation temperature and CTMax has been consistently reported by studies with a unifactorial experimental design, particularly regarding temperate species (MADEIRA et al., 2017; VINAGRE et al., 2018; GERVAIS et al., 2021). However, silversides' upper thermal tolerance did not shift after increasing temperature within each treatment, indicating that differences regarding acclimation conditions (i.e. warm-brackish, cold-marine treatments) likely result from a combined effect of temperature and salinity. Multiple driver studies are rather scarce in the literature, and often reveal species-dependent responses (see for example RE et al., 2012; REISER et al., 2017; MADEIRA et al., 2021). Here, we showed thermal tolerance can vary over a fine-spatial scale (<20 km), regarding a 2.2°C temperature and 7 ppt salinity difference. These findings further strengthen the importance of intraspecific variation (and its underlying mechanisms) for estimating species' risk of extirpation under short and long-term warming scenarios.

Interpopulation variation in heat tolerance is often overlooked on assessments of species' vulnerability to warming (BENNETT et al., 2019; FOX et al., 2019), leading to the development of predictive distribution models based on a single experimental population. However, our work revealed a significant change in fish upper thermal tolerance in response to distinct temperature and salinity conditions observed within an estuarine system. These findings demonstrate the importance of microhabitat for an accurate estimate of warming impacts at the individual, population and species levels (BENNETT et al., 2019; DUBOIS et al., 2022). For instance, silversides' exposure to cold-marine waters resulted in a CTMax of 39.9°C, and Thermal Safety Margin (TSM) of 11.9°C. However, treating these values as absolute would underestimate the impacts of warming on *A. brasiliensis*, since fish in the warm-brackish treatment showed lower TSM (i.e. 7.2°C), despite having a higher CTMax (i.e. 40.3°C). These results indicate that juveniles may be close to reaching their absolute upper thermal limits (VAN HEERWAARDEN; KELLERMANN, 2020), which may hinder silversides' persistence in the estuary over time. Microclimate variation can also anticipate organisms' exposure to temperatures predicted in climate change scenarios, enabling acclimation at a slower pace (BAY; PALUMBI, 2014; OLDFATHER; ACKERLY, 2019; DUBOIS et al., 2022). For instance, temperature in the warm-brackish treatment (i.e. current value) was similar to the one adopted for the cold-marine treatment under the SSP2-4.5 scenario (end of century prediction). However, fish from these treatments showed distinct CTMax, revealing a potential effect of salinity on silversides' thermal tolerance.

Salinity has been recognized as a "masking factor" regarding physiological responses such as metabolism, growth, and intra and inter-specific relationships (FRY, 1971; RE et al., 2005). The interaction with temperature has been particularly addressed in thermal tolerance studies (RE et al., 2005; 2012; REISER et al., 2017; MADEIRA et al., 2021) searching for additive, synergistic or antagonist effects that shape species vulnerability to warming. Here, we provide evidence of a negative relationship in silversides' physiological tolerance of temperature and salinity, as CTMax was higher in warmer and less saline waters (i.e. regarding both current and predicted scenarios). Failure to detect an isolated effect of each variable on CTMax can also be indicative of a combined effect, but evaluation of silversides' heat tolerance under additional salinity and temperature levels is required to strengthen these findings (see COLLINS et al., 2022). As a resident species in estuarine systems, *A. brasiliensis* has great osmoregulatory capacity, and has showed stability of plasma osmolality under short-term exposure to a range of salinities (i.e. 5 to 33 ppt; SOUZA-BASTOS; FREIRE, 2011). Nonetheless, energetic costs associated with osmotic regulation may hinder cellular-level processes underlying species' thermal tolerance, such as the heat-shock response (MADEIRA et al., 2014). For instance, production of heat-shock proteins declined after exposure to combined thermal and hyposaline stress in contrast to exclusive temperature exposure, regarding the crab *Pachygrapsus marmoratus* (MADEIRA et al., 2014). The decrease in HSP production was observed despite *P. marmoratus* inhabiting the dynamic intertidal zone, where temperature and salinity (among other factors) shift constantly - a variability that is also experienced by silversides in estuaries. However, molecular analyses are required to assess how single and combined exposure of distinct thermal and salinity levels affect the heat shock response of this particular species, since literature has reported a mix of positive and negative interactions (SPEES et al., 2002; RE et al., 2012; MADEIRA et al., 2014).

Phenotypic differences in silversides' heat tolerance were reversible, which may favor their persistence in the estuary. Rapid acclimation and de-acclimation are fundamental for maintaining species performance in ecosystems with diel, daily, and seasonal variability, otherwise conditions would change faster than individuals can adjust to (ANGILLETTA, 2009). Therefore, estuaries' heterogeneity in temperature and salinity (among other environmental conditions) probably favor generalist species, averting maladaptation, and increased energetic costs associated with acclimation time lags (ANGILLETTA, 2009). Plasticity in silversides' thermal tolerance can also be related to the fine spatial scale of our study, as strong genetic structuring has been detected among populations in the Brazilian coast (CORTINHAS et al., 2016). Range-wide studies could add to the results reported herein, and reveal the prevalence of local adaptation or niche conservatism at the regional level for silversides' heat tolerance.

Silversides' CTMax did not increase after exposure to temperatures predicted in the SSP2-4.5 and SSP5-8.5 scenarios, which may be related to a) tropical species' limited potential for plasticity (VAN HEERWAARDEN & KELLERMANN, 2020), and b) our experimental design. Low acclimation capacity has been reported for species living close to their absolute physiological limits, supporting a trade-off between tolerance and plasticity (TEWKSBURY et al., 2008; VINAGRE et al., 2018; VAN HEERWAARDEN; KELLERMANN, 2020). Such negative relationship is often reflected in the small thermal safety margins of tropical species, leading them particularly vulnerable to ocean warming. However, fine-scale intraspecific variation in thermal response could buffer from the impacts of heatwaves (Figures 8 and 9) and long-term increases in temperature predicted in intermediate warming scenarios, given that phenotypic plasticity is passed on to the next generations (BENNETT et al., 2019). Methodological limitations such as a narrow range of acclimation temperatures, can also influence the degree and slope of plasticity estimates, since reaction norms are not always linear (VAN HEERWAARDEN; KELLERMANN, 2020). Acclimation period may also underlie the trends reported herein, as some studies have detected increases in CTMax after long-term exposure (i.e. 30 days) to increased temperatures (MADEIRA et al., 2017; ROHR et al., 2018). Nonetheless, analysis of comprehensive data revealed that longer acclimation periods are particularly important for large-sized organisms, whereas adjustments in the CTMax of small-bodied species such as the Brazilian silversides often occur in a short-time span (i.e. 3 days; ROHR et al., 2018).

In summary, our work showed that fine-scale (< 20 km) environmental heterogeneity drives phenotypic plasticity for the estuarine fish species *A. brasiliensis*. Seawater conditions were associated with silversides' heat tolerance and thermal safety margins, demonstrating species vulnerability to warming is relative to microhabitat features in tropical, dynamic ecosystems. These findings show the importance of accounting for intraspecific variation not only at regional, but also the local level (GERVAIS et al., 2021; DUBOIS et al., 2022), in order to accurately estimate species climatic risks. Thermal tolerance of *A. brasiliensis* reached up to 40.6ºC, enabling species persistence in the estuary during heatwaves and short-term warming (i.e. within 2-3 generations). However, it is uncertain whether the high CTMax and phenotypic plasticity can buffer long-term impacts, as the relationship between phenotype and genotype is rather complex (BENNETT et al., 2019; FOX et al., 2019). Distinct thermal sensitivities reported for silversides likely result from a combined effect of temperature and salinity, since we were not able to detach each variable's influence on CTMax. Molecular analysis and response curves are recommended to unveil the mechanisms underlying the relationship between heat tolerance and the environment. Our findings match previous studies (GERVAIS et al., 2021; DUBOIS et al., 2022), which revealed we must stop treating species and their environments as static, homogeneous units, in order to protect them from warming.

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3. SHIPPING TRAFFIC, SALINITY AND TEMPERATURE SHAPE NON-NATIVE FISH RICHNESS IN ESTUARIES WORLDWIDE

Manuscrito a ser submetido no periódico *Science of the Total Environment* (Fator de Impacto = 10,754)

Abstract

Non-native species threaten biodiversity conservation and ecosystem functioning. Management at early-invasion stages can prevent ecological and socioeconomic impacts, but rely on the identification of drivers of non-native species occurrence at distinct scales. Here, we identify environmental and anthropogenic drivers of non-native fish richness across estuaries worldwide. We performed model selection using proxies of colonization pressure, habitat availability and connectivity, anthropogenic disturbance and climate, to assess the primary mechanisms underlying non-native species occurrence. Species traits (i.e. thermal and salinity affinities) were also used to investigate latitudinal and guild-related (i.e. freshwater, brackish, marine) trends in non-native occurrence. Data retrieved from a literature review revealed 147 non-native fish species in 147 estuaries worldwide. Shipping traffic, salinity (minimum and range values) and temperature (minimum value) were the main predictors of non-native fish richness. Hotspots of non-native species were under heavy levels of shipping traffic, had higher salinity (both minimum and range values) and colder waters (lower minimum temperature values). We also found evidence of thermal limits to species' geographic area of introduction. Latitude of invaded estuaries were negatively correlated with species' minimum, mean and maximum thermal affinities, and positively correlated with thermal affinity ranges. Most non-native species recorded in estuaries were freshwater, even though they tolerate maximum salinities of 25-35 pss. Conversely, marine species did not withstand minimum salinities below 30 pss. These contrasting tolerances may underlie the positive relationship between non-native richness and increased salinity. Our results indicate that colonization pressure and habitat filtering are the primary mechanisms underlying non-native fish richness in estuaries, contributing to the development of management strategies targeting early-invasion stages. Matching climate between native and non-native ranges was particularly important for predicting introductions at the global scale. Conversely, local fluctuations in salinity likely drove non-native richness through increased habitat availability for generalist species.

Keywords: Colonization pressure, Habitat filtering, Fluctuating Resource Availability, Invasiveness, Invasibility, Human activities

3.1 Introduction

Invasive species are recognized as a major threat to biodiversity conservation (IPBES, 2019), and have been associated with biotic homogenization, disruption of native communities, increased extinction risk for endangered species, and the impairment of ecosystem functions (STRAYER, 2012; BLACKBURN et al., 2019; JESSE et al., 2020; LIU et al., 2020a). Despite their pervasive impacts, management at early-invasion stages is often neglected (CUTHBERT et al., 2022), as control and eradication measures are frequently implemented after the detection of *in-situ* impacts (SIMBERLOFF et al., 2013). Prevention of biological invasions relies on the identification of anthropogenic and environmental correlates of non-native species occurrence, in order to understand niche-related processes underlying their establishment and growth in the novel environment (STRUBBE et al., 2014; LIU et al., 2020b). Further, the assessment of drivers of non-native richness operating at distinct scales (i.e. global, regional and local) can promote the development of suitable mitigation strategies (i.e. related to the scale of implementation; e.g. protected areas, country-wide spatial planning), reducing economic costs while enhancing control and eradication of invasive species (SIMBERLOFF et al., 2013; CUTHBERT et al., 2022).

Human activities are widely associated with non-native species occurrence (LEPRIEUR et al., 2008; BRABENDER et al., 2016; LIU et al., 2020a), and underlie invasion hypotheses such as those related to colonization pressure and disturbance (ENDERS et al., 2020). The number of species introduced to a given location represents a primary determinant of invasion success (i.e. colonization pressure hypothesis; LOCKWOOD et al., 2009), and takes place via anthropogenic pathways (e.g. trades of goods and aquaculture; LEPRIEUR et al., 2008; BLACKBURN et al., 2011). Intensified trade via shipping represents a central vector for invasive species spread, and is expected to boost translocations of both marine and terrestrial taxa by 2050, escalating global invasion risk up to 20 fold (SEEBENS et al., 2016; SARDAIN et al., 2019). Further, the presence of vectors and other anthropogenic pressures (e.g. habitat modification due to land-use change, dam construction and population growth) can increase ecosystem's invasibility as result of disturbance (ELTON, 1958; HOBBS; HUENNEKE, 1992). Human-induced environmental changes have been linked to biodiversity loss and altered biotic interactions (JENNINGS; POLUNIN, 1997; HILBORN et al., 2003; CORREA et al., 2015), which creates a “resource gap” that can be explored by non-native species (i.e. fluctuating resource hypothesis; ELTON, 1958; HOBBS; HUENNEKE, 1992; BERNARDO et al., 2003; DAVIS et al., 2000). However, in order to exploit feeding and reproductive resources, introduced species need to first overcome the abiotic filter (BLACKBURN et al., 2011).

Survival of non-native species is underpinned by either the local environment, species traits and/or the interaction between these components (BLACKBURN et al., 2011). Moreover, previous evidence indicates similarities in environmental processes underlying native and non-native richness, such as the species-area (BURNS et al., 2015; GUO et al., 2021) and species-energy (which is correlated with temperature) relationships (LEVINE; D'ANTONIO, 1999; EVANS et al., 2005). Despite some support for these invasibility-related mechanisms (TREASURE et al., 2019; GUO et al., 2021), invasion success has also shown strong signs of context-dependency (BLANCHET et al., 2009; GONZÁLEZ-MORENO et al., 2014), since pre-adaptation to environmental conditions may increase species' chance of establishment in the non-native area (i.e. habitat filtering hypothesis; WEIHER; KEDDY, 1995). Matching abiotic conditions between native and non-native ranges is particularly important to foreseen areas with high invasion risk at global scale, since conservatism of the climatic niche was detected for most invasive species (GONZÁLEZ-MORENO et al., 2014; LIU et al., 2020b). Non-native establishment is also underpinned by ecological specialization, and higher rates of success have been detected for generalist species (FISHER; OWENS, 2004). Flexibility in resource use is particularly important for ecological processes operating at the local scale, as it may enable species occurrence under a variety of environmental conditions, and provide competitive advantage over native specialists (DUNCAN et al., 2003; CLAVEL et al., 2011).

Anthropogenic and environmental factors mediating non-native species occurrence can be identified using data from estuarine systems. The concentration of vectors (e.g. aquaculture, shipping, recreational activities) and other anthropogenic pressures (e.g. habitat modification in response to urbanization; fishing) have been related to a greater susceptibility to invasion in these systems (WILLIAMS; GROSHOLZ, 2008; PREISLER et al., 2009).

However, estuaries are ruled by constant fluctuations in environmental conditions, especially temperature and salinity, which can prevent the establishment and spread of non-native species (CHENG; GROSHOLZ, 2016). Nonetheless, generalist traits often exhibited by invasive species (CLAVEL et al., 2011) may enable colonization of these dynamic systems, and further spread into adjacent areas (PREISLER et al., 2009). Therefore, the assessment of drivers of non-native richness in estuarine systems may thus elucidate anthropogenic and environmental processes underlying invasion at both global (e.g. climate, trade) and local (e.g. fluctuations in abiotic conditions) scales, which are needed for the development of effective mitigation strategies (SIMBERLOFF et al., 2013; GONZÁLEZ-MORENO et al., 2014). Moreover, the identification of donor and receiver areas, and hotspots of non-native species occurrence has not yet been carried out for estuaries worldwide, since previous studies were restricted to a regional scale (MEAD et al., 2011; KUME et al., 2021) and few model systems (NEHRING, 2006).

Here, we identify environmental and anthropogenic correlates of non-native richness, using compiled data on fish species occurrence across estuaries worldwide. We combine proxies of colonization pressure, habitat availability and connectivity, anthropogenic disturbance, and climate, to assess the primary mechanisms underlying non-native species occurrence. We expect a positive effect of a) colonization pressure, b) anthropogenic disturbance, c) habitat availability and connectivity and d) temperature, on non-native fish richness. Conversely, we predict lower richness at estuaries with greater variations in salinity (i.e. salinity range), which would hinder the occurrence of stenohaline species. Our expectations regarding the role of each driver were related to several hypotheses in invasion science (i.e. colonization pressure, disturbance, fluctuating resource availability and habitat filtering; ENDERS et al., 2020), and the species-area (i.e. habitat availability and connectivity; BURNS et al., 2015; GUO et al., 2021) and species-energy (i.e. temperature; LEVINE; D’ANTONIO, 1999; EVANS et al., 2005) relationships. We also assess the salinity and temperature affinities of non-native fish species in our database, to detect niche-related mechanisms underlying richness trends. Specifically, we test the association between species thermal affinity and latitude of the invaded estuary, and evaluate the tolerance of species within distinct salinity guilds (i.e. freshwater, brackish, marine).

3.2 Materials and Methods

3.2.1 Literature review and data compilation

Data on non-native fish species occurrence in estuaries were obtained through a literature search on Google Scholar online database (https://scholar.google.com), applying the keywords: [estuar*] AND [alien OR inva*] AND [fish]. The first thousand publications retrieved from the search were screened, and those that reported the occurrence of a single or multiple non-native fish species in estuarine systems were compiled into a database. Therefore, we excluded studies that did not report species' sampling location or that were performed outside estuaries, hereby defined as transitional systems under the influence of both inland and oceanic waters (ELLIOTT et al., 2007). Multiple studies reporting the occurrence of a single species in the same estuary were kept in the database whenever their data were obtained from separate surveys (i.e. represented distinct datasets). We also screened the references list of eligible studies to check for additional reports undetected in the primary search. Data were extracted from scientific articles, books that are freely available online, and grey literature (i.e. technical reports, monographs, theses and catalogs).

The year of manuscript publication, estuary's name and geographical coordinates, non-native fish species and fishing gear, were extracted from each eligible study. We also retrieved non-native fish species' potential vector of introduction from a subset of studies, which were grouped into eight categories: aquaculture, aquarium trade, commercial fishing, sport fishing, ballast water and biofouling, biological control, secondary expansion due to climate change and secondary expansion due to the development of man-made structures. Some studies reported more than one vector of introduction of non-native fish species, and each record was assigned to the suitable category (i.e. a single study could have more than one entry). The presence of a single non-native fish species in the estuary, the geographical coordinate of the estuary, and the study reporting such information, represented an occurrence record. Geographical coordinates were obtained from Google Earth (http://www.google.fr/intl/fr/earth/index.html), when not provided by the original study. We also estimated the area (km^2) covered by each estuary using Google Earth, and identified the respective marine ecoregion according to SPALDING et al. (2007). Non-native fish species cited on the retained publications were verified for terminology updates using the Eschmeyer's Catalog of Fishes online database (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp;

FRICKE et al., 2021). We also recorded the native distribution and salinity guild (i.e. freshwater, freshwater-brackish, marine, marine-brackish and freshwater-brackish-marine) of each non-native fish species listed in estuaries using this database.

3.2.2 Worldwide distribution of non-native fish species

The number of non-native fish species per ecoregion was assessed through a map built using the shapefile of the Marine Ecoregions of the World (MEOW) (http://www.marineregions.org/downloads.php; SPALDING et al., 2007) in the Quantum GIS 3.2.3 software (QGIS DEVELOPMENT TEAM, 2022). The most introduced fish species in estuaries were identified through a frequency of occurrence of ≥5% in all estuaries in our database. Latitude of the estuaries invaded by each of these species was compiled to assess their distribution range across the globe.

Chord diagrams were built to identify major donor and recipient areas of non-native fish species, using the '*circlize*' package (GU et al., 2014) for the R language and software (R CORE TEAM, 2021). To accomplish this goal, we divided the globe into seven continental regions: North and Central America, South America, Europe, Africa, North and East Asia, Central and South Asia, and Oceania (adapted from LIU et al., 2020a). The native distribution of each fish species was used to identify potential single (i.e. species native to only one continental region) or multiple (i.e. species native to at least two continental regions) donor areas, except when authors of the original studies reported the exact region as propagule source. Nonetheless, an additional link between species' native area and the reported propagule source was included as an entry in our spreadsheet, whenever the latter clearly represented a secondary introduction outside the geographical limits of species' original distribution. Recipient areas were represented by the continent-wide regions in which the invaded estuaries are located.

3.2.3 Predictors of non-native fish richness

The number of non-native species in a system has been associated with multiple drivers such as area, human interference and climate (LIU et al., 2020a; THEOHARIDES; DUKE, 2007). Here, we established 18 potential predictors of non-native fish richness in estuaries, which were divided into two groups: I) Environmental filtering, which encompassed proxies for habitat availability and connectivity, and climate; and II) Human activities, which comprised proxies for anthropogenic disturbance and colonization pressure (see Table 11 in Supplementary File 1 for data description and download source). Data were extracted by placing a 50 km buffer (diameter) at the center of each estuary, which was overlapped with the respective shapefile of each variable. Buffer scale was chosen after assessing estuaries' spatial coverage and the degree of overlap with adjacent systems under several distances (e.g. 10 km, 50 km, 100 km). These tests revealed a maximized coverage of most estuaries and reduced overlap with neighboring areas for the 50 km buffer. We only retained average values (i.e. mean of total pixels within the 50 km buffer) of each variable to perform the statistical analyses. Variables were tested for collinearity using the *correlate* function (method=”spearman”) in the *corrr* package (KUHN et al., 2022) for the R software (R CORE TEAM, 2022). We established a ≥0.6 correlation threshold to select variables for modeling the richness of non-native fish in estuaries (see section 2.4.). Therefore, the final set of variables (unit of measure) within each group was: I) Environmental filtering - area (km^2), mean annual discharge (m^3/s), minimum annual inundation (percent cover), minimum temperature ($^\circ$C), minimum salinity (pss) and salinity range (pss); and II) Human activities - dam area (km^2), shipping traffic (number of ship tracks recorded in a single 1km^2 cell), risk of invasive species (i.e. port volume; metric tons, mt), population density (people per km^2) and navigable waterways (index). All statistical analyses were performed in R language and environment (R CORE TEAM, 2022).

3.2.4 Model selection

Generalized linear mixed models (GLMM) for the negative binomial family were performed to test for predictors' effects on the richness of non-native fish species in estuaries. Statistical family and error distribution was chosen after detecting overdispersion for the response variable (LINDÉN; MÄNTYNIEMI, 2011). Richness of non-native species was corrected by the number of studies retrieved for each estuary, as previous tests showed a significant and positive correlation between these variables (linear regression: t-value=15.16, p<0.0001). Predictors (i.e. the final set of variables reported in section 2.3., and listed in Table 11 in Supplementary File 1; treated as fixed factors) were $\log_{10}$-transformed, and standardized using the *decostand* function in the *vegan* package (OKSANEN et al., 2022). Estuary's ecoregion was also included in the model, and treated as a random effect to control for spatial autocorrelation (LIU et al., 2020a). We ran a global model with all the predictors from the I) Environmental filtering and II) Human activities groups, using the function *glmer.nb* in the *lme4* package (BATES et al., 2015). Model selection was further performed to assess the best combinations of predictors in the global model, using the *dredge* function in the *MuMIn* package (BARTOŃ, 2022). Models were ranked according to the Corrected Akaike Information Criterion (AICc; BROCKWELL; DAVIES, 1991), and those with ΔAICc < 2 (i.e. difference between the AICc of each model and the model with the lowest AICc) were considered indistinguishable (BURNHAM; ANDERSON, 2002). Then, we averaged the parameter estimates across these models using the *model.avg* function in the *MuMIn* package (BARTOŃ, 2022). Model-averaged coefficients were calculated across all likely models (i.e. with ΔAICc < 2), including those where a given predictor was absent; in this scenario, the variance and coefficient of the predictor were set to zero (BURNHAM; ANDERSON, 2002). The main predictors of non-native fish species in estuaries were also identified by having a sum of Akaike weights equal to or higher than 0.80. Previous to running model selection, we assessed the variance inflation factor (VIF) of the global model, using the *multicollinearity* function in the *performance* package (LÜDECKE et al., 2021). We also simulated and tested model residuals for spatial autocorrelation (i.e. Moran's tests), using the functions *simulateResiduals* and *testSpatialAutocorrelation*, which are available in the *DHARMa* package (HARTIG, 2022).

3.2.5 Species' environmental affinity and invasiveness

Estuaries show diel, daily and seasonal variability in water conditions, mainly temperature and salinity, which may prevent the successful introduction and establishment of non-native species. Therefore, we estimated the thermal and salinity affinities of non-native fish species in our database to assess the relationship between these traits and invasiveness. First, we retrieved fish species occurrence from the Global Biodiversity Information Facility

(GBIF, http://www.gbif.org/). Data for each species was retrieved from native and non-native areas around the globe, as evidence supports niche conservatism for invasive species (STRUBBE et al., 2014; LIU et al., 2020b). Occurrence records were tested for duplicates, validity, zeros, equal coordinates, capitals, centroids, gbif, institutions and urban areas, using the *clean_coordinates* function in the *CoordinateCleaner* package (ZIZKA et al., 2019). Flagged records were removed from the dataset. The *sp* (PEBESMA; BIVAND, 2005; BIVAND et al., 2013) and *rgdal* (BIVAND et al., 2021) packages were used to transform species occurrence data from csv to shapefile format, and to create a polygon delimiting each species' range of occurrence. These data were then overlapped with surface temperature (i.e. minimum, mean, maximum and range values) and salinity (i.e. minimum and maximum values) shapefiles retrieved from BioOracle (https://www.bio-oracle.org/, TYBERGHEIN et al., 2012; ASSIS et al., 2018). We used the *extract* function in the *raster* package (HIJMANS; ETTEN, 2012) to retrieve temperature and salinity values throughout each species occurrence range (i.e. polygon). These values were then averaged to represent the thermal and salinity affinities of each non-native fish species. We only assessed the minimum and maximum salinity affinities of non-native fish species in our database, as BioOracle layers do not overlap with continental ecosystems (i.e. rivers and lakes). As consequence, estimates regarding freshwater species could be biased towards both higher (i.e. mean) and lower values (i.e. range).

Linear regressions were performed using non-native species thermal affinity as a function of estuary's latitude, to assess the relationship between species' realized thermal niche and geographic area of introduction. Entries for these analyses consisted of species thermal affinity and the absolute latitude of the invaded estuary; therefore, a single estuary had as many entries as the number of non-native species reported. Regressions were performed using the *lm* function in the *stats* package (R CORE TEAM, 2022). Model residuals were inspected for normality and heterogeneity of variance using the *check_model* function in the *performance* package (LÜDECKE et al., 2021).

We also produced raincloud plots using the salinity affinities (i.e. minimum and maximum values) of non-native species within each guild proposed by FRICKE; ESCHMEYER (2021), to assess whether distinct halotolerances may underlie invasiveness trends (e.g. more introductions reported for marine fish species). Raincloud plots were created using the *ggdist* (KAY, 2022) and *ggplot2* packages (WICKHAM, 2016).

3.3 Results

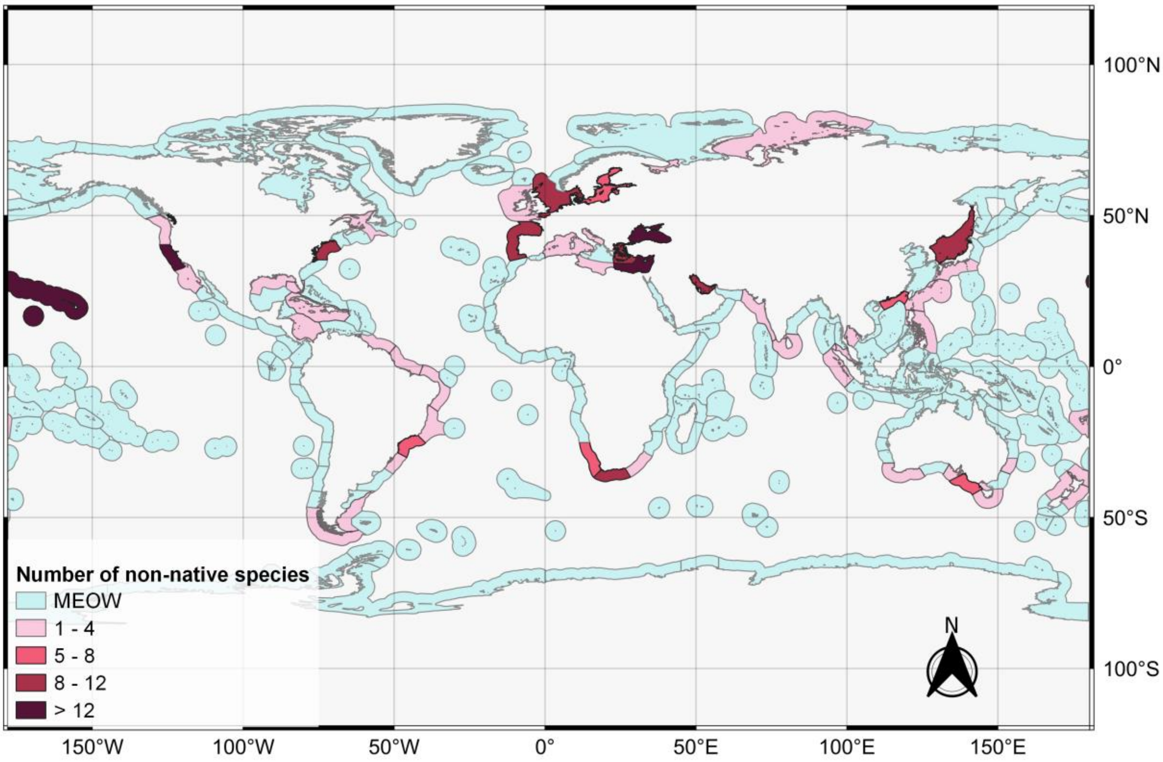
3.3.1 Review descriptive statistics

The literature review retrieved 1,279 publications, of which 215 fitted our eligibility criteria and were retained for data compilation (i.e. 759 occurrence records) and analysis (Supplementary File 2). Studies were published between 1928 and 2019, and reported data on 147 non-native fish species introduced in 147 estuaries worldwide (Table 12 in Supplementary File 3). Estuaries were distributed across all marine realms, excepting for the Southern Ocean, the Tropical Eastern Pacific and the African coast of the Tropical Atlantic, and covered |0° to 68°| degrees in latitude (Figure 10). Non-native fish species were sampled by several types of gear, such as nets (i.e. beach and purse seines, and cast, lift, drop, drift, gill, trammel, encircling, fyke and scoop nets), longline, trawl, electrofishing, hook and line, slurp gun, speargun, baited and plastic minnow traps. Few studies also reported data from underwater visual census, eDNA, catch landing sites and local markets, interviews with fishermen and museum collections. Aquaculture (N=56 records), commercial fishing (N=51 records) and ballast water and biofouling (N=41 records), were the main vectors of introduction of non-native fish species in estuaries, according to a subset of studies in our database. Sport fishing (N=30 records), biological control (N=24 records), aquarium trade (N=23 records), secondary expansion due to development of man-made structures (N=8 records) and climate change (N=1 record), were also cited as vectors by these publications.

3.3.2 Worldwide distribution of non-native fish species

Marine ecoregions with the highest number of non-native fish species were Northern California (S=37), Hawaii (S=13), Black Sea (S=13) and the Levantine Sea (S=13) (Fig. 10). Estuaries that represented hotspots of non-native fish species within these respective ecoregions were the San Francisco Bay (S= 37), Pearl Harbor (S=11), Dnieper-Bug (S=6) and Iskenderun Bay (S=8). Despite the worldwide distribution of estuaries included in our database (i.e. |0° to 68°| degrees in latitude), the majority of systems with at least five non-native species were located in the northern hemisphere (36º to 60º degrees in latitude; Fig. 10). Ecoregions with records of ≥ 5 non-native species (i.e. considering both the northern and southern hemispheres) represented 32% of our data. Conversely, 68% of marine ecoregions recorded up to four non-native fish species.

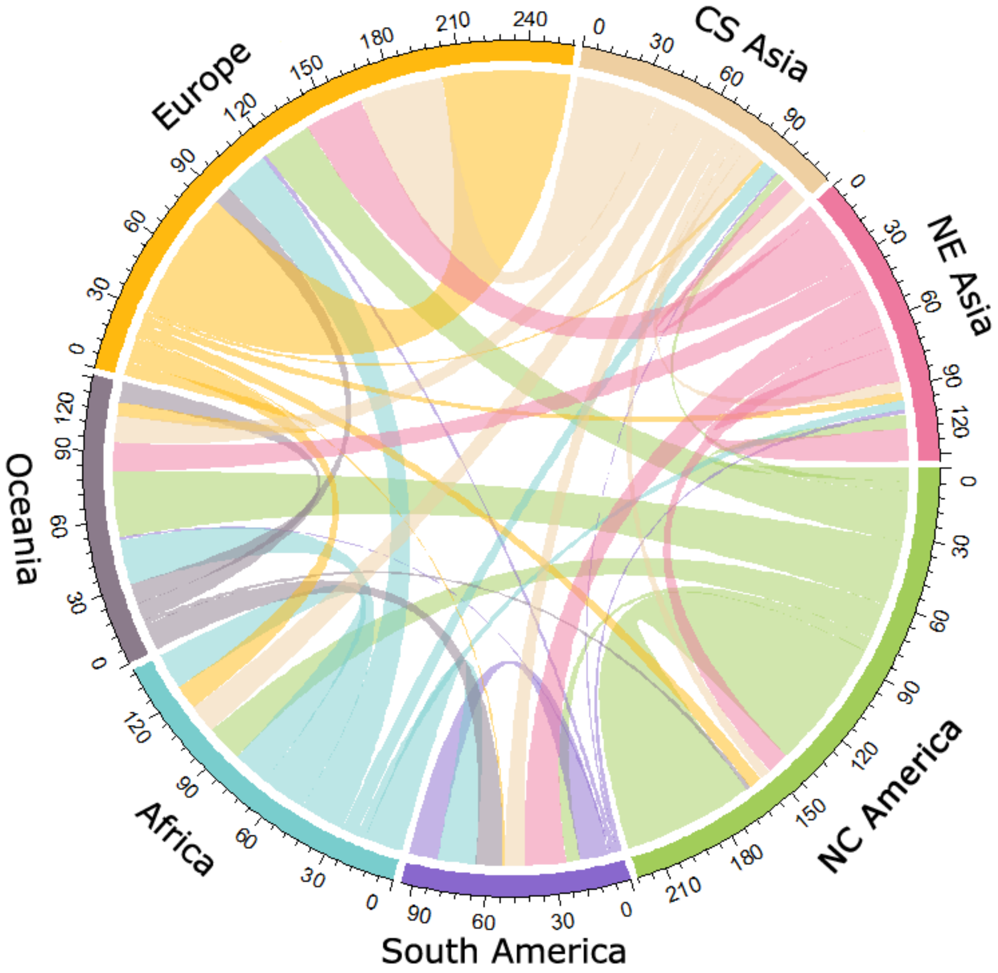
Figure 10 - Number of non-native fish species reported in estuaries per Marine Ecoregions of the World (SPALDING et al., 2007).



Source: The author, 2022.

Europe and North America are the major donors of non-native fish species recorded in estuaries across the globe (Figure 11). Europe is also the most important recipient area, followed by Oceania, South America and North America. Species introduced in Europe were mainly native to the continent, and to North and East Asia, North America and Africa (Fig. 11). Non-native species in Oceania and South America originate from several continents, while the majority of species established in the estuaries of North America are native to the same continent. The chord diagram also revealed Asia and Africa are donating more species than receiving, while the opposite pattern was observed for Oceania and South America (Fig. 11).

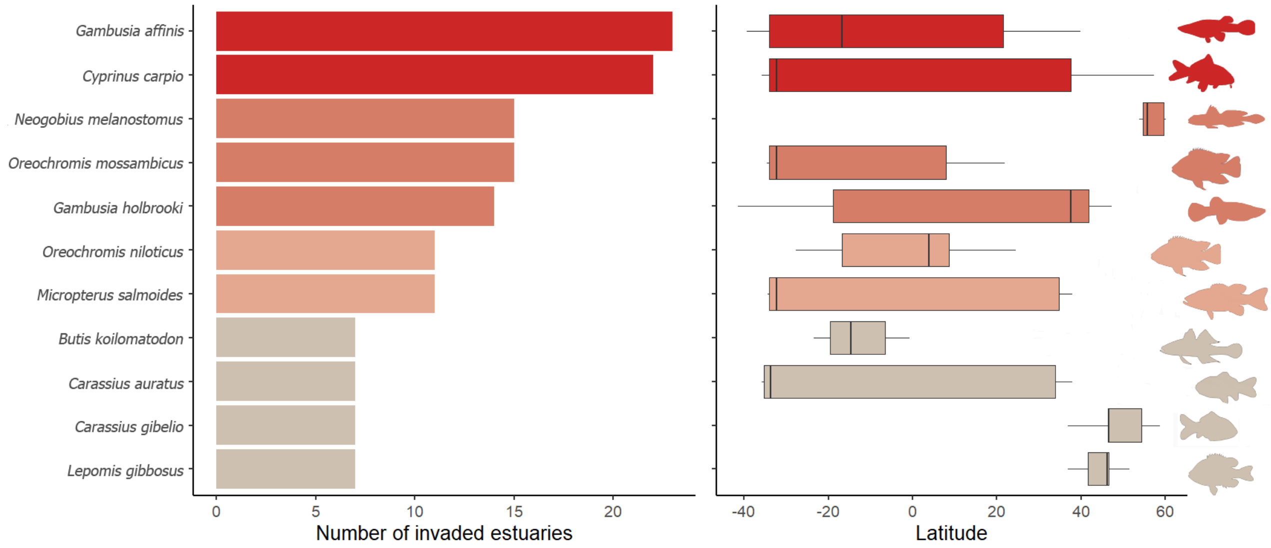
Figure 11 - Chord diagram showing the global flow of fish species from native to non-native areas.



Legend: Colors represent the continents where species are native and chord width depicts the number of introduction events in non-native areas. The size of the outer circle segments indicates the total number of introductions in or originating from the continent. CS Asia = Central and South Asia; NE = North and East Asia; NC America = North and Central America.
Source: The author, 2022.

Eleven non-native fish species were introduced in ≥ 5% of estuaries included in the present study. *Gambusia affinis* (Baird & Girard, 1853) and *Cyprinus carpio* Linnaeus, 1758 were recorded in the greatest number of estuaries (N=23 and 22, respectively), which were located across a broad latitudinal range (from -40ºS to 40ºN ; Figure 12). A wide latitudinal distribution was also noticed for *Oreochromis mossambicus* (Peters, 1852), *Gambusia holbrooki* Girard, 1859, *Micropterus salmoides* (Lacepède, 1802) and *Carassius auratus* (Linnaeus, 1758). Nonetheless, *Neogobius melanostomus* (Pallas, 1814) was recorded in estuaries across a narrower latitudinal range (between 40°N and 60°N), despite accounting for the third highest number of introductions in our database (Figure 12). A restricted latitudinal distribution was also observed for *Butis koilomatodon* (Bleeker, 1849), *Carassius gibelio* (Bloch, 1782; in contrast to its congener *C. auratus*) and *Lepomis gibbosus* (Linnaeus, 1758).

Figure 12 - Non-native fish species recorded in ≥ 5% of estuaries included in our database. The number of estuaries wherein each species was recorded, and its latitudinal range are shown in the figure.



Legend: Boxplots show medians (solid lines), with lower and upper hinges corresponding to the first and third quartiles, respectively. The color gradient was also established according to the number of estuaries non-native species were recorded.
Source: The author, 2022.

3.3.3 Predictors of non-native richness

Model selection revealed 22 indistinguishable combinations (i.e. models with ΔAICc < 2) of predictors from the I) Environmental filtering and II) Human activities groups. The selected variables and model-averaged coefficients are shown in Table 5. Richness of non-native fishes increased with shipping traffic (z=2.58, p=0.01), estuary's salinity range (z=3.11, p=0.002) and minimum salinity (z=2.53, p=0.01). Estuary's minimum temperature showed a negative, but marginal, effect (z=1.78, p=0.07) on the number of non-native fish species. These four variables were the most important (i.e. sum of Akaike weights ≥ 0.80) for predicting non-native fish richness in estuarine systems (Table 5). Our results were robust to collinearity (VIF<1.5) and spatial autocorrelation (p=0.49; both tests were performed on the global model).

Table 5 - Model-averaged coefficients of the selected predictors (i.e. included in top-ranking models ΔAICc < 2) of non-native fish richness in estuaries. Variable importance is expressed as the sum of Akaike weights across the top-ranking models, amounting to a maximum value of 1.

Selected variables in top-ranking models (ΔAICc < 2)	**Estimate**	**Adj. SE**	**z**	**p**	**Importance**
(Intercept)	0.37	0.09	4.22	<0.0001	
Environmental filtering					
Minimum annual inundation (percent cover)	0.06	0.09	0.71	0.48	0.47
Minimum salinity (pps)	0.33	0.13	2.53	**0.01**	**1**
Salinity range (pps)	0.30	0.10	3.11	**0.002**	**1**
Minimum temperature (^{o}C)	-0.16	0.09	1.78	0.07	**0.9**
Human activities					
Shipping traffic (number of ship tracks per 1km^2)	0.22	0.09	2.58	**0.01**	**1**
Risk of invasive species (metric tons, mt)	0.09	0.12	0.81	0.42	0.54
Population density (people per km^2)	-0.13	0.12	1.11	0.27	0.71
Dam area (km^2)	0.11	0.10	1.12	0.26	0.72
Navigable waterways (index)	-0.09	0.08	1.04	0.30	0.68

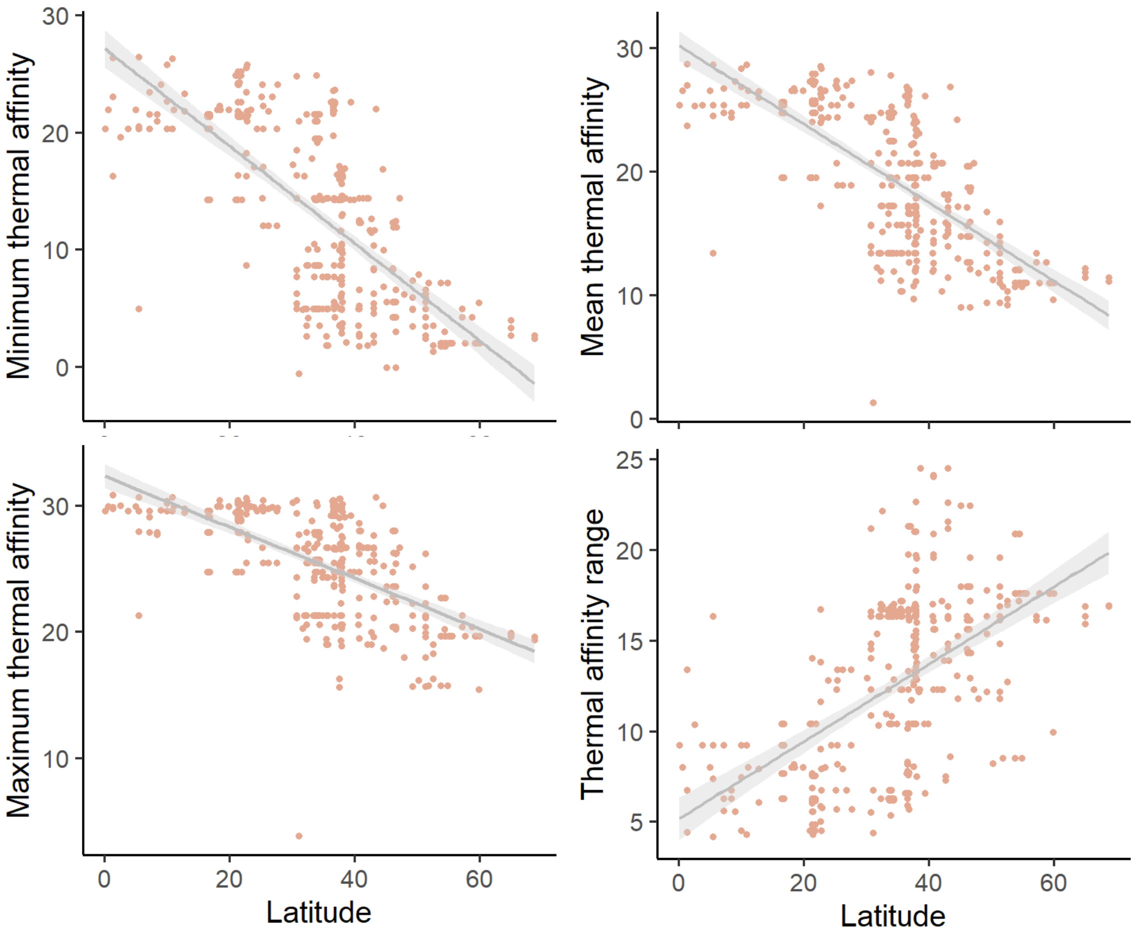
Legend: Statistically significant p-values (p<0.05) and variables with importance ≥0.8 are shown in bold. Adj. SE – adjusted standard error.

3.3.4 Species' environmental affinity and invasiveness

Latitude predicted the realized thermal niche of non-native fish species in estuaries (Figure 13). Estuaries located at higher latitudes recorded non-native species with lower minimum (t-value=-18.89, p<0.0001, adj. R^2=0.49), mean (t-value=-19.12, p<0.0001, adj. R2=0.50) and maximum (t-value=-15.56, p<0.0001, adj. R^2=0.40) thermal affinities, and wider thermal affinity ranges (t-value=13.24, p<0.0001, adj. R^2=0.32).

Most non-native fish species recorded in estuaries were freshwater (S=52), even though their maximum salinity affinity ranged from 25 to 35 pss (Figure 14). The freshwater-brackish-marine (S=36) and freshwater-brackish (S=34) guilds comprised the second and third highest number of non-native fish species in our database. Maximum salinity affinities within these guilds also reached 20 to 35 pss, and values were widely distributed in contrast to the freshwater guild (Fig. 14). Non-native species within the freshwater-brackish-marine guild also showed a wide range for minimum salinity affinity (Fig. 13). The marine (S=17) and brackish-marine (S=8) guilds had the lowest number of non-native fish species in our database. Minimum salinity affinities within the marine guild ranged between 30-35 pss, showing a narrow distribution. Conversely, affinities of non-native species within the brackish-marine guild varied mostly from 25 to 35 pss (Fig. 14).

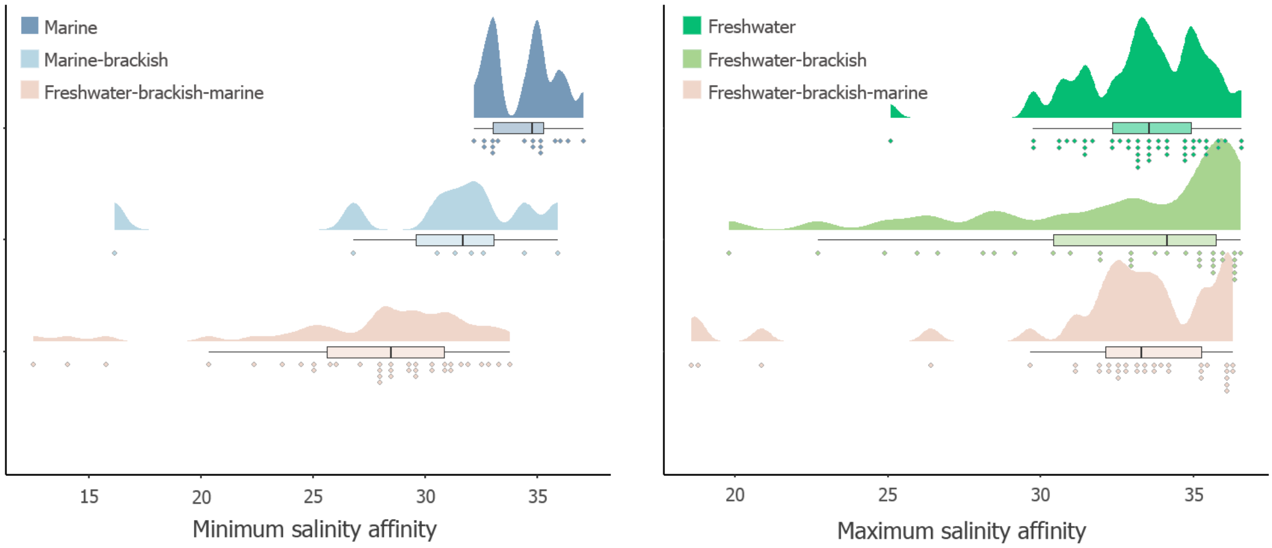
Figure 13 - Thermal affinity (minimum, mean, maximum and range values) of non-native fish species across latitude (i.e. absolute value) of the invaded estuary.



Legend: The light gray-shaded areas represent the 95% confidence interval.

Source: The author, 2022.

Figure 14 - Raincloud plots showing the minimum and maximum salinity affinities of non-native fish species per guild.



Legend: Data distribution is presented as unmirrored violin plots, combined with boxplots showing medians (vertical solid lines), with lower and upper hinges corresponding to the first and third quartiles, respectively. Vertical jitter below the boxplots represents individual data points.
Source: The author, 2022.

3.5 **Discussion**

Our work identified shipping traffic (as a proxy of colonization pressure), salinity and temperature (as proxies of environmental conditions and habitat filtering) as the main drivers of non-native fish richness in estuaries. Analysis of data revealed the number of non-native species increased with shipping traffic, supporting the well-documented and positive relationship between colonization pressure and non-native richness (LOCKWOOD et al., 2009). Temperature and salinity were also correlated with non-native richness, but the trends detected disagree with our preliminary expectations. A higher number of non-native species was recorded in estuaries with increased salinity (both minimum and range values) and colder (i.e. lower minimum temperature) waters. Moreover, the influence of temperature on non-native richness is likely related to the environmental conditions experienced by species in their native range, as we found an association between the realized thermal niche and geographic area of introduction (in accordance with the habitat filtering hypothesis; WEIHER; KEDDY, 1995). Distinct salinity affinities of marine and freshwater species also underpinned the trends in non-native richness, and represented an important component of species invasiveness (MOYLE; STOMPE, 2022). Conversely, habitat availability and connectivity, and other proxies of anthropogenic disturbance (e.g. population density, dam area) were not associated with the occurrence of non-native fish species. These results demonstrate that colonization pressure, rather than other human-related sources of disturbance, is a major driver of non-native fish richness in estuaries (LOCKWOOD et al., 2009). Nonetheless, pre-adaptation to environmental conditions in the recipient area is also a crucial invasiveness trait for non-native species occurrence (WEIHER; KEDDY, 1995; KELLER et al., 2011; SEEBENS et al., 2016).

Colonization pressure has been widely recognized as a primary determinant of invasion success (LOCKWOOD et al., 2009; ENDERS et al., 2020). The concept of “the more you introduce, the more you get” is underpinned by the likelihood of at least one introduced species experiencing favorable conditions in the invaded area (LOCKWOOD et al., 2009; ENDERS et al., 2020), which agrees with the trends detected in our study. Estuaries that represented hotspots of non-native species (e.g. San Francisco Bay, Pearl Harbor) were under heavy levels of shipping traffic, which represents an important vector for species introduction in aquatic ecosystems through ballast water (KELLER et al., 2011; HALPERN et al., 2015; SEEBENS et al., 2016). Successful invasions, and the overall occurrence of non-native species, may also be related to adverse effects on the native fauna (i.e. disturbance hypothesis; ELTON, 1958; HOBBS; HUENNEKE, 1992), since shipping traffic also represents a proxy for local disturbances, such as fishing (HALPERN et al., 2015). The removal of native species and individuals from the environment often leads to diversity loss, and alters the intensity of biotic interactions (JENNINGS; POLUNIN, 1997; HILBORN et al., 2003; CORREA et al., 2015), creating a “resource gap” that can be exploited by non-native species (i.e. fluctuating resource availability and disturbance hypothesis; ELTON, 1958; HOBBS; HUENNEKE, 1992; BERNARDO et al., 2003; DAVIS et al., 2000). Nonetheless, the deliberate introduction of target species (i.e. high commercial value) was widely reported by some studies included in our database, emphasizing this economic activity (i.e. fishing) represents not only a disturbance, but also a potential vector for non-native species introduction. Moreover, other proxies of anthropogenic disturbance (i.e. including the volume of ports, labeled as risk of invasive species) were not related to non-native species occurrence.

These results indicate that shipping traffic shapes non-native richness primarily as a result of colonization pressure.

Temperature also predicted non-native fish richness in estuaries, and the trends detected align with previous evidence of niche conservatism for invasive species (STRUBBE et al., 2014; LIU et al., 2020b). Non-native richness was higher in estuaries with cooler waters (i.e. lower minimum temperature), which may be related to species' ecological requirements in their native range. The majority of species in our database are native from the temperate zone (i.e. North America and Europe), and have affinity for lower temperatures. Such trait likely favors their occurrence in cold-water estuaries (leading to increased non-native richness), due to pre-adaptation to the environmental conditions experienced in the invaded area (in accordance with the habitat filtering hypothesis; WEIHER; KEDDY, 1995). The high number of within-continent introductions (Fig. 11), and the latitudinal trends detected for species' realized thermal niche, represents further evidence of a climatic constraint for non-native fish occurrence. Species with affinity for warmer waters (i.e. minimum, mean and maximum values) and narrower thermal ranges, were recorded in estuaries at lower latitudes; conversely, cold-affinity species with wider thermal ranges were recorded in estuaries at higher latitudes (Fig. 13). These trends have also been detected for the native fauna (STUART-SMITH et al., 2017), indicating that non-native species may conserve their climatic niche during invasions (STRUBBE et al., 2014; LIU et al., 2020b), despite their often generalist traits (CLAVEL et al., 2011). The narrow latitudinal distribution of *N. melanostomus*, *C. auratus* and *L. gibbosus* (i.e. species recorded in ≥ 5% of estuaries) may also be related to climate, or the absence of propagules arriving at systems distributed across a wider geographic range, which is unlikely since these species were recorded in estuaries under intense shipping traffic (e.g. San Francisco Bay, Dnieper-Bug). Nonetheless, climate change can favor non-native species spread (i.e. secondary introductions) to areas that are currently unsuitable for occurrence, as reported for *Alosa sapidissima* (WILSON, 1811) at Bahía Todos Los Santos (ROSALÉS-CASIAN, 2015). Warming has also been reported for driving dominance shifts in native communities (MCLEAN et al., 2021; STUART-SMITH, 2021; SOUZA; SANTOS, 2023), which may favor non-native species occurrence as result of disturbance and changes in resource availability (ELTON, 1958; HOBBS; HUENNEKE, 1992; BERNARDO et al., 2003; DAVIS et al., 2000). However, a global trend regarding the influence of climate change on non-native richness has not yet been detected (see HELLMANN et al., 2008 for potential scenarios), as studies often report species-dependent responses (e.g. CAPINHA et al., 2013; HILL et al., 2017; FULGÊNCIO-LIMA et al., 2021).

Salinity also shaped non-native richness, and represented an important proxy of environmental heterogeneity at local scale. Analysis of data revealed a higher number of non-native species in estuaries with greater salinity range, in contrast to our prior expectations. Habitat availability for species with distinct ecological requirements (i.e. salinity affinities) may underlie this trend. River discharge and seawater inflow create a salinity gradient along the estuary, which enables species colonization from both freshwater and marine realms (ELLIOT et al., 2007), leading to increased native and non-native richness. However, species incursions can be either permanent or temporary, in response to diel, daily and seasonal fluctuations in salinity; and lead to widespread or a restricted (e.g. near river's mouth) distribution within the estuary. Therefore, colonization success is not only related to increased habitat availability (i.e. resource availability hypotheses in ENDERS et al., 2020), but also to species traits, in particular plasticity (BAKER, 1965; REJMÁNEK; RICHARDSON, 1996; ENDERS et al., 2020). Generalist traits have been correlated with invasiveness (CLAVEL et al., 2011; ENDERS et al., 2020), as species with a wide niche breadth would have a greater chance of finding appropriate conditions for their survival and growth (DUNCAN et al., 2003; CLAVEL et al., 2011). Here, we found that most non-native species introduced in estuaries were freshwater, but with tolerance to maximum salinities around 25-35 pss (Fig. 14). Conversely, non-native species within the marine guild did not withstand minimum salinities below 30 pss, which likely hindered their occurrence in estuaries. Therefore, the positive relationship between non-native richness and minimum salinity may be a result of the combination of marine and freshwater species' contrasting salinity affinities. Lack of occurrence records for any marine species in ≥5% of estuaries further indicates their low invasiveness regarding these transitional systems, due to a potential low-salinity barrier. Conversely, tolerant species within freshwater guilds (e.g. *C. carpio* and *M. salmoides*) were recorded in several estuaries (Fig. 12), supporting the relationship between generalist traits and invasion (DUNCAN et al., 2003; CLAVEL et al., 2011).

Estuary's area and proxies of habitat connectivity (e.g. river discharge, runoff) were not correlated with non-native richness. Landscape features have been associated with the establishment and dispersal stages of invasion (THEOHARIDES; DUKE, 2007; BLACKBURN et al., 2011), which led to investigating whether non-native species respond similarly to mechanisms that predict native richness, such as the species-area relationship (LI et al., 2018; GUO et al., 2021). Nonetheless, we found considerable variation in the trends reported for non-native richness and ecosystem's area (BURNS, 2015; LEIHY et al., 2018; LI et al., 2018; GUO et al., 2021). Our study agrees with previous literature wherein such a relationship was not detected, but rather revealed colonization pressure and environmental heterogeneity as the primary proxies of non-native occurrence (LEIHY et al., 2018; LI et al., 2018). Proxies of habitat connectivity were also unrelated to non-native richness, despite the inclusion of minimum annual inundation in nearly half of the top-ranking models. Nonetheless, our results indicated that salinity range has a strong influence on estuary's connectivity with adjacent systems (discussed above), and was more important than other hydrological variables that were expected to increase the arrival of propagules in the estuary (THOMAZ, 2022). Human-related modifications in the riverine ecosystem (e.g. dam area, navigable waterways) also did not predict non-native richness, despite evidence supporting this relationship (BRABENDER et al., 2016; LIEW et al., 2016). Buffer size (i.e. 50 km diameter) may be related to this result, due to partial coverage (mainly) of dams, which are often located in intermediate and upstream river sections (LEHNER et al., 2011). Reduced coverage of the riverine environment may also have influenced the lack of population density's effect on non-native richness, as some urban centers are located upstream, i.e. outside of buffer's range (e.g. Dnieper-Bug). Nonetheless, we opted for keeping the 50 km diameter distance, since models ran with data extracted using a larger buffer (i.e. 100 km) revealed significant spatial autocorrelation.

Data retrieved from the literature search mainly depicts the initial stages of the invasion process (e.g. arrival and establishment), but non-native species also have to overcome biotic and landscape filters to become invasive (THEOHARIDES; DUKES, 2007; BLACKBURN et al., 2011). Despite the increasing rate of biological invasions as result of globalization (SEEBENS et al., 2017; BAILEY et al., 2020), early assessments revealed only a subset of introduced species accomplish the invasion process (LODGE, 1993; WILLIAMSON; FITTER, 1996). Nonetheless, probability of invasion has been correlated with non-native richness (JESCHKE; STRAYER, 2005; PYŠEK; RICHARDSON, 2006), and, therefore, the identification of predictors and mechanisms underlying non-native occurrence represents an important step towards biodiversity protection and conservation (PYŠEK; RICHARDSON, 2006). Moreover, the trends detected herein correlate with several invasion hypotheses, and emphasized the interdependence of colonization pressure, resource availability and species traits for non-native occurrence. Connection between these mechanisms was previously identified by ENDERS et al. (2020), who also investigated links with biotic interactions and eco-evolutionary hypotheses (e.g. Darwin's conundrum). However, we were not able to assess trends that could be related to these hypotheses, as few studies retrieved from the search provided data on native fauna. Nonetheless, mechanisms identified herein underlie the early stages of invasion, in which the implementation of control and eradication measures are more effective and less costly (MACK et al., 2000; CUTHBERT et al., 2022).

Our study emphasizes the major role of colonization pressure as a driver of non-native richness. However, climate filtering at global (i.e. temperature) and local (i.e. salinity) scales seemed to restrain non-native species occurrence. Pre-adaptation to the temperature regime at the novel area underpinned non-native richness (i.e. habitat filtering hypothesis; WEIHER; KEDDY, 1995), as we found evidence of thermal limits to species' geographic area of introduction, a relationship that has been previously detected for native fauna's distribution (STUART-SMITH et al., 2017). These findings support the use of ecological niche models (ENMs) for forecasting non-native species' distribution under future scenarios of climate change, and the identification of areas under high invasion risk (LIU et al., 2020b). Non-native richness was also correlated with wider salinity ranges, which may have increased habitat availability for freshwater and marine species in the estuary (i.e. resource availability hypotheses; ENDERS et al., 2020). Nonetheless, tolerant freshwater species were responsible for the majority of records in our database, strengthening the relationship between generalist traits and invasiveness (DUNCAN et al., 2003; CLAVEL et al., 2011). Our results indicate the existence of global (i.e. temperature) and local (i.e. salinity) barriers for non-native species occurrence, and revealed increased establishment potential for euryhaline fish species transported across estuaries under similar climate. Hence, we advise for targeted monitoring of shipping routes linking hotspots of non-native species with other systems under similar climatic conditions, in order to prevent further invasions and biodiversity loss.

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DISCUSSÃO GERAL

A presente tese revelou que mudanças na dominância de espécies residentes de diferentes afinidades térmicas contribuíram majoritariamente para a reorganização da ictiofauna estuarina sob influência do aquecimento global (Capítulo 1; SOUZA; SANTOS, 2023). Um aumento em espécies de afinidade térmica quente (i.e. tropicalização) foi registrado para dois terços das comunidades analisadas, porém este padrão não foi associado com a imigração de espécies, contrariando expectativas baseadas em estudos anteriores (CHEUNG et al., 2013; ANTÃO et al., 2020). A mudança no perfil térmico da comunidade foi, por outro lado, associada com poucas espécies registradas em pelo menos metade da série temporal (i.e. residentes). Estas espécies também apresentaram variações expressivas na abundância, em resposta à mudança de longo-prazo na temperatura. Esse padrão foi observado independente do balanço entre perdas e ganhos de espécies e indivíduos, e do principal processo relacionado com a mudança do perfil térmico da comunidade (i.e. tropicalização, borealização, detropicalização, deborealização), indicando um papel primário do *pool* local de espécies para a nova configuração das comunidades. Uma única exceção foi registrada para um sistema em região de transição entre a zona temperada e subtropical, onde a emigração foi o principal processo subjacente à reorganização da ictiofauna estuarina. Esta divergência da tendência principal reforça a necessidade de investigar a tolerância térmica de espécies residentes em ecossistemas tropicais, a fim de identificar potenciais mecanismos relacionados com sua persistência frente às mudanças climáticas.

Experimentos realizados com juvenis do peixe-rei *Atherinella brasiliensis*, espécie dominante e residente em estuários tropicais, revelaram diferentes limites e margens de segurança térmica para duas populações distantes 20 km entre si na Baía de Guanabara (Capítulo 2). A heterogeneidade local na temperatura e salinidade foi associada com a variação intraespecífica na tolerância térmica de *A. brasiliensis*, revelando a importância de considerar as condições do micro-habitat em estimativas de vulnerabilidade das espécies frente às mudanças do clima. Indivíduos aclimatados em águas quentes e salobras atingiram, em média, limite térmico máximo de 40,3^{o}C, enquanto peixes em águas frias e marinhas registraram, em média, um limite máximo de 39,9^{o}C. No entanto, um padrão oposto foi observado para as margens de segurança térmica (i.e. menor MST para peixes em águas quentes e salobras), indicando que os juvenis de *A. brasiliensis* podem estar perto de atingir seu limite térmico absoluto (VAN HEERWAARDEN; KELLERMANN, 2020). Essa tendência é especialmente preocupante considerando a falta de aclimatação da espécie à temperaturas previstas em cenários futuros, que levariam à MSTs negativas. No entanto, os limites térmicos registrados para as populações de *A. brasiliensis* mudaram de acordo com as condições de aclimatação (i.e. plasticidade fenotípica), o que pode favorecer a persistência desta espécie no estuário durante a ocorrência de ondas de calor e em cenários de aquecimento intermediário. A plasticidade na tolerância térmica pode, inclusive, estar associada com a persistência de espécies residentes detectada no Capítulo 1, visto que variações na temperatura em pequena escala (i.e. micro-habitat) podem antecipar condições previstas para o futuro, permitindo uma aclimatação gradual das espécies (BAY; PALUMBI, 2014; OLDFATHER; ACKERLY, 2019; DUBOIS et al., 2022). Divergências nos processos subjacentes à reorganização da ictiofauna em dois locais na Baía de Narragansett (i.e. *Narragansett Bay*), situada na costa lestes dos Estados Unidos (COLLIE et al., 2008), podem representar evidências desse processo. Neste sistema, a mudança no perfil térmico da ictiofauna residente em Fox Island foi relacionada com a deborealização, por meio da perda de indivíduos de afinidade térmica fria. Por outro lado, o aumento em espécies de afinidade térmica quente levou à tropicalização em Whale Rock (Capítulo 1). Tais divergências podem estar associadas com variações intraespecíficas na tolerância térmica (Capítulo 2), e outros processos em escala local (e.g. impactos antropogênicos; MCLEAN et al., 2021). Desta forma, os padrões detectados nestes capítulos suportam a adoção de uma abordagem fenotípica para o desenvolvimento de estratégias de manejo e conservação das espécies frente às mudanças climáticas.

O monitoramento, controle e erradicação de espécies invasoras também representa uma importante medida para a conservação da biodiversidade (HELLMAN et al., 2008; RAHEL; OLDEN, 2008). A síntese realizada no 3º Capítulo revelou que variáveis associadas com a pressão de colonização (i.e. tráfego de navios) e o clima (i.e. temperatura e salinidade), foram os principais preditores da riqueza de peixes não-nativos em estuários. O tráfego de navios é reconhecido como um importante vetor de introdução de espécies aquáticas e terrestres (KELLER et al., 2011; HALPERN et al., 2015), e está associado com o aumento no risco de invasão global previsto para 2050 (SEEBENS et al., 2016; SARDAIN et al., 2019). A chegada regular de espécies através do tráfego de embarcações pode favorecer o estabelecimento de populações não-nativas na região recipiente, em virtude da maior chance de um “*match*” favorável entre as condições ambientais na nova área e os requerimentos ecológicos de pelo menos uma espécie. A relação entre as características das espécies (i.e. potencial invasor) e o filtro ambiental foi observada, na presente tese, para a temperatura e a salinidade. Estas variáveis atuaram como uma barreira para a ocorrência de espécies não-nativas em diferentes escalas. Os limites térmicos das espécies foram associados com a latitude do estuário invadido, e revelaram padrões similares aos observados para a fauna nativa (STUART-SMITH et al., 2017), reforçando evidências prévias de conservação do nicho climático durante invasões (LIU et al., 2020). Por outro lado, flutuações locais na salinidade foram associadas com a ocorrência de espécies não-nativas marinhas e, principalmente, de água-doce nos estuários. As espécies pertencentes à esta última guilda demonstraram tolerância à salinidades máximas por volta de 25-35 pss, indicando um alto potencial invasor em estuários. Esta característica generalista em relação à salinidade pode estar, inclusive, associada com o maior número de introduções registrado para estas espécies em comparação às marinhas, que apresentaram uma estreita faixa de tolerância (i.e. afinidade mínima igual ou superior à 30 pss). Estes resultados indicam um efeito primário da temperatura (i.e. escala global) em relação à salinidade (i.e. escala local) para a ocorrência de peixes não-nativos em estuários, revelando maior chance de estabelecimento para espécies artificialmente transportadas (i.e. tráfego de navios) entre sistemas localizados em uma mesma zona climática. Neste sentido, os padrões detectados nesta tese indicam a necessidade de monitoramento prioritário de embarcações (i.e. água de lastro) conectando localidades sob condições climáticas similares, a fim de prevenir invasões biológicas e a perda de diversidade nativa.

Os dados gerados pela presente tese contribuíram para preencher importantes lacunas do conhecimento acerca de respostas da biodiversidade às mudanças climáticas. Alterações na dominância de espécies residentes apresentaram maior importância relativa para a reorganização das comunidades biológicas (Capítulo 1), contrariando expectativas de um papel primário da imigração e emigração (CHEUNG et al., 2013; ANTÃO et al., 2020). Diversos mecanismos podem estar associados com a persistência das espécies em seu habitat original, incluindo a tolerância térmica (BENNETT et al., 2019; FOX et al., 2019; MCKENZIE et al., 2021). A variação intraespecífica nos limites e margens de segurança térmica detectada para *A. brasiliensis*, espécie de peixe residente em estuários tropicais, apresentou potencial para favorecer sua persistência durante a ocorrência de ondas de calor, e em cenários de aquecimento intermediário previstos para o final do século 21 (Capítulo 2). No entanto, a avaliação dos limites térmicos de indivíduos desta espécie em outros estágios de vida é necessária para reforçar essa expectativa. As diferenças na tolerância térmica foram associadas com a heterogeneidade local na temperatura e salinidade característica de estuários, revelando a importância das condições do micro-habitat para estimativas acuradas da vulnerabilidade de ectotérmicos à eventos climáticos (BAY; PALUMBI, 2014; OLDFATHER; ACKERLY, 2019; DUBOIS et al., 2022), e o desenvolvimento de planos de conservação eficazes. Tais planos também devem considerar estratégias para o manejo, controle e erradicação de espécies invasoras, a fim de evitar pressões adicionais sobre a biodiversidade nativa, e prevenir a homogeneização biótica (CLAVEL et al., 2011). Para tal, sugere-se o monitoramento das rotas de embarcações, a fim de priorizar o manejo da água de lastro de navios conectando regiões com condições climáticas similares, visto que a ocorrência de espécies não-nativas está associada, principalmente, com a temperatura.

É importante ressaltar que os padrões reportados nesta tese se basearam na análise da ictiofauna estuarina, que apresenta uma alta plasticidade à mudanças nas condições ambientais (ELLIOTT et al., 2007). Desta forma, a persistência das espécies em seu habitat original, e seu papel primário para a reorganização das comunidades, podem estar relacionadas com essa característica. Neste sentido, recomenda-se a aplicação da abordagem metodológica desenvolvida no Capítulo 1 para a avaliação de dados de diversos táxons e/ou habitats, a fim de reforçar as tendências reportadas aqui, e/ou revelar divergências taxonômicas ou funcionais. Nossos resultados também demonstraram a necessidade da implementação de programas de monitoramento contínuo em regiões tropicais, visto que não foi possível avaliar os processos subjacentes à reorganização da biodiversidade nessa região tão rica. No entanto, o único estuário avaliado em região de transição entre a zona temperada e subtropical, revelou perda de espécies e declínio geral no número de indivíduos – tendências que podem se tornar ainda mais acentuadas caso as metas estipuladas para limitar o aquecimento global não sejam alcançadas.

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APÊNDICE A – Manuscrito aceito para publicação no periódico *Ecology* em 21 de Dezembro de 2022.

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CONCEPTS & SYNTHESIS

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Resident species, not immigrants, drive reorganization of estuarine fish assemblages in response to warming

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Abstract

Climate change is reshaping biological communities, as species track environmental temperature. Assemblage reorganization is underpinned by shifts in species abundance and distribution, but studies often focus on documenting compositional turnover. As a consequence, phenomena such as the tropicalization of temperate communities have been widely associated with increased occupancy of warm-affinity species. Abundance-weighted change in thermal affinity can be tracked with the Community Temperature Index (CTI), and decomposed into four processes: tropicalization (increasing warm-affinity), borealization (increasing cold-affinity), deborealization (decreasing cold-affinity), and detropicalization (decreasing warm-affinity). Further evaluation of these processes according to species persistence (i.e., immigrant, emigrant, and resident) may provide insights on whether novel communities emerge primarily from local shifts in species abundance or distribution. Using long-term data on fish assemblages undergoing climate change's effects across 19 temperate estuaries surveyed for at least 20 years, we hypothesized (1) deborealization is the main process reshaping communities under climate change, and (2) the contribution of resident species to processes reshaping communities surpass the ones from immigrants and emigrants. Community dissimilarity was calculated through the Temporal Beta Index (TBI), which was further decomposed into species and individual losses and gains. These values were then used as effect sizes in the meta-analyses performed to detect systematic trends in assemblage reorganization in response to climate change. We also calculated CTI and the strength of temperature-related processes for resident, immigrant and emigrant species. Species and individual gains outweighed losses in estuaries. Temperature was correlated with changes in species abundance, but not occurrence. Fish abundance decreased with warming, and initially cooler estuaries gained more fish than warmer ones. Novel communities were shaped by a variety of processes, but mainly tropicalization. Assemblage reorganization was primarily driven by shifts in abundance of resident species with distinct thermal affinities, while contributions of arriving and exiting species played a secondary role. These findings reveal that novel communities are drawn primarily from the local species pool, due to changes in climate-related drivers that favor distinct resident species.

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assembly rules, beta-diversity, climate change, community temperature index, deborealization, long-term, tropicalization

INTRODUCTION

Temporal dynamics in ecological communities have been extensively studied to unveil the mechanisms affected by global change. Assemblage-level regulation has been reported for metrics such as richness and abundance (Gotelli et al., 2017), but not for species composition (Dornelas et al., 2014). Change in species identity leads to novel communities, which may remain undetected by alpha diversity (Blowes et al., 2019; Dornelas et al., 2014; Vellend et al., 2013). Nonetheless, comprehensive analyses of assemblage data revealed increasing richness in temperate systems (Dornelas et al., 2014; Elahi et al., 2015). The raise in diversity has been associated with warming in the marine realm (Antão et al., 2020) and is underpinned by the influx of species tracking suitable isotherms (Lenoir et al., 2020; Pinsky et al., 2013). Colonization by species with warmer affinities has led to an increase in communities' thermal affinity (Brice et al., 2019; Cheung et al., 2013; Lehikoinen et al., 2021) and is considered as the main driver of tropicalization in temperate ecosystems. However, recent work by McLean et al. (2021) revealed this phenomenon may also be related to the loss and/or decline of cold-affinity species.

Four processes underlie assemblage reorganization in response to temperature change. These are non-exclusive (i.e., may occur concurrently in a given community), and are underpinned by temporal shifts in the relative abundance of species with distinct thermal affinities (McLean et al., 2021). For instance, tropicalization and borealization are described as the increase of warm and cold-affinity species, respectively. Conversely, the decline of these respective species is known as detropicalization and deborealization. These processes result from the decomposition of the Community Temperature Index (CTI), which measures the abundance-weighted mean thermal affinity of any given community (Devictor et al., 2008). Quantification of each process strength can provide a mechanistic view of temporal trends in diversity detected by synthesis studies (Antão et al., 2020), and point to ecosystems' resilience (in case of tropicalization or borealization) or vulnerability (in case of deborealization or detropicalization). For instance, increases in CTI may either result from tropicalization or deborealization; however, the first process is associated with a positive balance in community change (i.e., gain outweigh loss), which could maintain productivity under future warming, despite changes in species composition. Conversely, communities wherein loss prevails (i.e., deborealization) are more prone to population crashes and local extinctions in the near future (McLean et al., 2021). Prevalence of one process over the others has been associated with abiotic factors and species traits. Baseline temperature, long-term temperature change, depth and the incidence of species with high maximum thermal limits (among other characteristics) were positively associated with tropicalization. Conversely, deborealization prevails in sites close to human centers, and is positively correlated with the incidence of species with wide thermal ranges (for details on other features and processes, please see McLean et al., 2021). Yet, potential relationships between species occurrence over time and their respective contributions to CTI change have not been assessed, despite their valuable insights into the role of dispersal and dominance for assemblage reorganization.

Novel communities emerge from shifts in species occurrence and abundance over time (Dornelas et al., 2019), and both of these biodiversity components are temperature-dependent. Species thermal limits have been shown to predict their geographic ranges (Stuart-Smith et al., 2017; Sunday et al., 2012), while heating tolerance is tightly coupled with population size (Payne et al., 2021). Despite their separate contributions to community change, most studies focused primarily on understanding compositional change without further looking into potential shifts in dominance (Antão et al., 2020; Bates et al., 2014). As consequence, ecologists have been associating phenomena such as the tropicalization of temperate systems with increased occupancy of warm-affinity species. Novel communities would then emerge primarily via increased dispersal from the regional species pool to the local community (i.e., immigration). Nonetheless, increases in communities' mean thermal affinity could also result from (1) the increased abundance of resident species with warmer affinities or (2) deborealization (i.e., decline or exit of cold-affinity species; McLean et al., 2021) (Figure 1). In these cases, novel assemblages would arise either from local shifts in species dominance or via increased dispersal outside the local community (i.e., emigration). Classification of species according to their occurrence across time series (i.e., migrants versus residents) could provide insights into this matter, and either (1) support dispersal as the main process shaping the novel communities, in accordance with a growing number of studies reporting distribution shifts (Lenoir et al., 2020; Pinsky et al., 2013); or (2) reveal its

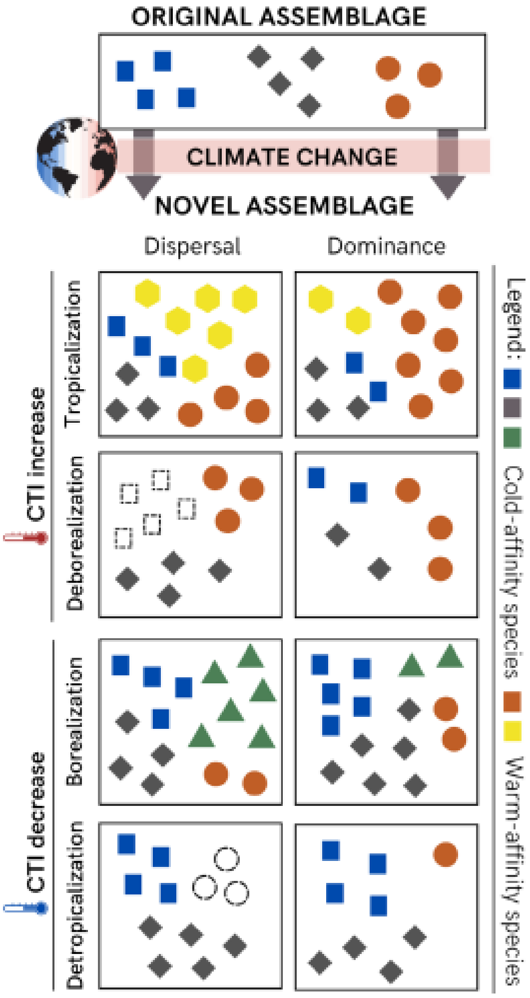

FIGURE 1 Conceptual figure combining Community Temperature Index (CTI) change, the temperature-related processes and species-level mechanisms underlying assemblage reorganization. CTI increase can result from either tropicalization or deborealization, whereas CTI decrease can be attributed to either borealization or detropicalization. Each of these processes may develop primarily from shifts in species dispersal (left column) or dominance (right column). In the first case, migrant species would have the greatest contribution to processes driving change; in the second case, community change would be driven by shifts in abundance of resident species.

minor role compared to shifts in abundance of resident species, as persistence over time is positively correlated with species dominance (Magurran & Henderson, 2003).

Here, we assessed the main temperature-related process (i.e., tropicalization, borealization, detropicalization, deborealization) and group of species (i.e., immigrants, emigrants and residents) driving community change, using long-term data on estuarine fish assemblages surveyed for at least 20 years. Our framework combined beta-diversity, meta-analyses, CTI decomposition and the evaluation of process strength at species-level, to examine the importance of shifts in species distribution (i.e., dispersal) and abundance (i.e., dominance) for communities under climate change. To accomplish this goal, we divided the time series into early and late periods, and labeled species according to their occurrence: resident—present during both periods; immigrant—present in the late period; or emigrant—present in the early period. We hypothesized (1) deborealization is the primary process reshaping communities, leading the loss of species and individuals in estuaries, and (2) the contribution of resident species to the temperature-related processes driving community change surpass the ones from immigrants and emigrants. Our expectations regarding the key role of deborealization over the other processes (including the often-reported tropicalization) were related to estuaries' heat-conservative properties, which may accentuate fish assemblage's exposure to warming, leading to a negative balance between losses and gains. Nonetheless, the great thermal ranges commonly exhibited by resident species inhabiting these dynamic systems (Elliott et al., 2007) may favor their persistence over time, despite declines in abundance.

MATERIALS AND METHODS

Search strategy

A literature search was conducted using Scopus, Web of Science and Google Scholar online databases, applying the keywords: [Climate Change OR Global Warming OR Warming OR Climate Warming OR Changing Climate] AND [Long-term] AND [Fish assemblage OR Ichthyofauna OR Fish species] AND [Estuar*]. Search string development was an iterative process conducted on the aforementioned platforms, and the chosen combination presented the best balance between comprehensiveness and relevance (see details on Appendix S1). As climate change is a subject of increasing interest in the scientific community, the number of studies on the topic is scaling up, but we found that only a few have assessed the relationship between climate-mediated drivers and fish assemblages in estuaries. Therefore, we added [Long-term] and level of organization (i.e., assemblage, ichthyofauna and species) to our search string, which increased the number of relevant entries for the meta-analysis (Appendix S1). Publications retrieved from the search were screened, and those that met the established criteria (see *Article screening and eligibility*) were compiled into a database. We also screened the references list of all retrieved studies for eligibility and included additional articles in our review whenever they fitted our criteria. Paleoclimatic and fishery-based studies were excluded from our database, as we were interested in current effects of climate change on fish assemblages and not just commercial species.

Article screening and eligibility

The screening process was divided in two parts: first, the title and abstract were examined for the following criteria: (1) Relevant subject, that is, long-term changes in estuarine fish communities; (2) Relevant exposure, that is, surveys performed for a minimum of 20 years, whether continuously or not; and (3) Relevant outcome, that is, availability of ecological data such as species occurrence and abundance. We established 20 years of sampling as the minimum time scale for selecting studies, since estuarine fish assemblages are very dynamic due to the occurrence of species from several guilds of functional use (marine and freshwater stragglers and migrants, anadromous, and catadromous, among others; Elliott et al., 2007), which may conceal long-term trends, even with a decade of data (James et al., 2018; Van der Veer et al., 2015). Studies with a discontinuous time series were also kept in the screening process, as several authors reported that fish assemblage similarity is higher between closer years and declines over time (Collie et al., 2008; Howell & Auster, 2012; Olsson et al., 2012); therefore, discontinuous samples far apart in time would still reveal shifts in community structure and composition. Articles that fit these criteria were then forwarded to the second part of the screening process, and had their full-texts reviewed. At this stage, articles were critically appraised in search of the following information: (1) Relevant subject (see description above); (2) Relevant study design, that is, similar fishing gear must have been employed during all surveys, which must also have been performed in the same areas within the estuary; (3) Relevant exposure (see description above); (4) Relevant results, that is, studies must have tested and found a statistical association between climate-mediated drivers and community change; and (5) Relevant outcome (see description above). Studies that met all these criteria were then compiled into a database. Statistically significant results were included as eligibility criterion, as we aimed to identify the ecological processes underpinning community reorganization in response to climate change. Therefore, studies must have reported an explicit effect of climate-related drivers on the fish assemblage, rather than just documenting changes in species occurrence and abundance over time (e.g., some studies retrieved by the search presented trends for temperature and assemblage descriptors, but did not test whether these were correlated; Appendix S2: Table S1). We are aware that statistical correlations may be biased by sample size; thus, excluding studies that did not find a relationship between environmental drivers and community change may narrow our results. However, we decided to adopt such conservative approach and retain the statistical test as a criterion, to increase confidence that trends reported herein are climate-driven. We also excluded studies performed with the same dataset, to avoid bias related to duplicated data (Appendix S2: Table S1). Studies with the longest time series were kept in the compiled database.

Data extraction and transformation

Fishing gear type, number of samples, fish position at the water column and life stage, taxonomic richness, species occurrence and abundance, statistical analysis performed in the study, and significant explanatory variables were extracted from the final set of articles. If these data were unavailable, the corresponding author was contacted twice. Failure to respond to these contact attempts or refusal to hand over the data led to study exclusion from the database (Appendix S2: Table S1). Data from each study was provided for a distinct sample unit (i.e., values for each survey replicate, month or year), and grouped in two time periods: early and late. These periods were defined according to the year of community shift described in the original paper. For instance, Collie et al. (2008) detected a major shift of the fish assemblage at Whale Rock, Narragansett Bay, between 1980 and 1981; therefore, the early and late periods comprised data before and after 1980, respectively. We adopted this approach for three main reasons: first, midpoint was not available for some studies with a discontinuous time series; second, pooling data into early and late periods reduces the likelihood of overestimating changes in species occurrence and abundance in contrast to adopting a single baseline year (e.g., first year of sampling); and third, most original studies tracked community change over time using ordination methods, which favors the establishment of early and late assemblages based on similarity, rather than as result of randomly splitting the time series. Abundance data were converted to densities (number of individuals per 100 meter square) to avoid bias, as the sampling effort (i.e., number of samples and total area sampled) between the early and late periods was different for some studies included in the review. Conversion of abundance data to density represents a suitable method for standardizing unbalanced sampling efforts in estuaries (Hollweg et al., 2020; Nicolas et al., 2010), and represents an alternative to downsampling procedures, which require data at sample unit level (an information that, unfortunately, was not available for all studies in our database).

Mean temperature values for the early and late periods were also extracted from the screened articles. Geographical coordinates of each estuarine system were obtained from Google Earth (http://www.google.fr/intl/fr/earth/index.html), and marine realm was identified according to Spalding et al. (2007). Species cited on the retained publications were verified for terminology updates using the Eschmeyer's Catalog of Fishes online database (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp; Fricke et al., 2020).

Temporal change in fish assemblages

Community change was evaluated through the Temporal Beta Index (TBI; Legendre, 2015). The TBI measures the dissimilarity (D) in community composition between the first (i.e., early period) and second (i.e., late period) surveys performed at a particular system, and has been considered a valuable tool for assessing anthropogenic impacts such as climate change (Legendre, 2019). Dissimilarity varies between 0 and 1, and can be further decomposed into losses (B) and gains (C), thus revealing the quantitative importance of each ecological process in shaping the novel assemblage (Legendre, 2015, 2019). TBI values were calculated based on species occurrence and abundance (i.e., density) matrices, using the *TBI.R* function (Legendre, 2015) in the *adespatial* package (Dray et al., 2020) for the R software (R Core Team, 2020). The percentage difference index ($D_{\%\text{diff}}$, also known as the Bray–Curtis index in other computer packages) was chosen for calculating dissimilarity, due to suitability for both occurrence and abundance data (Legendre, 2019). Dissimilarity values were calculated for each estuary separately unless systems were interconnected (i.e., sites at Narragansett Bay and some bays in the Texas coast). In the latter case, we also produced B–C plots (i.e., which show the relative importance of loss and gain processes in a study area) to identify whether adjacent sites share similar responses to climate change (e.g., all sites gained species) or not (e.g., some sites gained species while others lost) (Legendre, 2019).

Meta-analysis

Three-level meta-analyses were conducted to identify whether climate change is leading to the loss or gain of fish species and individuals in estuaries. TBI gain and loss values were each used as the observed effect sizes for the meta-analyses performed, while sampling variance was calculated as: $1/N_{\text{total}} - |N_{\text{pre-warming}} - N_{\text{post-warming}}|$. We adopted this innovative approach for three main reasons: first, solely looking at temporal differences in richness and total abundance may conceal community shifts, since several studies reported little change in these descriptors across years (Crosby et al., 2018; Gotelli et al., 2017; Olsson et al., 2012); second, the risk and odds ratio methods would not detect changes in species abundance (i.e., dominance); and third, community studies often perform multivariate statistical analyses, which returns non-linear coefficients that are inappropriate for conversion to the Fisher's z scale (Hunter & Schmidt, 1990).

We calculated the mean effect sizes for species and individual gains and losses using the random effects model with maximum-likelihood estimation (i.e., "REML") in the *metafor* package (Viechtbauer, 2010). To control for potential non-independence of effect sizes among studies performed in proximate areas (i.e., spatial autocorrelation; e.g., Collie et al., 2008; Pawluk et al., 2021), we nested "estuary" within "ecoregion" (Bates et al., 2015; Nakagawa et al., 2017). Model heterogeneity (I^2) was partitioned between two sources: variance explained by (I) estuary and (II) ecoregion, using the *dmetar* package (Harrer et al., 2019). Additionally, we reran the models using long-term temperature change (i.e., difference between early and late period values) and baseline temperature (i.e., mean value recorded in the early period) as moderators (Viechtbauer, 2010), since all studies in our database found an association between temperature and community change. Then, we compared the Corrected Akaike Information Criterion (AIC$_c$; Brockwell & Davies, 1991) and the percentage (%) of reduced variance exhibited by models with moderators, in order to assess the relationship between temperature and fish gain and loss. The model with the lowest AIC$_c$ value and highest % of reduced variance was retained for analysis; however, if the difference between AIC$_c$ values of models was lower than 4, these were considered as indistinguishable (Mazerolle, 2016) and the retained model was chosen based only on the % of reduced variance. Despite a subset of studies also reported an effect of variables other than temperature (e.g., salinity, sea level; see Table 1) on fish assemblages, these were not included as moderators in the meta-analyses due to lack of adequate sample size (i.e., number of entries per predictor). The number of missing studies (fail-safe N) was calculated to check for bias and outliers in the dataset using the methods proposed by Rosenthal (1979) and Rosenberg (2005), which are available in the *metafor* package for the R software (R Core Team, 2020).

CTI and process strength

Fish assemblage mean thermal affinity was calculated for the early and late periods, and the entire time series of

TABLE 1 Estuary (decimal coordinates), survey years (early and late periods), explanatory variables, long-term temperature change (°C), and baseline temperature (°C), extracted from each study included in the present review.

Study	Estuary	Survey years	Explanatory variables	Temperature	
				Change	**Baseline**
Kimball et al. (2020)	North Inlet (33.327011, −79.167301)	Early: 1981–1984 Late: 2013–2016	Mean temperature (annual)	1.7	18.4
Araújo et al. (2018)	Sepetiba Bay (−23.000671, −43.914823)	Early: 1983–1985 and 1993–1999 Late: **2000**–2006 and 2011–2015	Mean temperature (annual)	0.9	26
Howell and Auster (2012)	Long Island Sound (41.101207, −72.871826)	Early: 1984–1998 Late: **1999**–2008	Mean temperature (spring; autumn)	0.55	9.29
Henderson et al. (2011)	Bridgewater Bay (51.213902, −3.142063)	Early: 1981–1985 Late: **1986**–2009	Mean temperature (annual), salinity, NAO	1.36	12.08
Olsson et al. (2012)	Kattegat (Vendelsö) (57.30475, 12.158173)	Early: 1976–1986 Late: **1987**–2008	Mean temperature (annual), NAOw	0.68	5.56
	Baltic Proper (Kvädöfjärden) (58.050266, 16.774174)		Mean temperature (annual), salinity, NAOw	0.52	8
	Bothnian Sea (Forsmark) (60.399444, 18.18875)		Mean temperature (annual; spring), salinity, NAOw	1.23	16.33
Pawluk et al. (2021)	Sabine Lake (29.877478, −93.851353)	Early: 1986–1994 Late: **1995**–2008	Mean temperature (spring, autumn), salinity, sea level, dissolved oxygen	1.19	25.28
	Galveston Bay (29.510513, −94.847889)			0.61	26.32
	Matagorda Bay (28.564323, −96.312273)			0.99	26.2
	San Antonio Bay (28.300768, −96.72836)			1	26.25
	Aransas Bay (28.072052, −97.001494)			0.8	26.97
	Corpus Christi Bay (27.771875, −97.262627)			0.95	26.45
	Upper Laguna Madre (27.281196, −97.442972)			0.59	27.12
	Lower Laguna Madre (26.400829, −97.315607)			0.6	27.24
Crosby et al. (2018)	Norwalk Harbor at Long Island Sound (41.09265, −73.407723)	Early: 1990–2005 Late: **2006**–2016	Mean temperature (annual), salinity, dissolved oxygen, proportion of hypoxic days	1.26	20.45
Cloern et al. (2010)	San Francisco Bay (37.806234, −122.351122)	Early: 1980–1998 Late: **1999**–2008	NPGO	...	...
Collie et al. (2008)	Narragansett Bay: Fox Island (FI) and Whale Rock (WR) (41.554167, −71.41752)	FI—Early: 1959–1984 Late: **1985**–2005 WR—Early: 1959–1979 Late: **1980**–2005	Mean temperature (annual, spring, summer), chlorophyll-*a* concentration, NAOw	0.5	11.1

(Continues)

TABLE 1 (Continued)

Study	Estuary	Survey years	Explanatory variables	Temperature	
				Change	Baseline
van der Veer et al. (2015)	Mokbaai (53.004041, 4.764133)	Early: 1960–1984 Late: **1985**–2011	Mean temperature (summer), chlorophyll-*a* concentration, NAOw, nitrogen and phosphorus loadings, sand mining and beach nourishment, top predator	0.8	16.5

Note: The year of community shift described in each paper is indicated in bold.

Abbreviations: NAO, North Atlantic Oscillation Index; NAOw, North Atlantic Oscillation Index (winter); NPGO, North Pacific Gyre Oscillation.

each estuary, through the CTI (McLean et al., 2021). In CTI, species thermal affinity (STI) is weighted by its observed abundance (hereby, density; Devictor et al., 2008); therefore, changes in CTI are related not only to shifts in species occurrence, but also in their dominance. STI was estimated by overlapping occurrence data and mean sea surface temperature (SST; °C), which were extracted from the Global Biodiversity Information Facility (GBIF, 2022; http://www.gbif.org/) and BioOracle (https://www.bio-oracle.org/; Assis et al., 2017; Tyberghein et al., 2012) databases, respectively. Occurrence records were tested for duplicates, equal coordinates, validity, zeros, capitals, centroids, gbif, institutions, and urban areas, using the *clean_coordinates* function in the *CoordinateCleaner* package (Zizka et al., 2019). Flagged records were then removed from the dataset. The *sp* (Bivand et al., 2013; Pebesma & Bivand, 2005) and *rgdal* (Roger et al., 2021) packages were used to transform species occurrence data from csv to shapefile format, and to create a polygon delimiting each species range of occurrence; then, mean SST values were extracted for each polygon using the *extract* function in the *raster* package (Hijmans & van Etten, 2012) for the R software (R Core Team, 2020).

Next, STI was weighted by its density, which was calculated using the total abundance of each period (i.e., single value obtained from pooling samples within each period). The resulting values were then summed up and divided by total density (i.e., combined density of all species recorded in each period), determining CTI. CTI change was calculated as the difference between late and early CTI, whereas CTI based on the full time series was used to sort species as either warm- (i.e., STI > CTI full time series) or cold- (i.e., STI < CTI full time series) affinity, following the methods proposed by McLean et al. (2021). This classification was applied to assess the strength of each process (i.e., tropicalization, borealization, detropicalization, and deborealization) underlying CTI change across periods. First, we calculated the difference in species density between late and early periods. Next, we multiplied this value by the difference between STI and CTI based on the full time series. Process strength was determined by summing up the resulting values for all species within four categories: (1) tropicalization—warm-affinity species which increased in density; (2) detropicalization—warm-affinity species which decreased in density; (3) borealization—cold-affinity species which increased in density; and (4) deborealization—cold-affinity species which decreased in density (for more details see McLean et al., 2021). We further decomposed the strength of each process among resident (i.e., present during the early and late periods), immigrant (i.e., recorded only in the late period), and emigrant (i.e., recorded only in the early period) species, in order to assess the contribution of each group to assemblage reorganization. Permutational Analysis of Variance (PERMANOVA) was applied on the $\log_{10}$ × transformed strength values to detect the main process and group of species assembling the novel communities. We adopted a mixed-model design with "process" and "group of fish species" as fixed-factors, and nested "estuary" within "ecoregion" to control for potential spatial autocorrelation. Euclidean dissimilarity distance (1000 permutations) was used for the PERMANOVA tests, which were performed using the *adonis2* function in the *vegan* package (Oksanen et al., 2020) for the R software (R Core Team, 2020).

RESULTS

Review descriptive statistics

The literature search retrieved 4327 articles, of which 48 were screened at full-text. Details on the screening process and the list of studies screened at full-text with reasons for its inclusion or exclusion from the review can be found in Appendix S2: Figure S1 and Table S1. The final dataset consisted of 10 articles published between years 2008 and 2021, encompassing 19 estuaries (Table 1; Appendix S2: Table S1 and Figure S1). Estuaries were located in temperate realms (covering |23°–60°| degrees in latitude) mainly in the northern hemisphere, whereas the southern region was poorly represented in the data (Figure 2; Table 1). Fish assemblages were sampled using six types of gear, starting in 1959 (early period in the Narragansett Bay) and ending in 2016 (late period for the North Inlet and the Norwalk Harbor). The compiled articles recorded a total of 380 fish species; Cloern et al. (2010) captured the lowest number of species ($S = 11$) at the San Francisco Bay, while Araújo et al. (2018) surveyed 117 species at Sepetiba Bay (Appendix S2: Table S2). Fish assemblages were composed of pelagic, benthopelagic, and demersal species, excepting at the North Inlet (only pelagic and benthopelagic species), the San Francisco Bay (only demersal species), and the Norwalk Harbor (only demersal species). Also, communities assessed by Pawluk et al. (2021) in bays of Texas were composed exclusively of adult fishes.

Studies reported major community shifts between the mid 1980s and the end 1990s, excepting for the Norwalk Harbor at the Long Island Sound (Table 1). These shifts were primarily associated with temperature and regional climate such as the North Atlantic Oscillation (NAO) and the North Pacific Gyre Oscillation (NPGO), but also to changes in salinity, sea level, dissolved oxygen and proportion of hypoxic days, chlorophyll-*a* concentration, presence of top predators, habitat degradation, and pollution. Long-term temperature change ranged from 0.50°C at Narragansett Bay to 1.71°C at the North Inlet, while baseline temperature varied from 5.56°C at Kattegat to 27.24°C at the Lower Laguna Madre, in the Northern Gulf of Mexico (Table 1).

Temporal change in fish community

TBI values were higher for fish abundance (i.e., density; ranging from $D = 0.06$ to 0.77) than for occurrence (ranging from $D = 0.02$ to 0.25), revealing a greater shift in species dominance rather than composition (Figure 2; Appendix S2: Table S3). The highest TBI values were recorded at the North Inlet, for both occurrence ($D = 0.25$) and abundance ($D = 0.77$) data. Dissimilarity in species abundance was also high at Kattegat ($D = 0.64$), and for species occurrence at the Norwalk Harbor ($D = 0.21$) and Sepetiba Bay ($D = 0.2$). Systems with the lowest values were located in southern North America, between 26° N and 29° N latitude (Figure 2). The Baltic Proper (58° N latitude) also showed little dissimilarity in species occurrence (0.02) across the early and late periods (Appendix S2: Table S3).

Gains were higher than losses for most estuaries evaluated, excepting for Mokbaai (species occurrence and abundance data); the North Inlet, Norwalk Harbor, Fox Island at the Narragansett Bay, Lower Laguna Madre, and Galveston Bay (species abundance data); and the Bothnian Sea and Sepetiba Bay (species occurrence data; Figure 2; Appendix S2: Table S3). Species turnover was also quite balanced at the Long Island Sound and Corpus Christi Bay, as these systems showed nearly equal values between gain and loss components. Adjacent bays in the coast of Texas (Figure 2, letters J–Q) shared similar responses to climate change, excepting for species abundance data at Galveston Bay. Overall, sites gained more species and individuals than lost. Adjacent sites in Narragansett Bay showed distinct responses to climate change; loss of individuals prevailed at Fox Island, whereas gain was observed at Whale Rock (Appendix S2: Figure S2).

Meta-analysis

Mean effect sizes differed significantly from zero for species (loss: mean effect size = −0.04, $p = 0.001$; gain: mean effect size = 0.08, $p < 0.001$) and individual (loss: mean effect size = −0.17, $p = 0.003$; gain: mean effect size = 0.21, $p < 0.001$) meta-analyses (Figure 3). Estimates were higher for gains rather than losses (Figure 4), revealing a long-term increase in the number of fish species and individuals in temperate estuaries. The *Q*-test detected significant heterogeneity for species (loss: $I^2 = 56.42\%$, $Q(\mathrm{df} = 16) = 32.09$, $p = 0.01$; gain: $I^2 = 74.82\%$, $Q(\mathrm{df} = 16) = 55.52$, $p < 0.0001$) and individual (loss: $I^2 = 98.21\%$, $Q(\mathrm{df} = 19) = 463.08$, $p < 0.0001$; gain: $I^2 = 98\%$, $Q(\mathrm{df} = 19) = 1032.5268$, $p < 0.0001$) meta-analyses. Variance between estuaries within an ecoregion ($I^2 = 45.88\%–65.44\%$) was higher than between ecoregions ($I^2 = 28.95\%–32.56\%$) for species and individual gain meta-analyses, whereas the opposite pattern was observed for species and individual loss meta-analyses ($I^2 = 20.35\%–30.64\%$ within ecoregions; $I^2 = 36.06\%–67.57\%$ between ecoregions).

Heterogeneity was partially explained by long-term temperature change (mean effect size = −0.18, $p = 0.04$) and baseline temperature (mean effect size = −0.02, $p < 0.0001$) in the individual loss ($\mathrm{QM}(\mathrm{df} = 1) = 4.03$, $p = 0.04$) and gain ($\mathrm{QM}(\mathrm{df} = 1) = 15.96$, $p < 0.0001$) meta-analyses, respectively. Inclusion of these covariates in the models reduced variance by 15.80% and 42.23% (Table 2). Individual loss was positively correlated with warming (Figure 5), and

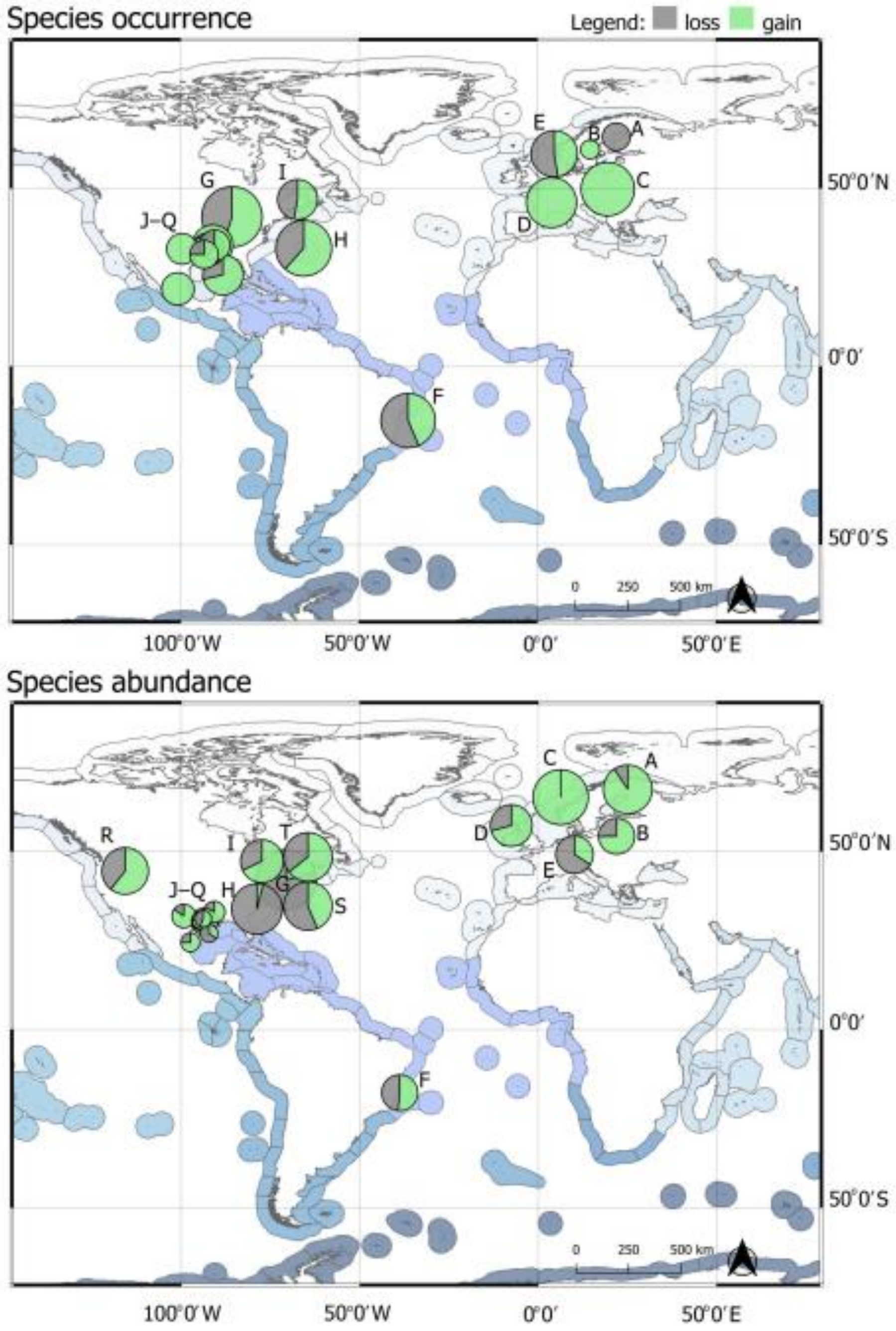

FIGURE 2 Map of Temporal Beta-Index (TBI) values, showing the loss (gray) and gain (green) components for each site evaluated in the present review, using species occurrence and abundance data. Circles are scaled according to TBI values. Blue shaded areas represent the marine realms established by Spalding et al. (2007). Letters indicate estuarine systems evaluated in the present review: A—Bothnian Sea; B—Baltic Proper; C—Kattegat; D—Bridgewater Bay; E—Mokbaai; F—Sepetiba Bay; G—North Inlet; H—Norwalk Harbor; I—Long Island Sound; J–Q—bays in the coast of Texas; R—San Francisco Bay; S—Narragansett Bay (Fox Island); T—Narragansett Bay (Whale Rock). Notice that TBI values based on fish species occurrence at Narragansett Bay and São Francisco Bay are not shown, since these studies only reported the occurrence of the most frequent fish species (FO% > 95%).

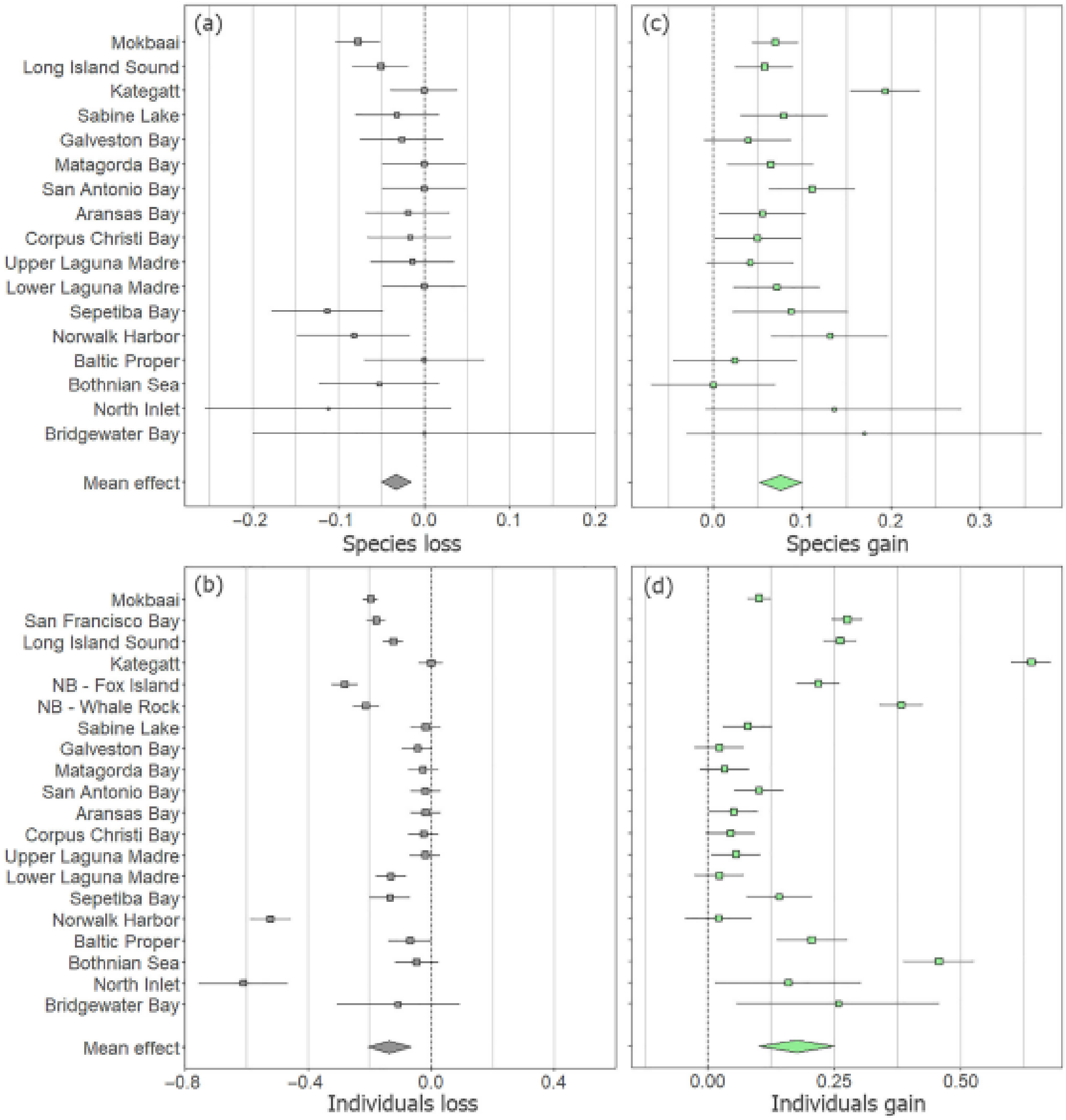

FIGURE 3 Species and individual losses (a,b) and gains (c,d) in response to climate change, as revealed by a three-level mixed-effects meta-analysis. Studies are ordered by sampling variance. Squares represent the estimated effect size and black lines represent the 95% confidence interval (CI) within each study. Polygons at the bottom of each graph indicate the mean effect sizes. Notice that data from the Narragansett Bay (i.e., NB—Fox Island and NB—Whale Rock) and São Francisco Bay are not shown in the species gain and loss meta-analyses, since these studies only reported the occurrence of the most frequent fish species (FO% > 95%).

prevailed as the main driver of community change in estuaries such as the North Inlet and Norwalk Harbor (Figure 3). Further, increases in fish species abundance were more pronounced in initially cooler estuaries, such as the Baltic Proper and the Long Island Sound (Figures 3 and 5).

Residual heterogeneity was detected for both loss ($I^2 = 82.42\%$, QE(df = 17) = 450.7237, $p < 0.0001$) and gain ($I^2 = 55.77\%$, QE(df = 17) = 540.9812, $p < 0.0001$) meta-analyses even after accounting for the temperature-related covariates. Variance between estuaries within

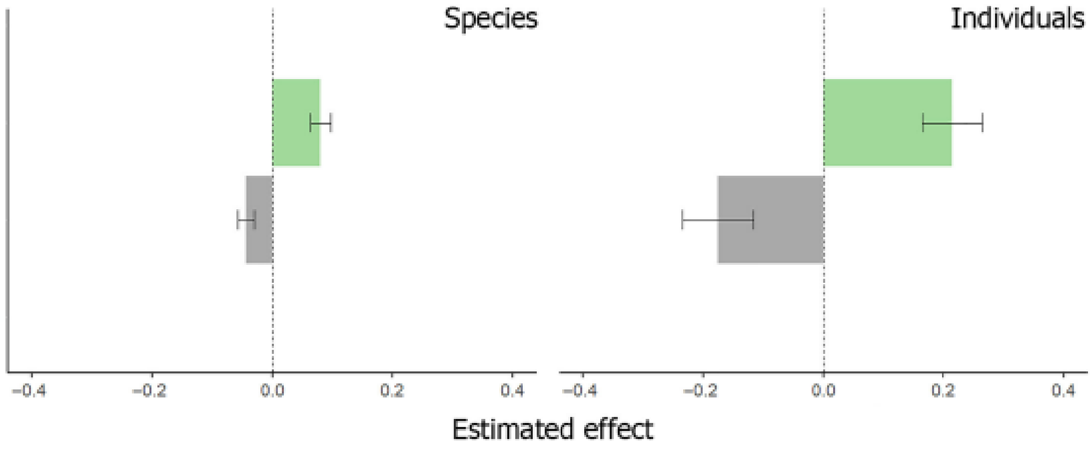

FIGURE 4 Species and individual gains (green) and losses (gray) in response to climate change, as revealed by three-level mixed-effects meta-analyses. Bars represent the mean effect sizes and whiskers indicate the standard errors. Polygon at the bottom of each figure represents the mean effect size, and polygon width represents the standard errors.

TABLE 2 Corrected Akaike Information Criterion (AIC_c) and percentage of reduced variance for species and individual gain and loss meta-analyses.

Model		Without moderators	Long-term temperature change	Baseline temperature	Long-term temperature change and baseline temperature
Species loss	**AIC_c**	**−53**	−45.9787	−46.8426	−45.9787
	% of reduced variance	...	0	0	0
Species gain	**AIC_c**	**−42.0671**	−38.6226	−38.8904	−30.6101
	% of reduced variance	...	0	0	0
Individuals loss	**AIC_c**	−11.5991	**−10.2164**	−12.5782	−5.8428
	% of reduced variance	...	**30.15**	0	0
Individuals gain	**AIC_c**	−10.6048	−3.4523	**−11.4044**	−4.9486
	% of reduced variance	...	0	**43.29**	41.89

Note: The model retained for analysis is indicated in bold.

an ecoregion ($I^2 = 55.76\%$) was higher than between ecoregions ($I^2 = 0\%$) in the individuals gain meta-analyses; the opposite pattern was detected for the individuals loss test ($I^2 = 29.48\%–52.94\%$ within and between ecoregion, respectively). Regarding occurrence data, neither the loss nor gain of species were significantly correlated with long-term temperature change ($QM(df = 1) = 1.1090–1.8416$, $p \geq 0.1748$) and/or baseline temperature ($QM(df = 1) = 2.4886–0.3007$, $p \geq 0.1147$); therefore, initial models (i.e., without covariates) were retained for analysis (Table 2). These results were robust to publication bias, since Rosenthal's (species loss = 165; species gain = 903; individual loss = 3857; individual gain = 7950) and Rosenberg's fail-safe *N* (species loss = 152; species gain = 724; individual loss = 3254; individual gain = 6868) revealed a high number of studies would be necessary to reduce the significance level of mean effect sizes to >0.05.

CTI and process strength

Fish assemblages' mean thermal affinity (CTI) changed across time periods in the 19 estuaries evaluated (Table 3). Increases in CTI were noticed for 16 systems, and ranged from 0.004 to 1.65. However, half of these communities showed a subtle increase in CTI of less than 0.1°C. Fish assemblages at three estuaries located in eastern North America exhibited the largest increases in CTI, reaching over 1°C. Tropicalization was the main process

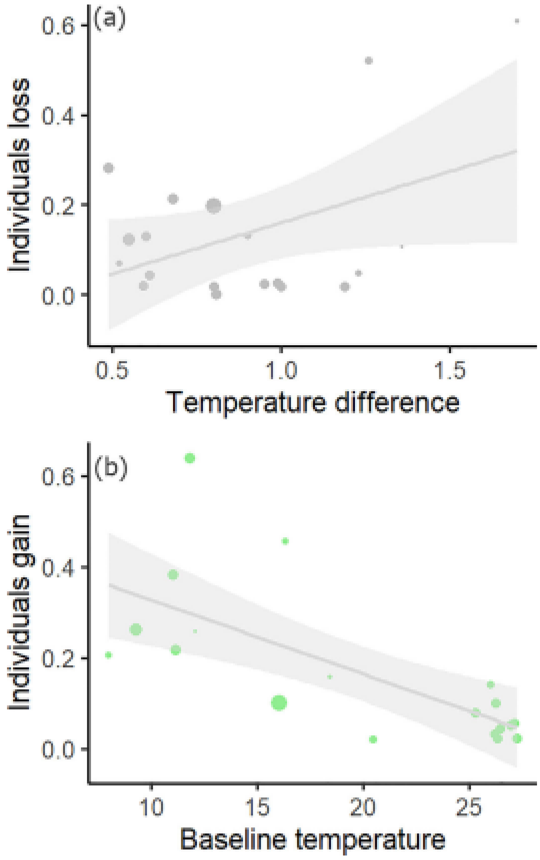

FIGURE 5 Observed effect sizes of individuals loss (gray) and gain (green) meta-analyses in response to long-term temperature change (a) and baseline temperature (b). Point size is scaled according to study weight and light gray-shaded areas represent the 95% confidence interval.

TABLE 3 Temperature-related process and fish group that contributed the most to changes in the Community Temperature Index (CTI) per estuary.

Estuary	CTI change	Process	Fish group
Bridgewater Bay	−0.192	Borealization	Residents
Sepetiba Bay	−0.153	Detropicalization	Emigrants
Matagorda Bay	−0.01	Borealization	Residents
Baltic Proper	−0.004	Borealization	Residents
Sabine Lake	0.004	Tropicalization	Residents
Upper Laguna Madre	0.013	Tropicalization	Residents
Galveston Bay	0.014	Deborealization	Residents
Bothnian Sea	0.019	Tropicalization	Residents
Lower Laguna Madre	0.036	Deborealization	Residents
Aransas Bay	0.057	Tropicalization	Residents
San Antonio Bay	0.068	Tropicalization	Residents
Corpus Christi	0.091	Tropicalization	Residents
Mokbaai	0.149	Deborealization	Residents
Kattegat	0.273	Tropicalization	Residents
San Francisco Bay	0.463	Tropicalization	Residents
North Inlet	0.822	Deborealization	Residents
Norwalk Harbor	1.165	Deborealization	Residents
Long Island Sound	1.262	Tropicalization	Residents
Narragansett Bay (Whale Rock)	1.452	Tropicalization	Residents
Narragansett Bay (Fox Island)	1.652	Deborealization	Residents

underlying community change in 10 sites where CTI increased ($F(3,54) = 2.33$, $p = 0.01$; Figure 6), including two out of the four estuaries that warmed the most, that is, Long Island Sound and Whale Rock at Narragansett Bay. Nonetheless, deborealization prevailed in the remaining six fish assemblages with increased CTI, namely at the Norwalk Harbor, Fox Island at Narragansett Bay, North Inlet, Galveston Bay, Lower Laguna Madre, and Mokbaai. Decreases in community mean thermal affinity (CTI) were observed at three locations, and values ranged from −0.19 to −0.004. Borealization was the main process shaping the novel communities in all sites, with exception for the Sepetiba Bay (Table 3), but this pattern was not statistically significant ($F(3,16) = 0.16$, $p = 0.32$; Figure 6). Differences in CTI and the processes shaping the novel fish assemblages were also noticed for adjacent bays in Texas coast, but Galveston Bay was the only estuary among them where deborealization and loss of individuals prevailed (Appendix S2: Figure S2).

Tropicalization was also the strongest process underlying community change across all sites (i.e., estuaries with increased and decreased CTI; $F(3,76) = 1.96$, $p = 0.01$). Resident species contributed most to each and every one of the four temperature-related processes (Figure 6), while immigrants and emigrants played a secondary role (all estuaries: $F(7,152) = 25.09$, $p = 0.0009$; increased CTI: $F(7,112) = 22.92$, $p = 0.0009$; decreased CTI: $F(7,32) = 3.30$, $p = 0.0009$). Tropicalization was also the strongest process underlying community change across all sites ($F(3,68) = 1.34$, $p = 0.04$), and sites with increased CTI ($F(3,52) = 1.60$, $p = 0.05$), when we reran analyses excluding data from the San Francisco and Narragansett bays (Appendix S2: Figure S3), which only comprised the most frequent species in the assemblage (FO > 95%). These tests also revealed resident species had the greatest contribution to the four temperature-related processes underlying CTI change ($F(7,136) = 16.6$, $p < 0.001$ for all sites; $F(7,104) = 13.45$, $p < 0.001$, for sites with increased CTI).

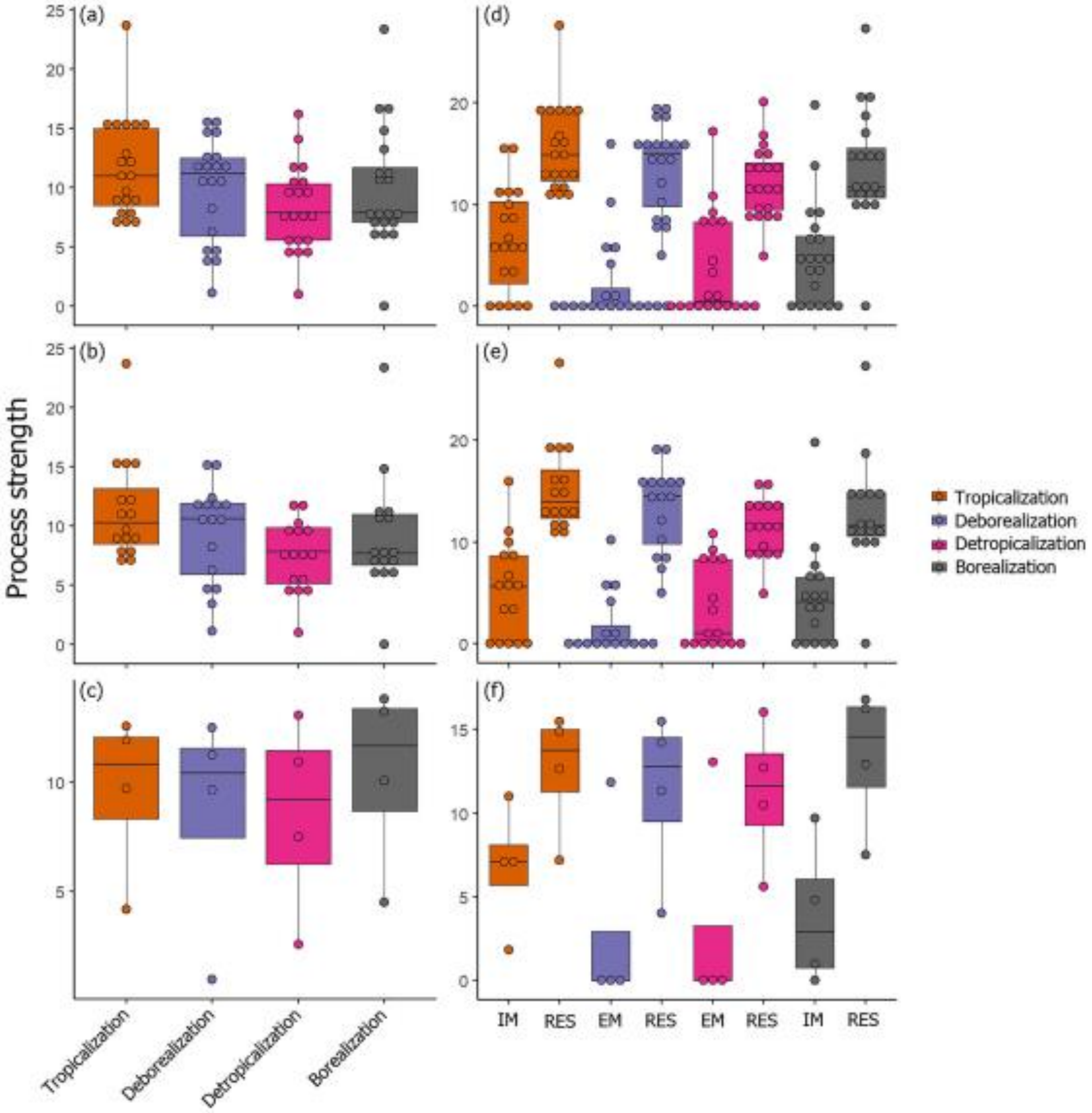

FIGURE 6 Strength of each process underlying Community Temperature Index (CTI) change for all sites pooled (a)–(d), sites where CTI increased over time (b)–(e), and sites where CTI decreased over time (c)–(f). The left panels show the value for each process regarding all species combined; the right panels show the value of each process per species groups. EM, emigrants; IM, immigrants; RES, residents.

DISCUSSION

Our work summarized evidence of long-term fish assemblage reorganization in response to warming, and explored the underlying mechanisms at assemblage (i.e., CTI change and processes) and species-level (i.e., persistence-related groups). Analysis of data did not support our first hypothesis that deborealization is the main temperature-related process underlying community change. Instead, we found tropicalization is the strongest process driving CTI change for most assemblages evaluated in the present review, agreeing with the formerly reported rise of warm-affinity species in temperate systems (Antão et al., 2020; Cheung et al., 2013; McLean et al., 2021). However, this process (and the three others) was primarily underpinned by changes in resident species abundance, while immigrants and emigrants had minor contributions. These results demonstrate that novel communities emerge primarily from local shifts in dominance of persistent species with distinct thermal affinities, despite the high turnover in occupancy rates reported for the marine realm (Blowes et al., 2019; Dornelas et al., 2014). Our study provides novel and timely insights on climate-driven biodiversity change, and revealed warming reshapes communities by favoring thermally distinct species from the local pool (i.e., dominance shift) rather than through increased dispersal.

Temperature has been proposed as one of the main drivers of biodiversity change, as it predicts species distribution and abundance (Payne et al., 2021; Stuart-Smith et al., 2017; Sunday et al., 2012). Such influence on species dispersal and dominance has been associated, in turn, with assemblage dissimilarity at both local and regional scales (Henriques et al., 2017), and across time (Antão et al., 2020). Nonetheless, most studies have associated the rise of novel communities with the replacement of original species by new settlers (i.e., increased dispersal; Blowes et al., 2019; Dornelas et al., 2014), without further looking into potential shifts in dominance. For instance, increases in CTI are frequently associated with the influx of tropical species at temperate areas (Bates et al., 2014; Cheung et al., 2013); in such cases, immigrant species would account for the largest proportion of CTI change, surpassing residents. However, our work showed that species that were already present in temperate estuaries during the early period had the biggest contributions for shifts in CTI, irrespective of the dominant process (i.e., tropicalization, borealization, and others). These findings provide some unexpected insights on how assemblages are coping with climate change, starting with the uncoupled relationship between the main group of species driving community reorganization and temperature-related processes.

The importance of resident versus immigrant and emigrant species for novel assemblages was predicted to be dependent on the strongest temperature-related process driving CTI change. For instance, resident and emigrant species were expected to have greater contributions to CTI change at systems where the loss of individuals prevailed, either through deborealization or detropicalization. In addition, immigrant species would account for the greatest proportion of CTI change whenever a positive balance in community change was detected (i.e., gains outweigh losses). Disagreeing with these expectations, we found that resident species were more important for CTI change regardless of individual losses and gains, and the prevailing temperature-related process. This pattern may be underpinned by (1) the correlation between species abundance and their persistence within a community, with dominant species being the ones present in a system for a large number of years (Magurran & Henderson, 2003), and (2) the tight relationship between temperature and species abundance (Payne et al., 2021), since we did detect a shift in the dominance of residents according to their thermal preference. These results suggest that, under ocean warming, novel fish assemblages are drawn primarily from the local pool rather than via dispersal. Poleward shifts in species distribution have been increasingly documented over the years (Bates et al., 2014; Cheung et al., 2013), and were expected to have a key role in assemblage reorganization. However, recent findings revealed warming also leads to large-scale shifts in species abundance (McLean et al., 2021), which we have found to surpass the contribution of immigrants to the processes underlying community change in temperate estuaries. Secondary contributions of immigrants to CTI change also raises concern on whether temperature-tracking species (range-shifting or not) are prone to a successful establishment at colonizing sites. These species were expected to show increased abundance under the new thermal regime, and ultimately replace the original core species (Magurran & Henderson, 2003). However, our findings suggest that other ecological pressures may hinder the growth of immigrant species in novel environments, which can increase their vulnerability to extinction while tracking suitable isotherms.

The largest contribution of residents to processes underlying CTI change could also be related to the greater number of species in this category (Appendix S2: Table S4), as result of splitting the time series into early and late periods. For instance, species sampled twice were labeled as residents, given their capture occurred in each time period. Nonetheless, few species accounted for 75% of CTI change, and these were recorded in estuaries for over half of the time series (Appendix S2: Table S4). These species also experienced large shifts in abundance, but were not necessarily among the most abundant ones within the community. Species traits were consistent across all studies with a continuous time series, as we could not assess temporal occurrence at systems with disrupted surveys, such as Sepetiba Bay (where residents and emigrants accounted for 75% of process strength) and the North Inlet. Remaining residents, immigrants, and emigrants accounted for only 25% of CTI change. Most of these species popped in and out of the community over years, which may underlie turnover rates reported by previous studies assessing biodiversity change, as these often adopt the first year of sampling as baseline for temporal comparison (Antão et al., 2020; Dornelas et al., 2014). Nonetheless, low contribution to CTI change suggests these species occurrence is less related to warming's effects. Hence, it is unlikely the number of species in resident, immigrant and emigrant categories biases the trends reported herein, which corroborate with previous reports showing that few species drive assemblage reorganization (Gotelli et al., 2022).

Evidence supporting the patterns detected in our study were mostly retrieved from temperate systems. However, divergence from the "residents trend" was found for Sepetiba Bay, which is located in a climatic transitional zone between subtropical and warm-temperate waters (22°–23° S latitude; Araújo et al., 2018). Detropicalization was the strongest process underlying assemblage reorganization at this estuary, which was underpinned by emigrant species. Abundance declines and/or retraction are expected for tropical species in response to warming, due to their low thermal safety margins and acclimation capacity (Tewksbury et al., 2008; Vinagre et al., 2019). Unfortunately, the lack of long-term data in the tropical region hinders a comprehensive estimation of beta-diversity components in our and previous studies (Antão et al., 2020), and prevent from further investigating latitude-related variation in the group of species leading community reorganization. Nonetheless, data retrieved from Sepetiba Bay agrees with the high vulnerability reported for the tropical fauna (Tewksbury et al., 2008; Vinagre et al., 2019). Therefore, assessing the upper thermal tolerance of resident, dominant species, in tropical communities may be critical for determining the risk of collapse in future scenarios of change.

Our meta-analyses only covered estuaries that warmed, since the literature search did not retrieve any study performed in cooling areas. Nonetheless, decreases in CTI were detected at four systems (Table 3). Borealization was the strongest process reshaping these communities, excepting for Sepetiba Bay (discussed above). Similar results were reported by McLean et al. (2021), which revealed wider thermal ranges for cold-affinity species driving borealization. Tolerance to distinct temperatures can buffer species against warming impacts, favoring persistence within their original habitat over dispersal (Moran et al., 2016)—which is aligned with the main findings of our study. Such ecological trait is common to estuarine species, which are subject to continuous shifts in temperature and other environmental conditions (Elliott et al., 2007). However, generalist species often show a trade-off between thermal plasticity and tolerance and, thus, are highly vulnerable to subtle increases in maximum temperature (Tewksbury et al., 2008; Vinagre et al., 2019). Hence, tolerance to current warming may not prevent from major species and individuals loss in future scenarios of change (McLean et al., 2021), despite the generalist trait of estuarine species.

Assemblage reorganization was correlated with other climate-mediated drivers besides temperature in the original studies. Sea level and salinity were associated with community change in bays along the coast of Texas, and in the Baltic Proper and the Bothnian Sea, respectively. These systems also showed little change in CTI (Table 3), revealing drivers other than temperature can have a greater influence in assemblage reorganization. The synergistic effect of climate and other anthropogenic threats also represents a topic of interest for further studies in the field, since ecosystems under several human-induced pressures (e.g., high population density and fishing) have been associated with deborealization (McLean et al., 2021). Unfortunately, we did not have enough entries to evaluate the relationship between these factors and community change, as several studies retrieved by the literature search had significant methodological inconsistencies and, thus, were excluded from our database (e.g., surveyed distinct areas or used distinct sampling methods across time periods; Appendix S2: Table S1). Lack of a significant relationship between climate-related drivers and community change also led to exclusion of 12 studies (out of the 48 screened at full-text) from the compiled database (Appendix S2; Table S1). However, the majority of these studies ($N = 11$) did not test for such relationship, but rather reported on spatial and temporal patterns of the fish assemblage. As consequence, losses and gains estimated from these data could be related to confounding factors, compromising the identification of climate-related processes underpinning assemblage reorganization. We recognize our methodological approach may overestimate meta-analyses mean effects; thus, results should be interpreted with caution. Nonetheless, the ecological patterns reported herein agree with the ones detected by Antão et al. (2020). Moreover, studies with significant results are more likely to get published (i.e., file drawer problem; Borenstein et al., 2021; Rosenberg, 2005; Rosenthal, 1979), leading potential bias in meta-analysis regardless of the criteria we have established. However, Rosenthal's and Rosenberg's fail-safe N tests revealed our results were robust to publication bias.

Loss and gain of species and individuals over time may also have been influenced by sampling effort. Number of years and samples were quite balanced across the early and late periods for all but five sites (Appendix S2: Table S5). Nonetheless, studies with higher sampling variance are given less weight when performing a meta-analysis, thus contributing little to the mean effect (Borenstein et al., 2021). For instance, among the five estuaries with unbalanced samples, only Sepetiba Bay and Kattegat had significant effect sizes (Figure 3), and the first system lost species despite increased sampling in the late period. Meta-analyses estimates based on species abundance data are also unlikely biased, as we corrected the number of individuals per sampled area (i.e., density; Appendix S2: Table S5). Therefore, mean effect sizes are likely robust and effectively controlled the unbalanced sampling effort detected for some studies in our database.

In summary, our study revealed that novel communities arise primarily via temperature-mediated shifts in resident species dominance, rather than distribution (i.e., immigration and emigration). We also demonstrated this mechanism is uncoupled from (1) the final balance between individual losses and gains in a given community, and (2) the strongest temperature-related process underlying CTI change (i.e., tropicalization, detropicalization, borealization, deborealization). These results emphasize the importance of management practices for the local species pool, since original species remained the core of novel communities, despite increased colonization rates in response to warming (Antão et al., 2020; Cheung et al., 2013). Dispersal to novel environments is particularly important for tropical species, but lack of long-term data prevented from detecting the main processes reshaping these communities. Future synthesis studies combining evidence from distinct taxa and realms may help to elucidate whether the main group of species driving community reorganization change across climatic zones, and further strengthen the results reported herein.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data supporting this research were retrieved from a literature search performed using Google Scholar, Scopus and Web of Science databases. Studies and their respective datasets are listed in Appendix S2: Table S1. Raw data was transformed in Temporal Beta-Diversity values, which are reported in Appendix S2: Table S3. Mean sea surface temperature (°C) data was downloaded from BioOracle (https://www.bio-oracle.org/) by choosing the "Present" option regarding the period of layers; "Surface layers" option regarding the depth of layers; "Tiff Raster File" option regarding the format of file; and "Mean temperature" option regarding the layers to download. Global occurrence data was downloaded from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) by searching the scientific names in the species list provided in Souza (2023) in Figshare at https://doi.org/10.6084/m9.figshare.22006493.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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APÊNDICE B – Material suplementar referente ao Apêndice 1 (Appendix S1) do manuscrito “Resident species, not immigrants, drive reorganization of estuarine fish assemblages in response to warming”, aceito para publicação no periódico *Ecology* em 21 de Dezembro de 2022.

Protocol for search string development

The search string employed in the meta-analysis was developed through a series of tests in three online databases: Web of Science, Scopus and Google Scholar. A step-by-step process was followed (see below), according to the results obtained from each combination of terms tested. We recorded the total number of hits per database, and the first 100 titles ordered by relevance (or all results, whichever was smaller) were screened for eligibility. When comparing search strings a higher number of eligible studies was considered more valuable than the number of hits.

Alternative A – *Climate Change and synonyms + fish:*

Keywords: [Climate Change OR Global Warming OR Warming OR Climate Warming OR Changing Climate] AND [Fish*]

Results per database:

- Web of Science: 25,818 results; of the first 100 entries screened, 2 fitted the eligibility criteria
- Scopus: 1,576 results; of the first 100 entries screened, 1 fitted the eligibility criteria
- Google Scholar: 47,800 results; of the first 100 entries screened, 0 fitted the eligibility criteria

Comments: This search string returned studies that discussed a) future scenarios of climate change for marine ecosystems and single species (*in situ* or experimental), b) management policies and conservation targets, c) models for environmental processes under regional warming, d) societal perception of climate change's impacts and e) impacts at other types of organisms such as algae and invertebrates.

Conclusion: Unwieldy number of studies, given return rate.

Alternative B – *Adding a term for the system of interest:*

Keywords: [Climate Change OR Global Warming OR Warming OR Climate Warming OR Changing Climate] AND [Fish*] AND [Estuar*]

Results per database:

- Web of Science: 1,819 results; of the first 100 entries screened, 2 fitted the eligibility criteria
- Scopus: 72 results; 1 fitted the eligibility criteria
- Google Scholar: 19,200 results; of the first 100 entries screened, 3 fitted the eligibility criteria

Comments: This search string returned studies that discussed a) molecular alterations of fish species due to climate change, b) experimental protocols to evaluate a single species vulnerability to climate change, c) impacts at other types of organisms such as algae and invertebrates, d) potential impacts in estuarine ecosystems (temperature, tides, hydrodynamics, etc) and e) reports on species range shifts.

Conclusion: Lack of precision and further refinement required.

Alternative C – *Adding level of organization:*

Keywords: [Climate Change OR Global Warming OR Warming OR Climate Warming OR Changing Climate] AND [Fish assemblage OR Ichthyofauna OR Fish species] AND [Estuar*]

Results per database:

- Web of Science: 195 results; of the first 100 entries screened, 4 fitted the eligibility criteria
- Scopus: 44 results; 2 fitted the eligibility criteria

- Google Scholar:22,400 results; of the first 100 entries screened, 3 fitted the eligibility criteria

Comments: This search string returned a lot of studies that were performed in a short-term time period.

Conclusion: Significant improvement but further refinement worth attempting.

Alternative D – *Adding long-term:*

Keywords: [Climate Change OR Global Warming OR Warming OR Climate Warming OR Changing Climate] AND [Long-term] AND [Fish assemblage OR Ichthyofauna OR Fish species] AND [Estuar*]

Results per database:

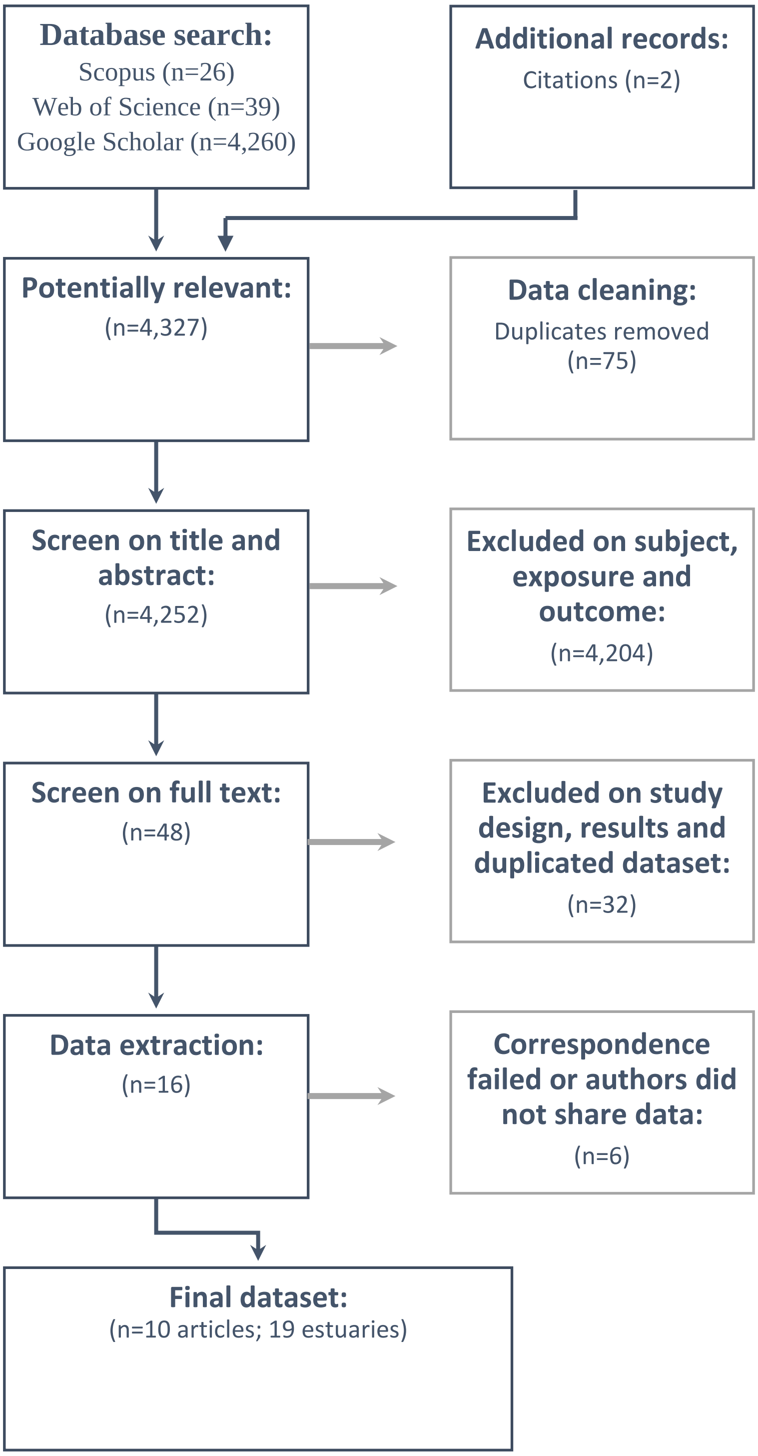
- Web of Science: 39 results; 6 fitted the eligibility criteria
- Scopus: 26 results; 6 fitted the eligibility criteria
- Google Scholar: 4,260 results; of the first 100 entries screened, 4 fitted the eligibility criteria

Comments: This search string returned a lower total number of studies, but increased the number of relevant entries for the meta-analysis.

Conclusion: Search string was deemed appropriate, as we have recorded the greatest number of eligible studies while employing less effort in screening.

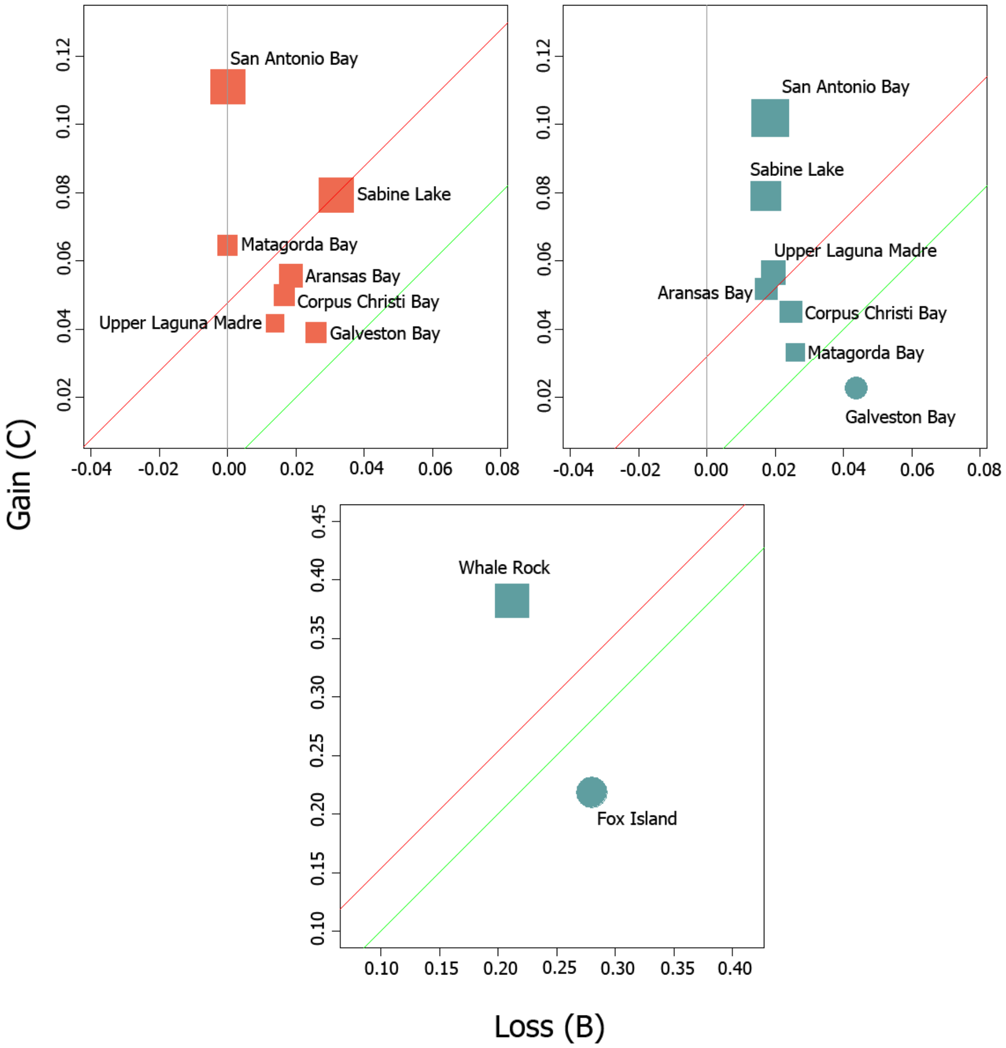
APÊNDICE C – Material suplementar referente ao Apêndice 2 (Appendix S2) do manuscrito "Resident species, not immigrants, drive reorganization of estuarine fish assemblages in response to warming", aceito para publicação no periódico *Ecology* em 21 de Dezembro de 2022.

Figure 15. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA).



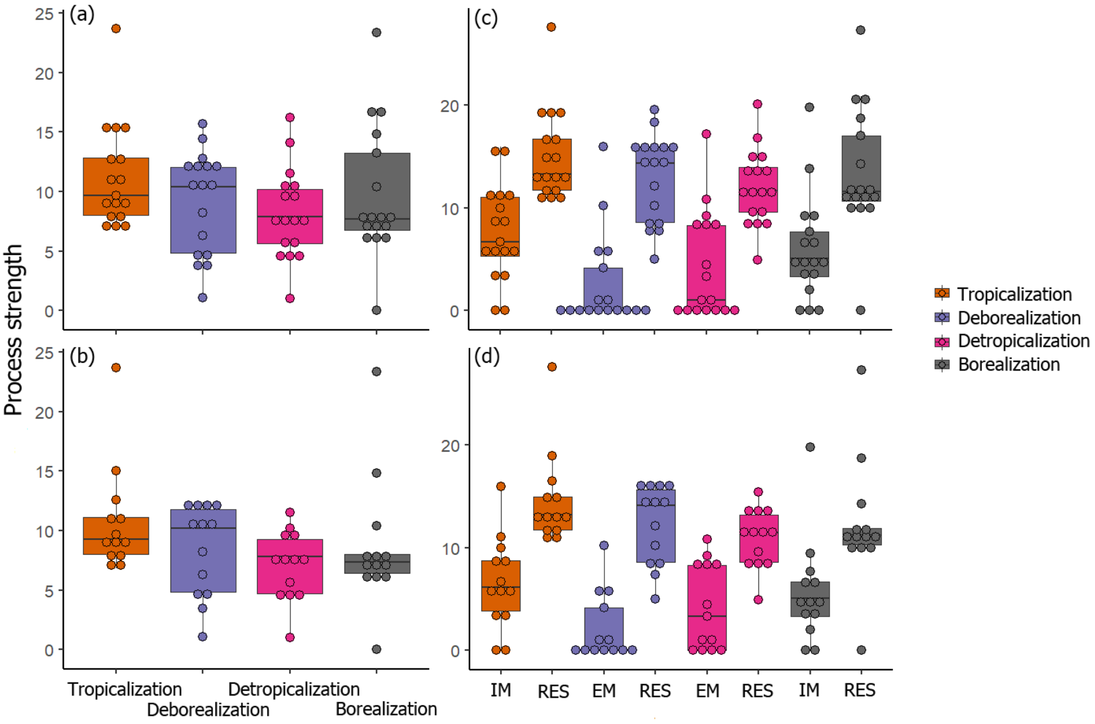
Legend: Dark blue boxes contain the number of articles (n) forwarded to the next level of screening; grey boxes show the number of articles that did not meet the eligibility criteria and were removed from the review.
Source: The author, 2022.

Figure 16. B-C plots for species occurrence (orange) and abundance (i.e. density; blue) data.



Legend: Square symbols indicate sites where gain > loss, whereas circles represent sites where loss > gain (notice the different scales for different metrics). Green line with slope of 1: line where gains equal losses. The red line was drawn parallel to the green line (i.e. with slope = 1) and passing through the centroid of the points. In estuarine systems where the average (i.e. all sites) gain was higher than the average loss, the red line is positioned above the green line; B-C plots of systems where the average loss was higher than the average gain show the red line below the green one.
Source: The author, 2022.

Figure 17 **-** Strength of each process underlying CTI change for all estuaries pooled (a-c), and estuaries where CTI increased over time (b-d). Boxplots were produced without data from Collie et al., 2008 (i.e. Narragansett Bay) and Cloern et al., 2010 (San Francisco Bay), since these authors only reported data on the most frequent species in the assemblage (FO>95%).



Legend: The left panels show the value for each process regarding all species combined; the right panels show the value of each process per species groups. Legend: IM – immigrants, EM – emigrants, RES – residents.
Source: The author, 2022.

Table 6. Eligibility and data availability for the 48 studies retrieved from the literature search that were screened at full-text. Data included in the review were retrieved from studies in bold.

Study	Eligibility	Data availability	Dataset reference/Contact details
KIMBALL et al., 2020	Eligible	Available on the paper. DOI: 10.1007/s12237-019-00692-1	-
HENDERSON et al., 2011*	Eligible	Shared by authors upon request	Data on temperature, species occurrence and abundance at the Bridgewater Bay (years 1981-2009) should be requested to Dr. Peter Henderson, Director at Pisces Conservation, via email peter@pisces-conservation.com.
VAN DER VEER et al., 2015	Eligible	Available on GBIF. DOI: 10.15468/ztbuho	VAN DER VEER HW; DE BRUIN T, 2019
ARAÚJO et al., 2018	Eligible	Available on the paper. DOI: 10.1007/s10750-018-3537-8	-
COLLIE et al., 2008	Eligible	Available at the link: web.uri.edu/gso/research/fish-trawl/data/	University of Rhode Island (URI) Graduate School of Oceanography (GSO) and Rhode Island Department of Environmental Management (DEM), 2020
OLSSON et al., 2012*	Eligible	Shared by authors upon request	Data on temperature, species occurrence and abundance at Kattegat, the Baltic Proper and the Bothnian Sea (years 1976-2008) should be requested to Dr. Jens Olsson, researcher at the Department of Aquatic Resources (SLU), Swedish University of Agricultural Sciences, via email jens.olsson@slu.se
PAWLUK et al., 2021	Eligible	Available on GBIF. Sabine Lake, DOI: 10.15468/qvitpx Matagorda Bay, DOI: 10.15468/gq5ghl San Antonio Bay, DOI: 10.15468/1j4zcw Aransas Bay, DOI: 10.15468/qyyvdr Corpus Christi Bay, DOI: 10.15468/borr1c Upper Laguna Madre, DOI: 10.15468/scwtde Lower Laguna Madre, DOI: 10.15468/t7auq9	United States Geological Survey, 2021. For information regarding species occurrence and abundance data at Galveston Bay, please contact researcher Abigail Benson, Science Analytics and Synthesis (SAS) program at USGS, via email albenson@usgs.gov
CROSBY et al., 2018*	Eligible	Shared by authors upon request	Data on temperature, species occurrence and abundance at the Norwalk Harbor (years 1990-2016) should be requested to Dra. Sarah Crosby, Director of Harbor Watch, via email s.crosby@earthplace.org
HOWELL; AUSTER, 2012*	Eligible	Shared by authors upon request	Data on species occurrence and abundance at the Long Island Sound (years 1984-2008) should be requested to Dr. Peter Howell, researcher at the Department of Marine Sciences, University of Connecticut, via email peter.auster@uconn.edu

CLOERN et al., 2010	Eligible	Available at the link: filelib.wildlife.ca.gov/Public/BayStudy/AccessDatabase/	California Department of Fish and Wildlife and Interagency Ecological Program for the San Francisco Estuary (IEP), 2019
AUBER et al., 2017	Eligible	Awaiting authorization from authors’ funding agencies to use data	-
BARCELÓ et al., 2016	Eligible	Full dataset was not available	-
CHAALALI et al., 2013	Eligible	Authors did not respond to contact	-
CHEVILLOT et al., 2016	Eligible	Authors did not respond to contact	-
SNYDER et al., 2019	Excluded on results	-	-
FEYRER et al., 2015	Excluded on results	-	-
GENNER et al., 2003	Excluded on duplicated dataset	Similar dataset of HENDERSON et al., 2011	-
HUGHES et al., 2015	Excluded on results	-	-
LEKVE et al., 2003	Eligible	Full dataset was not available	-
MEYER et al., 2016	Eligible	Authors did not respond to contact	-
POSSAMAI et al., 2018	Excluded on exposure	-	-
WALRAVEN et al., 2017	Excluded on subject		-
BAPTISTA et al., 2015	Excluded on study design	-	-
DENCKER et al., 2017	Excluded on subject	-	-
DZOGA et al., 2018	Excluded on subject	-	-
FRODIE et al., 2010	Excluded on subject	-	-
GREENE et al., 2015	Excluded on study design	-	-
HENDERSON et al., 2017	Excluded on results	-	-
JAMES et al., 2018	Excluded on results	-	-
KENDALL et al., 2021	Excluded on results	-	-
MATERN et al., 2002	Excluded on study design	-	-
MATICH et al., 2016	Excluded on results	-	-
O’CONNOR et al., 2012	Excluded on study design	-	-
PASQUAUD et al., 2012	Excluded on study design	-	-
POTTER et al., 2016	Excluded on results	-	-

PUNZÓN et al., 2016	Excluded on study design	-	-
PUNZÓN et al., 2021	Excluded on study design	-	-
SEMUSHIN et al., 2019	Excluded on results	-	-
SGUOTTI et al., 2016	Excluded on subject	-	-
SHAN et al., 2013	Excluded on subject	-	-
SNICKARS et al., 2015	Excluded on subject	-	-
SOBOCINSKI et al., 2013	Excluded on study design	-	-
TULP et al., 2008	Excluded on results	-	-
TULP et al., 2017	Excluded on results	-	-
VINAGRE et al., 2019	Excluded on study design	-	-
WOODLAND et al., 2021	Excluded on subject	-	-
XIANSHI et al., 2013	Excluded on subject	-	-
ZHANG et al., 2020	Excluded on results	-	-

* Data from HENDERSON et al., 2011 and CROSBY et al., 2018 are owned by private organizations, and therefore require authorization for usage by third parties. Data from Galveston Bay reported by PAWLUK et al., 2021 are not available on GBIF due to formatting issues, but can be requested through the email address detailed in the table. OLSSON et al., 2012 and HOWELL; AUSTER, 2012 share data upon request via the email addresses provided in the details for their studies in this table.

Table 7 - Estuary, marine ecoregion, estuary area (km^2), fishing gear and fish assemblage richness extracted from each study included in the present review.

Study	**Estuary**	**Ecoregion**	**Area (km^2)**	**Fishing gear**	**Number of species**
KIMBALL et al., 2020	North Inlet	Carolinian	33	Trawl	78
ARAÚJO et al., 2018	Sepetiba Bay	Southeastern Brazil	426	Beach seine	117
HOWELL; AUSTER, 2012	Long Island Sound	Virginian	2704	Trawl	87
HENDERSON et al., 2011	Bridgewater Bay	Celtic Seas	48	Cooling water filter screen	79
OLSSON et al., 2012	Kattegat (Vendelsö)	North Sea	0.1	Fykenet	36
	Baltic Proper (Kvädöfjärden)	Baltic Sea	7.3	Gillnet	21
	Bothnian Sea (Forsmark)	Baltic Sea	21	Gillnet	20
PAWLUK et al., 2021	Sabine Lake	Northern Gulf of Mexico	271	Gillnet	36
	Galveston Bay	Northern Gulf of Mexico	1333	Gillnet	41
	Matagorda Bay	Northern Gulf of Mexico	785	Gillnet	34
	San Antonio Bay	Northern Gulf of Mexico	508	Gillnet	30
	Aransas Bay	Northern Gulf of Mexico	520	Gillnet	30
	Corpus Christi Bay	Northern Gulf of Mexico	424	Gillnet	32
	Upper Laguna Madre	Northern Gulf of Mexico	633	Gillnet	38
	Lower Laguna Madre	Northern Gulf of Mexico	1179	Gillnet	30
CROSBY et al., 2018	Norwalk Harbor at Long Island Sound	Virginian	1.27	Trawl	36
CLOERN et al., 2010	San Francisco Bay	Northern California	902	Trawl	11
COLLIE et al., 2008	Narragansett Bay: Fox Island (FI) and Whale Rock (WR)	Virginian	343	Trawl	16
VAN DER VEER et al., 2015	Mokbaai	North Sea	1.84	Kom-fyke trap	73

Table 8 - Temporal Beta Index (TBI), loss and gain values regarding species occurrence and abundance data for each site evaluated in the present review.

Study	**Estuary**	**Occurrence**			**Abundance**		
		TBI	**Loss**	**Gain**	**TBI**	**Loss**	**Gain**
KIMBALL et al., 2020	North Inlet	0.248	0.112	0.136	0.769	0.610	0.159
ARAÚJO et al., 2018	Sepetiba Bay	0.200	0.113	0.087	0.274	0.133	0.141
HOWELL; AUSTER, 2012	Long Island Sound	0.108	0.051	0.057	0.384	0.123	0.261
HENDERSON et al., 2011	Bridgewater Bay	0.170	0.000	0.170	0.364	0.106	0.258
OLSSON et al., 2012	Kategatt (Vendelsö)	0.194	0.000	0.194	0.639	0.000	0.639
	Baltic Proper (Kvädöfjärden)	0.024	0.000	0.024	0.275	0.069	0.205
	Bothnian Sea (Forsmark)	0.053	0.053	0.000	0.504	0.047	0.457
PAWLUK et al., 2021	Sabine Lake	0.111	0.032	0.079	0.096	0.017	0.079
	Galveston Bay	0.065	0.026	0.039	0.066	0.044	0.023
	Matagorda Bay	0.065	0.000	0.065	0.059	0.026	0.033
	San Antonio Bay	0.111	0.000	0.111	0.120	0.018	0.102
	Aransas Bay	0.074	0.019	0.056	0.069	0.017	0.052
	Corpus Christi Bay	0.07	0.02	0.05	0.070	0.025	0.045
	Upper Laguna Madre	0.056	0.014	0.042	0.076	0.020	0.056
	Lower Laguna Madre	0.071	0.000	0.071	0.154	0.131	0.023
CROSBY et al., 2018	Norwalk Harbor at LIS	0.213	0.082	0.131	0.543	0.522	0.021
CLOERN et al., 2010	San Francisco Bay	-	-	-	0.454	0.179	0.275
COLLIE et al., 2008	NB - Fox Island	-	-	-	0.499	0.28	0.22
	NB - Whale Rock	-	-	-	0.594	0.21	0.38
VAN DER VEER et al., 2015	Mokbaai	0.147	0.078	0.070	0.298	0.196	0.102

Table 9 - Number of resident, immigrant and emigrant species in each estuary evaluated in the present review. The number of species that accounted up to 25%, 50% and 75% of the strength of temperature-related processes underlying CTI change (i.e. tropicalization, borealization, deborealization, detropicalization), and the number of years species in the latter category (75% of processes strength) were present in the estuary are also shown.

Estuary	**Number of species**			**Number of species that contributed to % of processes strength**			**Years present in the estuary**
	Residents	**Immigrants**	**Emigrants**	**25%**	**50%**	**75%**	
North Inlet	46	17	14	1	2	3	-
Sepetiba Bay	78	17	22	2	5	12	-
Long Island Sound	74	9	9	1	2	3	25
Bridgewater Bay	56	23	0	1	3	7	29 - 28
Kattegat (Vendelsö)	24	12	0	1	1	3	32
Baltic Proper (Kvädöfjärden)	20	1	0	1	2	3	33 - 20
Bothnian Sea (Forsmark)	18	0	2	1	2	4	33 - 18
Sabine Lake	28	6	2	2	4	8	23 - 5
Galveston Bay	34	4	3	1	3	6	23
Matagorda Bay	29	5	0	2	3	7	23 - 21
San Antonio Bay	24	6	0	1	2	4	23
Aransas Bay	25	4	1	1	2	3	23 - 22
Corpus Christi Bay	28	3	1	1	2	5	23 - 19
Upper Laguna Madre	34	3	1	2	5	9	23 - 8
Lower Laguna Madre	29	1	0	2	5	9	23 - 22
Norwalk Harbor at Long Island	24	7	5	1	2	5	-
San Francisco Bay	11	-	-	1	3	4	-
Fox Island at Narragansett Bay	17	-	-	1	1	1	-
Whale Rock at Narragansett Bay	17	-	-	1	1	2	-
Mokbaai	56	9	9	3	7	21	52 - 25

Table 10 - Number of years, number of samples, richness and total fish density (i.e. abundance per 100 m^2 of sampled area) for the early and late periods of each estuary evaluated in the present review.

Estuary	**Number of years**		**Number of samples**		**Richness**		**Density**	
	Early	**Late**	**Early**	**Late**	**Early**	**Late**	**Early**	**Late**
North Inlet	4	4	94	93	61	64	6.62	2.5
Sepetiba Bay	10	12	46	276	100	95	60.75	61.79
Long Island Sound	15	10	1599	1159	78	84	5.98	7.69
Bridgewater Bay	5	24	48	276	56	79	416.61	565.3
Kattegat (Vendelsö)	11	22	1260	2772	24	36	2392.47	10858.14
Baltic Proper (Kvädöfjärden)	11	22	396	792	20	21	186.26	244.78
Bothnian Sea (Forsmark)	11	22	396	666	18	17	1484.58	3551.22
Sabine Lake	9	14	405	630	30	54	1.71	1.94
Galveston Bay	9	14	405	630	37	38	29.58	28.35
Matagorda Bay	9	14	405	630	30	34	5.24	5.31
San Antonio Bay	9	14	405	630	24	30	3.74	4.41
Aransas Bay	9	14	405	630	26	29	3.7	3.96
Corpus Christi Bay	9	14	405	630	29	31	3.28	3.41
Upper Laguna Madre	9	14	405	630	35	37	2.75	2.96
Lower Laguna Madre	9	14	405	630	26	30	3.12	2.56
Norwalk Harbor at Long Island	16	11	446	774	29	31	3.293	1.092
San Francisco Bay	19	10	4003	2112	11	11	5.219	6.328
Fox Island	26	21	1240	1070	17	17	64.88	57.21
Whale Rock	21	26	1061	1248	17	17	47.68	67.25
Mokbaai	25	27	3602	3466	64	64	9.47	7.84

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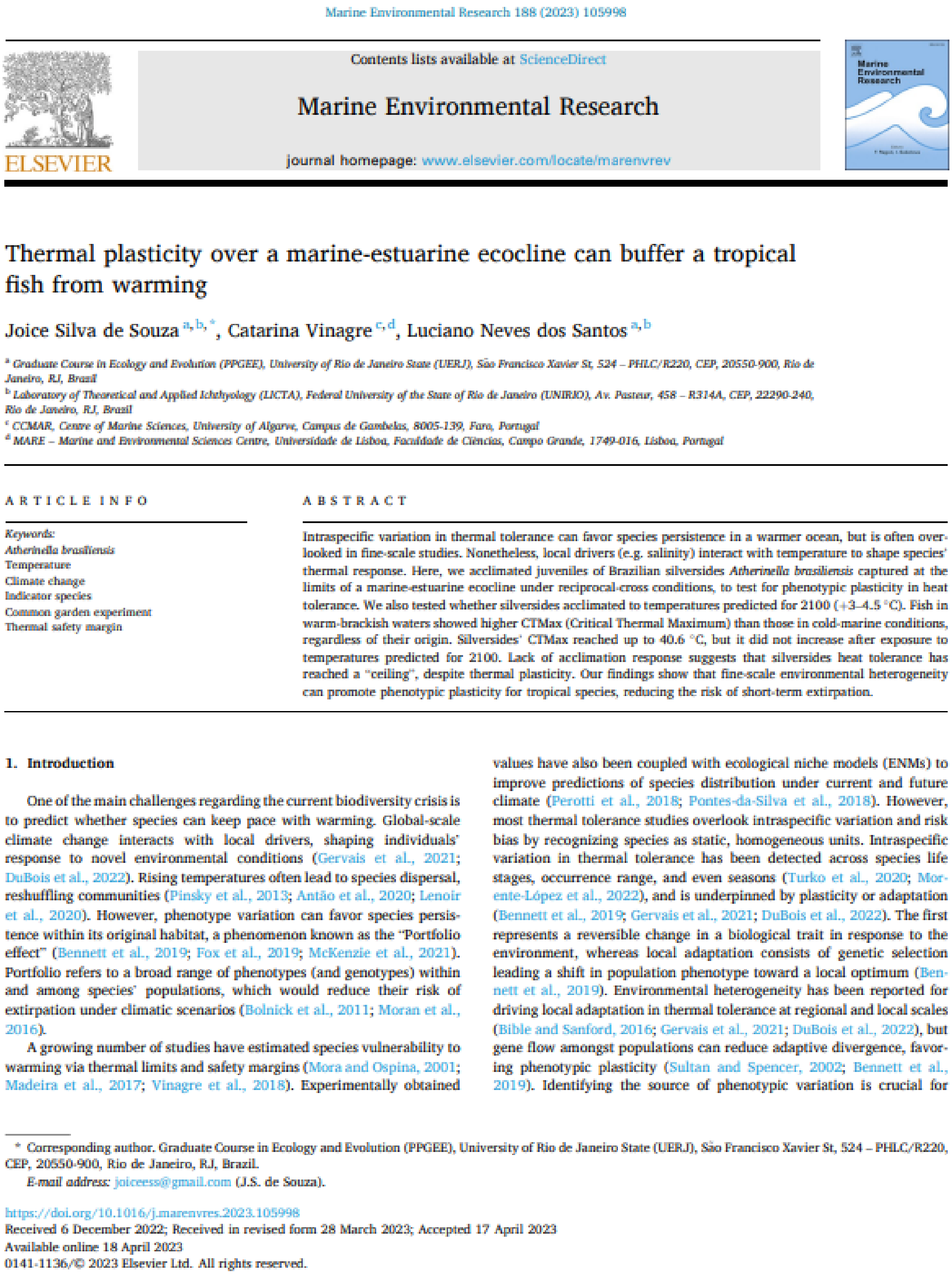

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Thermal plasticity over a marine-estuarine ecocline can buffer a tropical fish from warming

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ABSTRACT

Intraspecific variation in thermal tolerance can favor species persistence in a warmer ocean, but is often overlooked in fine-scale studies. Nonetheless, local drivers (e.g. salinity) interact with temperature to shape species' thermal response. Here, we acclimated juveniles of Brazilian silversides *Atherinella brasiliensis* captured at the limits of a marine-estuarine ecocline under reciprocal-cross conditions, to test for phenotypic plasticity in heat tolerance. We also tested whether silversides acclimated to temperatures predicted for 2100 (+3–4.5 °C). Fish in warm-brackish waters showed higher CTMax (Critical Thermal Maximum) than those in cold-marine conditions, regardless of their origin. Silversides' CTMax reached up to 40.6 °C, but it did not increase after exposure to temperatures predicted for 2100. Lack of acclimation response suggests that silversides heat tolerance has reached a "ceiling", despite thermal plasticity. Our findings show that fine-scale environmental heterogeneity can promote phenotypic plasticity for tropical species, reducing the risk of short-term extirpation.

1. Introduction

One of the main challenges regarding the current biodiversity crisis is to predict whether species can keep pace with warming. Global-scale climate change interacts with local drivers, shaping individuals' response to novel environmental conditions (Gervais et al., 2021; DuBois et al., 2022). Rising temperatures often lead to species dispersal, reshuffling communities (Pinsky et al., 2013; Antão et al., 2020; Lenoir et al., 2020). However, phenotype variation can favor species persistence within its original habitat, a phenomenon known as the "Portfolio effect" (Bennett et al., 2019; Fox et al., 2019; McKenzie et al., 2021). Portfolio refers to a broad range of phenotypes (and genotypes) within and among species' populations, which would reduce their risk of extirpation under climatic scenarios (Bolnick et al., 2011; Moran et al., 2016).

A growing number of studies have estimated species vulnerability to warming via thermal limits and safety margins (Mora and Ospina, 2001; Madeira et al., 2017; Vinagre et al., 2018). Experimentally obtained values have also been coupled with ecological niche models (ENMs) to improve predictions of species distribution under current and future climate (Perotti et al., 2018; Pontes-da-Silva et al., 2018). However, most thermal tolerance studies overlook intraspecific variation and risk bias by recognizing species as static, homogeneous units. Intraspecific variation in thermal tolerance has been detected across species life stages, occurrence range, and even seasons (Turko et al., 2020; Morente-López et al., 2022), and is underpinned by plasticity or adaptation (Bennett et al., 2019; Gervais et al., 2021; DuBois et al., 2022). The first represents a reversible change in a biological trait in response to the environment, whereas local adaptation consists of genetic selection leading a shift in population phenotype toward a local optimum (Bennett et al., 2019). Environmental heterogeneity has been reported for driving local adaptation in thermal tolerance at regional and local scales (Bible and Sanford, 2016; Gervais et al., 2021; DuBois et al., 2022), but gene flow amongst populations can reduce adaptive divergence, favoring phenotypic plasticity (Sultan and Spencer, 2002; Bennett et al., 2019). Identifying the source of phenotypic variation is crucial for

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preventing maladaptation in a management context, since each mechanism has implications at distinct time scales (e.g. plasticity is expected to buffer from immediate impacts of warming such as heatwaves, while adaptation also has potential to dampen against decadal warming; Bennett et al., 2019). Evidence on the main mechanism underlying intraspecific variation can be retrieved from common garden experiments, which are based on the acclimation of individuals from distinct sites under similar environmental conditions (Gervais et al., 2021; DuBois et al., 2022).

Thermal history (i.e. the temperature range experienced by an individual in their natural environment) often shapes species' thermal tolerance (Giomi et al., 2016; Olsen et al., 2021). Nonetheless, multiple abiotic variables can interact with temperature, creating additive, synergistic or antagonist effects in heat tolerance (i.e. combined effect equal, greater or smaller than the sum of each independent variable, respectively; Re et al., 2012; Fong et al., 2018; Reiser et al., 2017; Madeira et al., 2021). The interplay between temperature and salinity has been the subject of several studies performed with coastal species, as salinity interacts with temperature to shape species thermal tolerance (Reiser et al., 2017; Madeira et al., 2021). Local-scale mosaics regarding temperature and salinity can be observed in estuaries, due to overlapping marine-estuarine (i.e. ocean to mid-estuary) and estuarine-freshwater (i.e. mid-estuary to river) ecoclines (Attrill and Rundle, 2002). The environmental gradient in temperature and salinity drives community turnover between the upper, middle and lower estuary, filtering species from distinct functional-use guilds according to their tolerance, particularly regarding salinity (Attrill and Rundle, 2002; Chaves et al., 2018). However, resident species inhabiting these systems often show phenotypic variation to cope with heterogeneity in environmental conditions (Gervais et al., 2021). Therefore, these species represent a good model for assessing the combined effects of temperature and salinity in heat tolerance, as well as to unveil potential mechanisms underlying fine-scale intraspecific variation.

Brazilian silversides *Atherinella brasiliensis* (Quoy and Gaimard, 1825) is a resident fish species in estuaries along the southwestern Atlantic, and thrives under varied salinity and temperature conditions within these systems (de Souza et al., 2018; Damasceno, 2020). Despite their wide distribution across the estuary, site-fidelity has been reported for Atherinidae species, particularly during early life stages (Green et al., 2012; Claudino et al., 2013). Limited dispersal between estuarine zones and a partially dispersive reproductive strategy (i.e. adhesive bottom eggs followed by a larval stage; Fávaro et al., 2003; del Río et al., 2005) may lead to distinct phenotypes between local populations (Bennett et al., 2019). Intraspecific variation can play an important role in protecting species from warming in heat-conservative systems, since spatial and temporal (i.e. from hours to years) microclimate variation may exceed the thermal limits of individuals distributed across the estuary. These fine-scale assessments are particularly important for determining tropical species vulnerability to rising temperatures, since they have been reported to have low acclimation capacity despite their high Critical Thermal Maximum (CTMax; Tewksbury et al., 2008; Vinagre et al., 2018).

Here, we investigated intraspecific variation in heat tolerance and the potential for phenotypic plasticity and local adaptation over a fine-spatial scale (<20 km), using experimental data from a resident estuarine fish species, *Atherinella brasiliensis*. Experiments were performed exclusively with juveniles in order to avoid confounding effects related to ontogenetic variation; we chose this particular life stage to test our hypotheses due to their lower mobility and high site-fidelity (Green et al., 2012; Claudino et al., 2013). Fish were acclimated under the average temperature and salinity of two sites at the opposite limits of a marine-estuarine ecocline, using a reciprocal-cross design (i.e. silversides were acclimated to original and alternate conditions of their capture site). Therefore, experimental treatments mirrored the cold-marine (27.5 °C and 32 ppt) and warm-brackish (29.7 °C and 25 ppt) conditions observed at each site. We expected a higher CTMax for fish in warmer and less saline waters, regardless of specimens' capture site (i.e. phenotypic plasticity). We also predicted CTMax of fish from both treatments would increase after exposure to temperatures predicted under the SSP2-4.5 and SSP5-8.5 scenarios. A second set of experiments was performed to disentangle current temperatures' effect on CTMax of silversides acclimated in marine and brackish salinities. Higher CTMax was expected for fish in warmer waters, irrespective of treatment's salinity. Silversides' life-history traits (i.e. site-fidelity and a partly dispersive reproductive strategy) justify our expectations regarding phenotypic plasticity at local scale. Further, euryhalinity would underlie the lack of a salinity effect on species thermal tolerance, as fish were acclimated under regular habitat conditions (i.e. as opposed to stressful hypo or hypersaline levels, e.g. Júnior et al., 2021). Therefore, we hypothesized that thermal history would be the main factor underlying intraspecific variation in *A. brasiliensis* thermal tolerance.

2. Materials and methods

2.1. Animal collection and husbandry

Brazilian silversides were caught using a seine net with a codend (20m width x 2m height – 7 mm mesh size; 3 mm mesh size for codend) in two beaches located at the entrance and northwest zones of Guanabara Bay, Rio de Janeiro, Brazil (Fig. 1). These sites are ca. 20 km apart from each other, and were chosen for this study as they represent the opposite boundaries of a marine-estuarine ecocline, particularly regarding temperature (Chaves et al., 2018). Urca Beach (22°56′52″S, 43°09′48″W) is located near Guanabara Bay entrance, where marine conditions prevail (Kjerfve et al., 1997). Mean salinity ranges from 29 to 32 ppt throughout the year, and mean temperature from 23°C to 28 °C (de Souza et al., 2018; Damasceno, 2020). Zumbi Beach (22°49′13″S, 43°10′23″W) is located in the inner western portion of the bay, where hydrodynamic energy is low. As consequence, water residence time is high (Fistarol et al., 2015), and temperatures reach up to 33 °C during summer - the highest value recorded for the entire bay (Rosman et al., 2017; Damasceno, 2020). Discharge from polluted rivers and the decreased velocity of tidal currents results in salinities around 25 ppt in the region (Chaves et al., 2018).

Fish were captured in early 2022 at both Urca and Zumbi beaches. Silversides were placed in coolers and plastic bags filled with *in situ* seawater, which were continuously aerated using a portable oxygen compressor (Boyu D-200) during transport to the Laboratory of Theoretical and Applied Ichthyology (LICTA) at Federal University of the State of Rio de Janeiro (UNIRIO). Fish were transported within 1 h, and placed in aerated recipients filled with *in situ* seawater upon arrival at the laboratory. Then, an equal volume of artificial seawater was gradually added to each recipient to avoid osmotic and thermal stress during fish acclimation to experimental conditions. After this process, 40 fish were randomly placed in each of two individual aquariums of 472 L (68 x 150 × 53 cm, Model Ea-150L.h^{-} - Boyu). Each tank was filled with artificial seawater of temperature and salinity similar to the average levels at Zumbi and Urca beaches (see section 2.2. for more details). Temperatures were controlled using thermostats (Kintons Kth-8800, Minjiang MJ-HF500), and experimental salinities were achieved by adding synthetic salt (Ocean Tech Reef Active) to filtered water. Tanks were also equipped with a diffuser stone connected to an air pump (Maxxi Power Pro-2000), ceramic rings (Professional Sera Siporax), fine gravel (i.e. Aragonite Aquarium Sand) and fluorescent white lights. Fish were conditioned for 48 h prior to the start of experimental trials, under a summer photoperiod of 14h light: 10h dark. Juveniles were fed *ad libitum* with *Artemia salina* once a day during housing in the laboratory. Water quality parameters were monitored every 24 h, and kept within the standard range regarding organisms' welfare (mean ± S.E): pH = 8.0 ± 0.02, dissolved oxygen = 5.88 ± 0.18 ppm, ammonia = 0.08 ± 0.01 ppm and nitrite = 0.33 ± 0.03 ppm (values were monitored using Labcon tests for the respective variables). Tanks were allowed to

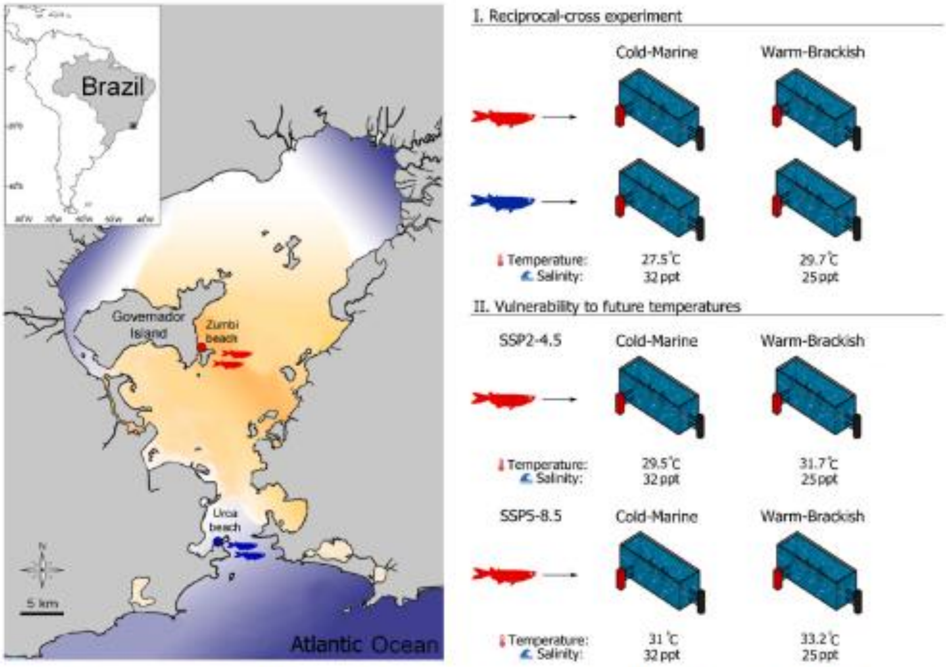

Fig. 1. Map of Guanabara Bay, Brazil, showing the two sites where Brazilian silversides were collected (i.e. Urca Beach and Zumbi Beach). The conceptual color gradient represents cold (blue) and warm (orange) areas within the bay, and is based on hydrodynamic models of water residency time and field data retrieved from previous studies (Rosman et al., 2017; Chaves et al., 2018; de Souza et al., 2018; Damasceno, 2020). Experimental design and treatments regarding the reciprocal-cross and future vulnerability tests are also shown. Color legend: blue fish – captured at Urca Beach; red fish – captured at Zumbi Beach.

stabilize for 6 weeks before housing silversides. Animal collection, husbandry and experimental protocols were authorized by the Brazilian Institute of Environment and Natural Resources (IBAMA, license n° 70942).

2.2. *Reciprocal-cross experiment*

Fish were acclimated to mean temperature and salinity recorded during summer at Urca (i.e. designed as the cold-marine treatment hereafter) and Zumbi (i.e. designed as the warm-brackish treatment hereafter) beaches. Water temperature was stable at 27.5 °C ± 0.2 (mean ± SE) and salinity at 32 ppt ± 0.1 in the cold-marine treatment; these respective variables were maintained at 29.7 °C ± 0.02 and 25 ppt ± 0.1 in the warm-brackish treatment (Fig. 1). Silversides were acclimated under original and alternate (reciprocal-cross) temperature and salinity of their respective capture site. Therefore, we had four groups of acclimated fish: a) cold-marine treatment (original), b) cold-marine treatment (cross), c) warm-brackish treatment (original), and d) warm-brackish treatment (cross) (Fig. 1). In the original-labeled treatments, fish were kept under similar conditions of their respective capture site; in the cross-labeled treatments, silversides were exposed to alternate conditions (i.e. fish captured at Urca Beach was acclimated to the temperature and salinity of Zumbi Beach and vice-versa). We adopted this experimental design to detect whether differences in silversides' heat tolerance varied with environmental conditions or not (i. e. home-site advantage). Fish were acclimated for five days, during which we performed a daily check of their health status (i.e. wounds or disease symptoms). Afterwards, a subset of individuals had their upper critical limits assessed (see section 2.5. for details). Acclimation duration was defined based on previous literature that reported tropical species fully acclimate to elevated temperatures within 2–5 days (Schmidt-Nielsen, 1997). Moreover, a comprehensive meta-analysis also revealed a short period (i.e. 3 days) is required for CTMax acclimation regarding species with a small body size (Rohr et al., 2018), such as the Brazilian silversides.

2.3. *Silversides' vulnerability to temperatures predicted for 2100*

Subsequent experiments were performed to evaluate *A. brasiliensis*' vulnerability to warming scenarios predicted for 2100. These trials were performed using only fish from the cold-marine (cross) and warm-brackish (original) treatments, as statistical analyses of reciprocal-cross experiments revealed a significant effect of acclimation condition but not specimen's origin on CTMax. Fish in the cold-marine and warm-brackish treatments were acclimated for five more days under temperatures increased by +2 °C (i.e. cold-marine treatment: 29.5 °C ± 0.1 temperature, 32 ppt ± 0.2 salinity; warm-brackish treatment: 31.7 °C ± 0.04 temperature, 25 ppt ± 0.2 salinity) (Fig. 1). Then, we estimated CTMax for a subset of individuals. The experimental +2 °C rise in temperature, combined with the currently reported +1 °C in the natural environment, amounts to a warming of +3 °C, which is expected by 2100 under the SSP2-4.5 scenario (IPCC, 2021). We adopted temperature values from this "inequality" scenario, since an increase of +2 °C to +3 °C degrees has been proposed as the likely range of warming by the end of the century (Bauer et al., 2017; Burgess et al., 2022). After the end of this acclimation period, we further exposed the remaining fish in both treatments to an increase of +1.5 °C in temperature, thus achieving the mean value predicted for 2100 under the SSP5-8.5 scenario (IPCC et al., 2021). Therefore, the cold-marine treatment had 31 °C ± 0.4 temperature and 32 ppt ± 0.25 salinity, and the warm-brackish treatment had

33.2 °C ± 0.1 temperature and 25 ppt ± 0.2 salinity (Fig. 1). Despite SSP-8.5 has been considered as an unlikely scenario (Burgess et al., 2022), the temperature values predicted may be reached during extreme events in heat-conservative systems, such as estuaries. Therefore, we used values from this "fossil-fueled development" scenario for conservation and comparative purposes. Fish were acclimated for five days, and then another subset of individuals had their CTMax estimated. No individual was exposed to CTMax trials more than once.

2.4. *Temperature's isolated effect on CTMax*

We performed a second set of experiments to assess temperature change's effect on *A. brasiliensis* CTMax, using values currently observed at each capture site. Silversides were conditioned for 48 h before the start of acclimation period (see section 2.1.), and 15 fish were randomly placed in each of two individual aquariums of 472 L (68 x 150 × 53 cm, Model Ea-150L.h^{-} - Boyu). These aquariums were set with salinities from the marine (i.e. 32 ppt) and brackish (i.e. 25 ppt) treatments (see section 2.2.), and had a starting temperature of 27.5 °C ± 0.1. Fish were acclimated for five days, and then a subset of individuals had their upper critical limits (CTMax) assessed. Afterwards, we increased the aquariums' temperature to 29.7 °C ± 0.1 for five more days. At the end of this period, CTMax was estimated for another subset of individuals. No fish was exposed to more than one CTMax trial.

2.5. *Critical Thermal Maxima*

Silversides' upper thermal limits were estimated through the CTMax method (Mora and Ospina, 2001; Vinagre et al., 2015; Madeira et al., 2017). Fish from each trial (see sections 2.2., 2.3. and 2.4.) were transferred to two individual aquariums of 40 L (35.2 x 53.5 × 32.3 cm, Model ZJ 401 - Boyu), which were equipped with a digital thermostat (TIC-17RGT - Full Gauge), a diffuser stone connected to an air pump (Maxxi Power Pro-2000), ceramic rings (Professional Sera Siporax), fine gravel (aragonite) and fluorescent white lights. Temperature and salinity were set according to acclimation conditions of each experiment described in the previous sections. For instance, to assess CTMax of fish acclimated to temperatures predicted for SSP5-8.5 (section 2.3.), we set the cold-marine tank with a stable temperature of 31 °C and salinity at 32 ppt, while the warm-brackish tank's temperature and salinity was 33.2 °C and 25 ppt, respectively. CTMax was estimated by exposing fish to a constant rate of temperature increase of 1 °C per 15 min, and loss of equilibrium was defined as end-point (i.e. specimen turned upside down and failed to return to the original position). Warming rate was chosen based on Vinagre et al. (2015), and represents an ecologically suitable estimate for coastal ecosystems, such as estuaries. The critical upper temperature (CTMax) of each individual was recorded through the digital thermostat (TIC-17RGT - Full Gauge). Fish were anesthetized with eugenol and euthanized by freezing in ice, before having their total length (mm) and weight (0.00 gr) recorded.

2.6. *Data analysis*

We calculated the arithmetic mean of thermal endpoints (CTMax) obtained for individuals from each treatment (Mora and Ospina, 2001). Intraspecific variability (%CV) of CTMax was determined by dividing standard deviation by the mean, multiplied by 100 (Madeira et al., 2017). Thermal safety margins (TSM) were estimated as the difference between fish CTMax and maximum habitat temperature (i.e. values were retrieved from Damasceno, 2020), to investigate specimens' risk of ecological function loss (Madeira et al., 2017). We also provided TSM estimates considering heatwave events (i.e. +5 °C above the average maximum temperature of a location; Vinagre et al., 2018) in present-day conditions, and the maximum temperatures predicted for 2100 under SSP2-4.5 e SSP5-8.5 scenarios.

Permutational Analysis of Variance (PERMANOVA) was performed to assess the effect of specimen's origin (i.e. capture site) and acclimation condition (i.e. cold-marine and warm-brackish treatments) on silversides' CTMax and TSM, using $\log_{10}x$ transformed total length (cm) as covariate. The Euclidean distance (1000 permutations; $p \leq 0.05$) was chosen for PERMANOVA tests, which were performed using the *adonis2* function in the *vegan* package (Oksanen et al., 2022) for the R software (R Core Team, 2022). We also assessed homogeneity of data variance between levels of each factor (e.g. treatment, species origin) using the *betadisper* function in the *vegan* package (Oksanen et al., 2022). Linear Mixed Models (LMM) were performed to assess the effect of acclimation temperature on silversides' CTMax and TSM (i.e. experiments described in section 2.3.). Acclimation temperature (fixed factor; levels = current, SSP2-4.5 and SSP5-8.5 scenarios) was nested within treatment (fixed factor; levels = cold-marine, warm-brackish) for these tests. We also included trial number as a random effect, to account for the lack of temporal independence between acclimation scenarios (e.g. fish from CTMax trial number 2 were exposed to acclimation temperatures of both current and SSP2-4.5 scenarios, and so on). Our mixed-model also tested for an effect of $\log_{10}x$ transformed total length (cm) on silversides' CTMax. The same statistical design was employed to analyze current temperatures' influence on fish CTMax (i.e. experiments described in section 2.4.). Acclimation temperature (fixed factor; levels = 27.5 °C and 29.7 °C) was nested within salinity treatment (fixed factor; levels = 25 ppt and 32 ppt), and a random effect was specified for trial number. Total length ($\log_{10}x$ transformed; cm) was also included in the model. LMMs were performed using the *lme* function from the *nlme* package (Pinheiro and Bates, 2000; Pinheiro and Bates, 2022). Post-hoc pairwise comparisons were calculated using the *lsmeans* package (Lenth, 2016). Prior to performing LMM models, we confirmed the Gaussian distribution of the response variable through the visual inspection of histograms. Model residuals were also checked for normality and homogeneity of variance using qqplots from the *stats* package (R Core Team, 2022).

3. Results

3.1. *Reciprocal-cross experiment*

Heat tolerance (CTMax) was influenced by acclimation conditions ($F_{1,29} = 20.91$, $p = 0.001$, $R^2 = 0.43$), but not silversides' origin ($F_{1,29} = 2.30$, $p = 0.15$, $R^2 = 0.05$) or the interaction between these factors ($F_{1,27} = 0.03$, $p = 0.85$, $R^2 = 0$). Fish acclimated in warm-brackish conditions showed a higher CTMax than ones from the cold-marine treatment (both original and cross) (Table 1; Fig. 2). Fish size did not influence CTMax ($F_{1,30} = 0.01$, $p = 0.91$, $R^2 = 0$), nor interacted with acclimation conditions ($F_{1,29} = 1.98$, $p = 0.17$, $R^2 = 0.04$) and specimen's origin ($F_{1,29} = 0.007$, $p = 0.93$, $R^2 = 0$). We also did not detect a significant interaction between CTMax and acclimation condition, specimen's origin and size ($F_{1,27} = 0.21$, $p = 0.64$, $R^2 = 0$). Variance regarding CTMax data was homogeneous between acclimation treatments ($F_{1,29} = 1.25$, $p = 0.27$) and specimen's origin ($F_{1,29} = 0.31$, $p = 0.58$). Intraspecific CTMax variation (%CV) within treatments was low, and ranged from 0.31% to 0.66% (Table 1).

Fish from the cold-marine treatment had higher thermal safety margins (TSM) than ones from the warm-brackish treatment, regarding both regular and heatwave scenarios ($F_{1,29} = 4093.96$, $p = 0.001$, $R^2 = 0.99$; values for both tests) (Table 1; Fig. 2). Specimen's origin ($F_{1,29} = 2.79$, $p = 0.09$, $R^2 = 0$), size ($F_{1,30} = 0.01$, $p = 0.9$, $R^2 = 0$), the interaction between these factors ($F_{1,29} = 0.97$, $p = 0.33$, $R^2 = 0$), and with acclimation condition ($F_{1,27} = 0.21$, $p = 0.65$, $R^2 = 0$) did not have a significant effect on silversides' TSM (i.e. values given refer to regular temperature and heatwave tests). Acclimation condition also did not interact with specimen's origin ($F_{1,27} = 0.03$, $p = 0.86$, $R^2 = 0$) nor size ($F_{1,27} = 1.03$, $p = 0.32$, $R^2 = 0$), regarding regular and heatwave TSMs. Variance of TSM data was homogeneous between acclimation treatments ($F_{1,29} = 1.25$, $p = 0.27$) and specimen's origin ($F_{1,29} = 0.05$, $p = 0.82$), for both regular and heatwave scenarios. Differences between

Table 1
CTMax (°C) and intraspecific variability (%CV), Thermal Safety Margin (TSM, °C; calculated using maximum habitat and heatwave temperatures), number of individuals tested and their mean size (cm), with respective standard errors (SE), for each treatment and experimental trial.

	CTMax	SE	%CV	N	Size	SE	TSM	SE	TSM (heatwave)	SE
Reciprocal-cross experiment										
Cold-Marine (original)	39.86	0.10	0.66	7	6.50	0.05	11.86	0.10	6.86	0.10
Cold-Marine (cross)[a]	39.96	0.07	0.50	8	5.38	0.25	11.96	0.07	6.96	0.07
Warm-Brackish (original)[a]	40.31	0.04	0.31	8	5.56	0.17	7.31	0.04	2.31	0.04
Warm-Brackish (cross)	40.18	0.06	0.46	8	5.25	0.40	7.18	0.06	2.18	0.06
Vulnerability to temperatures predicted for 2100										
Current[a]										
SSP2-4.5										
Cold-Marine	39.98	0.09	0.23	6	5.85	0.28	9.48	0.09	4.48	0.09
Warm-Brackish	40.31	0.12	0.80	7	5.59	0.22	4.81	0.12	−0.19	0.12
SSP5-8.5										
Cold-Marine	40.02	0.13	0.74	5	6.02	0.16	7.32	0.13	2.32	0.13
Warm-Brackish	40.36	0.12	0.65	5	6.10	0.11	2.66	0.12	−2.34	0.12
Temperature's isolated effect on CTMax										
Salinity 32										
27.5 °C	40.12	0.04	0.21	5	4.76	0.26	–	–	–	–
29.7 °C	40.07	0.09	0.38	3	4.57	0.41	–	–	–	–
Salinity 25										
27.5 °C	39.94	0.10	0.55	5	4.66	0.09	–	–	–	–
29.7 °C	40.18	0.10	0.51	4	4.35	0.09	–	–	–	–

[a] Experiments to assess silversides' vulnerability to future warming were subsequently performed using fish from these treatments, since PERMANOVA results revealed acclimation conditions had a significant effect on CTMax, but not specimens' origin. Therefore, values from the referred treatments represented the current scenario in subsequent statistical tests concerning silversides' vulnerability to predicted temperatures.

silversides' upper tolerance and habitat's maximum temperature ranged from 11.96 °C (TSM of fish in the cold-marine treatment) to 2.18 °C (TSM of fish in the warm-brackish treatment during a heatwave) (Table 1; Fig. 2).

3.2. *Vulnerability to temperatures predicted for 2100*

Acclimation conditions had a significant effect on silversides' upper tolerance (t-value = 2.80, p = 0.009). Fish acclimated in warm-brackish waters showed higher CTMax than the ones from the cold-marine treatment, regarding both current and predicted temperatures (Table 1; Fig. 3). However, silversides' CTMax did not increase after exposure to temperatures predicted under SSP2-4.5 (Cold-marine treatment: t-value = −0.02, p = 0.97; Warm-brackish treatment: t-value = 0.002, p = 0.99) and SSP5-8.5 scenarios (Cold-marine treatment: t-value = 0.06, p = 0.95; Warm-brackish treatment: t-value = 0.06, p = 0.96). Fish size also did not influence CTMax (t-value = 0.81, p = 0.42). Intraspecific CTMax variation (%CV) ranged from 0.23% to 0.80% (Table 1).

Silversides' thermal safety margins (TSMs) were influenced by acclimation condition and warming scenario (Table 1; Fig. 3). Fish from the cold-marine treatment had higher TSM than the ones acclimated in warm-brackish waters (t-value = −38.69, $p < 0.001$, values given refer to regular and heatwave tests). TSMs were also higher in current scenarios, and decreased in SSP2-4.5 (Cold-marine: t-value = −16.68 and −8.85, $p < 0.001$; Warm-brackish: t-value = −17.69 and −8.96, $p < 0.001$; t-values are given for regular and heatwave tests, respectively) and SSP5-8.5 (Cold-marine: t-value = −29.22 and −16.21, $p < 0.001$; Warm-brackish: t-value = −29.76 and −16.30, $p < 0.001$; t-values are given for regular and heatwave tests, respectively). Tukey's post-hoc test revealed TSM values differed between all treatments and scenarios ($p < 0.001$), excepting for the TSM of warm-brackish fish in the current scenario and that of cold-marine fish under temperatures predicted for SSP5-8.5 (p = 1; Fig. 3). Fish size did not influence TSM values under regular and heatwave conditions (t-value = 0.81, p = 0.42, values given refer to both tests).

3.3. *Temperature's isolated effect on CTMax*

Silversides' upper thermal tolerance did not change between salinity treatments (t-value = 1.54, p = 0.15), nor after exposure to increased temperatures within each treatment (salinity 32: t-value = −0.11, p = 0.91; salinity 25: t-value = 1.09, p = 0.30) (Supplementary Fig. 1). We also did not detect any differences in CTMax regarding fish size (t-value = 1.53, p = 0.15). Intraspecific variability (%CV) of CTMax was also low within each treatment, and ranged from 0.21% to 0.55% (Table 1).

4. Discussion

Our work revealed intraspecific variation in heat tolerance of Brazilian silversides over a fine-spatial scale (<20 km), is best explained by site acclimatization (i.e. phenotypic plasticity) and not local adaptation. Analysis of data revealed fish acclimated in warm, brackish waters had higher CTMax than those in cold, marine conditions. The relationship between acclimation temperature and CTMax has been consistently reported by studies with an unifactorial experimental design, particularly regarding temperate species (Madeira et al., 2017; Vinagre et al., 2018; Gervais et al., 2021). However, silversides' upper thermal tolerance did not shift after increasing temperature within each treatment, indicating that differences regarding acclimation conditions (i.e. warm-brackish, cold-marine treatments) likely result from a combined effect of temperature and salinity. Multiple driver studies are rather scarce in the literature, and often reveal species-dependent responses (see for example Re et al., 2012; Reiser et al., 2017; Madeira et al., 2021). Here, we showed thermal tolerance can vary over a fine-spatial scale (<20 km), regarding a 2.2 °C temperature and 7 ppt salinity difference. These findings further strengthen the importance of intraspecific variation (and its underlying mechanisms) for estimating species' risk of extirpation under short and long-term warming scenarios.

Interpopulation variation in heat tolerance is often overlooked on assessments of species' vulnerability to warming (Bennett et al., 2019; Fox et al., 2019), leading to the development of predictive distribution models based on a single experimental population. However, our work revealed a significant change in fish upper thermal tolerance in response to distinct temperature and salinity conditions observed within an estuarine system. These findings demonstrate the importance of microhabitat for an accurate estimate of warming impacts at the individual, population and species levels (Bennett et al., 2019; DuBois et al., 2022). For instance, silversides' exposure to cold-marine waters resulted in a CTMax of 39.9 °C, and Thermal Safety Margin (TSM) of 11.9 °C.

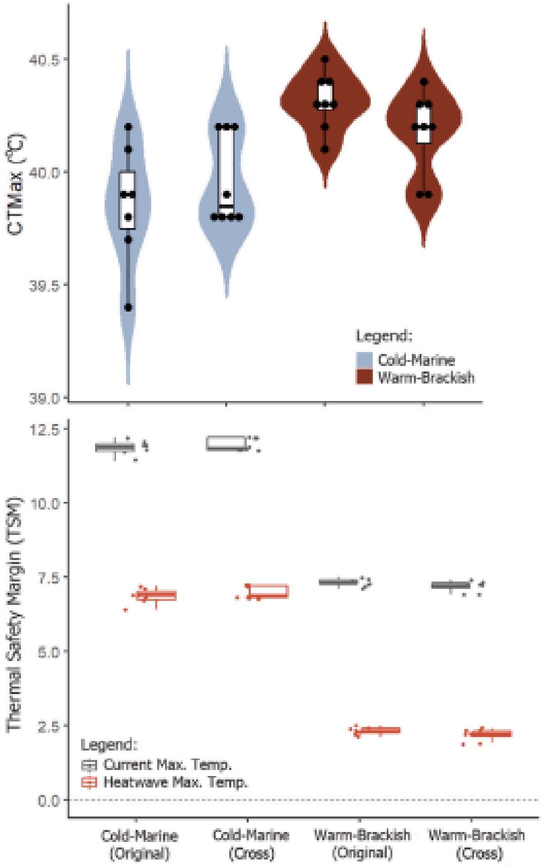

Fig. 2. Critical Thermal Maxima (CTMax, °C) and Thermal Safety Margin (TSM, °C) of Brazilian silversides acclimated under cold-marine (27.5 °C, 32 ppt) and warm-brackish (29.7 °C, 25 ppt) waters. Fish were acclimated under original and crossed habitat temperatures and salinities. Boxplots represent the first and third quartiles around the median (solid line), and the whiskers (errors) represent the minimum and maximum values of outliers.

However, treating these values as absolute would underestimate the impacts of warming on *A. brasiliensis*, since fish in the warm-brackish treatment showed lower TSM (i.e. 7.2 °C), despite having a higher CTMax (i.e. 40.3 °C). These results indicate that juveniles may be close to reaching their absolute upper thermal limits (van Heerwaarden and Kellermann, 2020), which may hinder silversides' persistence in the estuary over time. Microclimate variation can also anticipate organisms' exposure to temperatures predicted in climate change scenarios, enabling acclimation at a slower pace (Bay and Palumbi, 2014; Oldfather and Ackerly, 2019; DuBois et al., 2022). For instance, temperature in the warm-brackish treatment (i.e. current value) was similar to the one adopted for the cold-marine treatment under the SSP2-4.5 scenario (end of century prediction). However, fish from these treatments showed distinct CTMax, revealing a potential effect of salinity on silversides' thermal tolerance.

Salinity has been recognized as a "masking factor" regarding physiological responses such as metabolism, growth, and intra and interspecific relationships (Fry, 1971; Re et al., 2005). The interaction with temperature has been particularly addressed in thermal tolerance studies (Re et al., 2005, 2012; Reiser et al., 2017; Madeira et al., 2021) searching for additive, synergistic or antagonist effects that shape species vulnerability to warming. Here, we provide evidence of a negative relationship in silversides' physiological tolerance of temperature and salinity, as CTMax was higher in warmer and less saline waters (i.e. regarding both current and predicted scenarios). Failure to detect an isolated effect of each variable on CTMax can also be indicative of a combined effect, but evaluation of silversides' heat tolerance under additional salinity and temperature levels is required to strengthen these findings (see Collins et al., 2022). As a resident species in estuarine systems, *A. brasiliensis* has great osmoregulatory capacity, and has showed stability of plasma osmolality under short-term exposure to a range of salinities (i.e. 5–33 ppt; Souza-Bastos and Freire, 2011). Nonetheless, energetic costs associated with osmotic regulation may hinder cellular-level processes underlying species' thermal tolerance, such as the heat-shock response (Madeira et al., 2014). For instance, production of heat-shock proteins declined after exposure to combined thermal and hyposaline stress in contrast to exclusive temperature exposure, regarding the crab *Pachygrapsus marmoratus* (Madeira et al., 2014). The decrease in HSP production was observed despite *P. marmoratus* inhabiting the dynamic intertidal zone, where temperature and salinity (among other factors) shift constantly - a variability

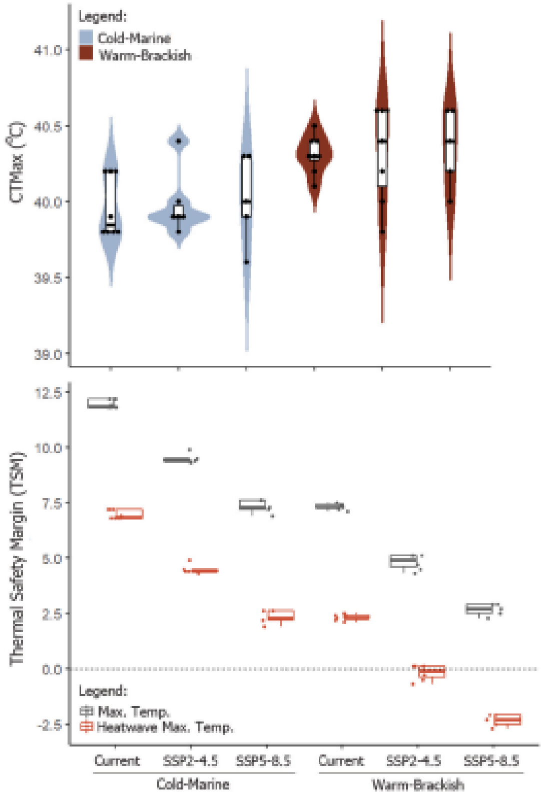

Fig. 3. Critical Thermal Maxima (CTMax, °C) and Thermal Safety Margin (TSM, °C) of Brazilian silversides acclimated under cold-marine (27.5 °C, 32 ppt) and warm-brackish (29.7 °C, 25 ppt) waters. CTMax and TSM values are also reported after fish acclimation to temperatures predicted under the SSP2-4.5 (C–M: 29.5 °C, W–B: 31.7 °C) and SSP5-8.5 (C–M: 31 °C, W–B: 33.2 °C) scenarios. Boxplots represent the first and third quartiles around the median (solid line), and the whiskers (errors) represent the minimum and maximum values of outliers.

that is also experienced by silversides in estuaries. However, molecular analyses are required to assess how single and combined exposure of distinct thermal and salinity levels affect the heat shock response of this particular species, since literature has reported a mix of positive and negative interactions (Spees et al., 2002; Re et al., 2012; Madeira et al., 2014).

Phenotypic differences in silversides' heat tolerance were reversible, which may favor their persistence in the estuary. Rapid acclimation and de-acclimation are fundamental for maintaining species performance in ecosystems with diel, daily, and seasonal variability, otherwise conditions would change faster than individuals can adjust to (Angilletta, 2009). Therefore, estuaries' heterogeneity in temperature and salinity (among other environmental conditions) probably favor generalist species, averting maladaptation, and increased energetic costs associated with acclimation time lags (Angilletta, 2009). Plasticity in silversides' thermal tolerance can also be related to the fine spatial scale of our study, as strong genetic structuring has been detected among populations in the Brazilian coast (Cortinhas et al., 2016). Range-wide studies could add to the results reported herein, and reveal the prevalence of local adaptation or niche conservatism at the regional level for silversides' heat tolerance.

Silversides' CTMax did not increase after exposure to temperatures predicted in the SSP2-4.5 and SSP5-8.5 scenarios, which may be related to a) tropical species' limited potential for plasticity (van Heerwaarden and Kellermann, 2020), and b) our experimental design. Low acclimation capacity has been reported for species living close to their absolute physiological limits, supporting a trade-off between tolerance and plasticity (Tewksbury et al., 2008; Vinagre et al., 2018; van Heerwaarden and Kellermann, 2020). Such negative relationship is often reflected in the small thermal safety margins of tropical species, leading them particularly vulnerable to ocean warming. However, fine-scale intraspecific variation in thermal response could buffer from the impacts of heatwaves (Figs. 2 and 3) and long-term increases in temperature predicted in intermediate warming scenarios, given that phenotypic plasticity is passed on to the next generations (Bennett et al., 2019). Methodological limitations such as a narrow range of acclimation temperatures, can also influence the degree and slope of plasticity estimates, since reaction norms are not always linear (van Heerwaarden and Kellermann, 2020). Acclimation period may also underlie the trends reported herein, as some studies have detected increases in CTMax after long-term exposure (i.e. 30 days) to increased temperatures (Madeira et al., 2017; Rohr et al., 2018). Nonetheless, analysis of comprehensive data revealed that longer acclimation periods are particularly important for large-sized organisms, whereas adjustments in the CTMax of small-bodied species such as the Brazilian silversides often occur in a short-time span (i.e. 3 days; Rohr et al., 2018).

In summary, our work showed that fine-scale ($<$20 km) environmental heterogeneity drives phenotypic plasticity for the estuarine fish species *A. brasiliensis*. Seawater conditions were associated with silversides' heat tolerance and thermal safety margins, demonstrating species vulnerability to warming is relative to microhabitat features in tropical, dynamic ecosystems. These findings show the importance of accounting for intraspecific variation not only at regional, but also the local level (Gervais et al., 2021; DuBois et al., 2022), in order to accurately estimate species climatic risks. Thermal tolerance of *A. brasiliensis* reached up to 40.6 °C, enabling species persistence in the estuary during heatwaves and short-term warming (i.e. within 2–3 generations). However, it is uncertain whether the high CTMax and phenotypic plasticity can buffer long-term impacts, as the relationship between phenotype and genotype is rather complex (Bennett et al., 2019; Fox et al., 2019). Distinct thermal sensitivities reported for silversides likely result from a combined effect of temperature and salinity, since we were not able to detach each variable's influence on CTMax. Molecular analysis and response curves are recommended to unveil the mechanisms underlying the relationship between heat tolerance and the environment. Our findings match previous studies (Gervais et al., 2021; DuBois et al., 2022), which revealed we must stop treating species and their environments as static, homogeneous units, in order to protect them from warming.

Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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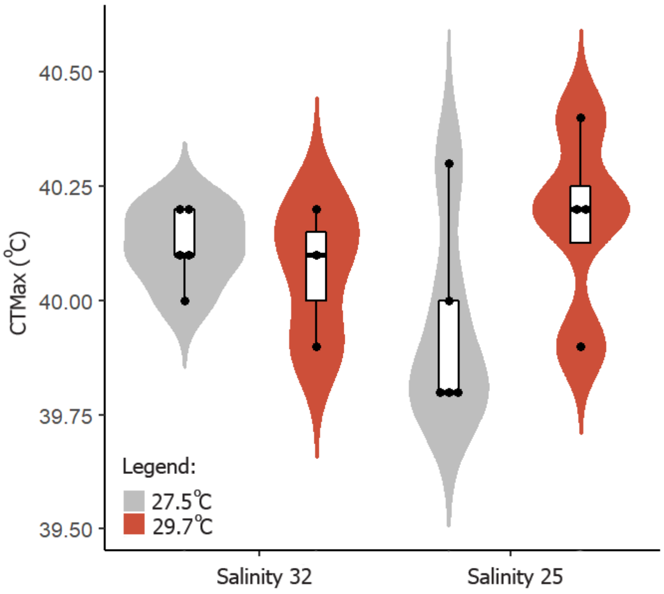
Figure 18 - Critical Thermal Maxima (CTMax, °C) of Brazilian silversides in 25 and 32 salinity treatments. Within each treatment, CTMax values are reported after acclimation under 27.5 °C and 29.7 °C temperatures.



Legend: Boxplots represent the first and third quartiles around the median (solid line), and the whiskers (errors) represent the minimum and maximum values of outliers.
Source: The author, 2022.

APÊNDICE F – Material suplementar 1 (*Supplementary File 1* em inglês) do manuscrito “Shipping traffic, salinity and temperature shape non-native fish richness in estuaries worldwide”, que será submetido no periódico *Science of the Total Environment*.

Table 11 - Description, source and details for download of each variable used as a potential predictor of non-native fish richness in estuaries worldwide.

Variable (unit of measure)	**Description**	**Source**	**Details for download**
	Environmental filtering		
Area (km^2)	Area of each estuary.	Google Earth. Available at http://www.google.fr/intl/fr/earth/index.html	Estimated using the "Measure" tool available on Google Earth
Mean annual runoff (mm)	Land surface runoff. Estimates are based on long-term (1971-2000) average ‘naturalized’ runoff values provided by the state-of-the-art global integrated water balance model WaterGAP v2.2 (DÖLL et al., 2003).	HydroATLAS, BasinATLAS (LINKE et al., 2019). Available at https://www.hydrosheds.org/hydroatlas	Suffix: "syr"
Mean annual discharge (m^3/s)	Natural discharge. Estimates are based on long-term (1971–2000) average ‘naturalized’ discharge values provided by the state-of-the-art global integrated water balance model WaterGAP v2.2 (DÖLL et al., 2003).		Suffix: "pyr"
Maximum annual discharge (m^3/s)			Suffix: "pmax"
Minimum annual inundation (percent cover)	Inundation extent (FLUET-CHOUINARD et al. 2015). Annual minimum values represent areas permanently inundated, estimated from the Global Inundation Extent from Multi-Satellites (GIEMS, PRIGENT et al., 2007) for the years		Suffix: ""smn"

	1993-2004, and adjusted with wetland extents from the Global Lakes and Wetlands Database (GLWD, LEHNER; DÖLL, 2004).		
Temperature ($^{\circ}$C)	Sea surface temperature (maximum, mean, minimum and range values).	Bio-ORACLE: Marine data layers for ecological modeling (TYBERGHEIN et al. 2012; ASSIS et al., 2018). Available at: https://www.bio-oracle.org/downloads-to-email.php	Choose the "Present" option regarding the period of layers; "Surface layers" option regarding the depth of layers; "Tiff Raster File" option regarding the format of file
Salinity (pss)	Sea surface salinity (maximum, mean, minimum and range values).		
Human activities			
Dam (km^2)	Number and surface area of large dams (i.e. greater than 15m in height or with a reservoir of more than 0.1km3).	Global Reservoir and Dam Database version 1.3 (GRanD; LEHNER et al., 2011). Available at: https://www.globaldamwatch.org/directory	Choose "GRanD v1.3" in the DW Directory; Click "Download"
Gross Domestic Product - GDP ($)	GDP per capita based on purchasing power parity (THE WORLD BANK, WORLD DEVELOPMENT INDICATORS, 2021). Data are in constant 2017 international dollars.	Our World in Data (ROSER, 2013). Available at https://ourworldindata.org/grapher/gdp-per-capita-worldbank	Choose "Chart" and then click in "Download"
Artificial Light at Night (index)	Light visible at night due to human activities. The radiance values were estimated from satellite imagery fostered by the United States National Oceanic and Atmospheric Administration - Earth Observation Group, and processed by the Radiance Light Trends web application (STARE; KYBA, 2019).	United States National Oceanic and Atmospheric Administration, National Centers for Environmental Information. Available at: https://ngdc.noaa.gov/eog/download.html	Choose "Global DMSP-OLS Nighttime Lights Time Series 1992 - 2013 (Version 4)" under DMSP Data Download
Shipping traffic (number of ship tracks recorded in a single 1 km^2 cell)	Shipping lanes map considering eight broad classes of vessels: authority, cargo, fishing, high-speed, passenger, pleasure, support, tanker and an ‘other’ class. Data represent the number of ship tracks (i.e. movement paths) per km^2, created by connecting location data of mobile ships.	Spatial and temporal changes in cumulative human impacts on the world’s ocean (HALPERN et al., 2015). Available at: https://knb.ecoinformatics.org/view/doi%3A10.5063%2FF1S180FS	Object name: "raw_2013_shipping_mol.zip"
Risk of invasive	Measures the relative risk of invasive species based on the amount of cargo		Object name: "raw_2013_invasives_mol.zip"

species - ports (metric tons, mt)	traffic in a port (metric tons, mt).		
Ocean pollution (metric tons, mt)	Combined data from shipping traffic and risk of invasive species.		Object name: "raw_2013_ocean_pollution_mol.zip"
Urban extent (percent cover)	Spatial information regarding human presence on the planet over time (PESARESI; FREIRE, 2016).	HydroATLAS, BasinATLAS (LINKE et al., 2019). Available at: https://www.hydrosheds.org/hydroatlas	Suffix: "cse"
Road density (m/km^2)	Spatial dataset on road infrastructure (MEIJER et al., 2018).		Suffix: "sav"
Population density (people per km^2)	Distribution of human densities on a continuous global surface (CIESIN, 2016).		Suffix: "sav"
Human footprint (index value x 10)	The relative human influence in every biome on the land's surface (VENTER et al., 2016).		Suffix: "s09"
Navigable waterways (km)	Navigable coastlines and rivers with signs of human settlement (VENTER et al., 2016).	Global terrestrial Human Footprint maps for 1993 and 2009 (VENTER et al., 2016). Available at: https://doi.org/10.5061/dryad.052q5	-

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APÊNDICE H – Material suplementar 3 (*Supplementary File 3* em inglês) do manuscrito “Shipping traffic, salinity and temperature shape non-native fish richness in estuaries worldwide”, que será submetido no periódico *Science of the Total Environment*.

Table 12 **-** Raw data of the non-native species detected in each of the worldwide estuaries compiled and analysed as described in the Methods section. FID = Number designated to each of the estuaries evaluated.

FID	Estuary	Latitude	Longitude	Alien species	Vector	Reference
0	Aceh River	5,597471	95,349665	*Aplocheilus panchax* *Cyprinus carpio* *Oreochromis niloticus* *Pterygoplichthys pardalis*		DEKAR et al., 2018
1	Aksu River Estuary	36,860496	30,963297	*Carassius gibelio*		INNAL, 2012
2	Altea	38,601476	-0,04524	*Gambusia holbrooki*		VIDAL et al., 2010
3	Baakens River	-33,96382	25,629469	*Tilapia sparrmanii*		MULLER et al., 2015
4	Babitonga Bay	-26,230911	-48,651946	*Odontesthes bonariensis*		VILAR et al., 2011
				Omobranchus punctatus	Ship biofouling	GERHARDINGER et al., 2006; FREITAS; VELASTIN, 2010; COSTA et al., 2011; SOUZA-CONCEIÇÃO et al., 2013
5	Bahía de San Juan	18,453802	-66,116072	*Pterois volitans*	Aquarium trade	OTERO; GONZÁLEZ, 2017
6	Bahía Todos Los Santos	31,804545	-116,640362	*Alosa sapidissima*	Range expansion due to altered oceanic conditions (climate change), secondary introduction	ROSALES-CASIÁN, 2015
7	Bay of Plenty	-37,743745	177,129636	*Gambusia affinis*	Biological control	PURCELL; STOCKWELL, 2015

8	Berezansky	46,727775	31,515108	*Syngnathus abaster*		MOVCHAN, 1988
9	Bizerte Lake	37,257414	9,864003	*Stephanolepis diaspros*		SHAIEK; HAJ, 2019
10	Boddengewässer Ost	53,768717	14,373021	*Acipenser gueldenstaedtii*		GESSNER et al., 1999
				Neogobius melanostomus	Ballast water	CZERNIEJEWSKI; BRYSIEWIC, 2018
11	Broken Bay	-33,541145	151,323613	*Acanthogobius flavimanus*	Ballast water	BELL et al., 1987
12	Burgas Bay	42,510917	27,544914	*Pomatoschistus marmoratus*		APOSTOLOU et al., 2011
13	Canning & Swan Rivers Estuary	-32,014683	115,860105	*Phalloceros caudimaculatus*	Aquarium trade	MADDERN, 2008
14	Charlotte Harbor	26,93376	-82,082117	*Mayaheros urophthalmus*		ADAMS; WOLFE, 2007
15	Chesapeake Bay	37,979348	-76,239395	*Cyprinus carpio*		HILDEBRAND; SCHROEDER, 1928; STEVENSON; CONFER, 1978; JENKINS; BURKHEAD, 1993
				Dorosoma petenense		JENKINS; BURKHEAD, 1993
				Ictalurus furcatus	Sport fishing; Recreational fishing; Commercial fishing	CHANDLER, 1998; FABRIZIO et al., 2018; SCHMITT et al., 2019a; SCHMITT et al., 2019b
				Ictalurus punctatus	Commercial fishing	JENKINS; BURKHEAD, 1993; SCHMITT et al., 2019
				Lepomis macrochirus		FLEMER; WOOLCOTT, 1966; JENKINS; BURKHEAD, 1993
				Micropterus salmoides		HILDEBRAND; SCHROEDER, 1928; KILLGORE et al., 1989; JENKINS; BURKHEAD, 1993
				Pylodictis olivaris	Commercial fishing	CHANDLER, 1998
				Channa argus		ODENKIRK; OWENS, 2007
				Gambusia holbrooki	Biological control	VIDAL et al., 2010
16	Ciénaga Grande de Santa Marta	10,853366	-74,393311	*Oreochromis niloticus*	Aquaculture	LEAL-FLÓREZ, 2003
				Trichopodus pectoralis	Aquarium trade	
17	Complexo Lagoas	-30,018224	-50,188614	*Trachelyopterus*		MORAES, 2012

	Costeiras RS			*lucenai*		
18	Conceição da Barra	-18,530086	-39,731567	*Butis koilomatodon*		MACIEIRA et al., 2012
19	Curuçá	-0,673978	-47,83791	*Butis koilomatodon*		MACIEIRA et al., 2012
20	Danube Delta	45,216007	29,755427	*Lepomis gibbosus*		KVACH et al., 2018
				Perccottus glenii		
21	De HoopVlei	-34,459728	20,393944	*Oreochromis mossambicus*		VAN RENSBURG, 1966
22	Derwent River Estuary	-42,783641	147,264439	*Forsterygion gymnotum*	Ballast water	HICKEY et al., 2004
				Forsterygion varium		
23	Diep River Estuary	-33,886475	18,48795	*Gambusia affinis*	Biological control	VISKICH et al., 2016
				Tilapia sparrmanii		
24	Dnieper-Bug Estuary	46,575925	31,958033	*Carassius gibelio*		SEMENCHENKO et al., 2015
				Lepomis gibbosus		BOLTACHEV et al., 2003;
				Neogobius fluviatilis		SMIRNOV, 2001
				Perccottus glenii	Aquaculture	SEMENCHENKO et al., 2015; KVACH et al., 2016
				Pseudorasbora parva		KARABANOV et al., 2010
				Sparus aurata		TKACHENKO, 2012
25	Doubtless Bay	-34,918958	173,453882	*Carassius auratus*		HUGHEY et al., 2013
				Cyprinus carpio		
				Gambusia affinis		
26	Dreketi River Estuary	-16,555265	178,861376	*Gambusia affinis*		JENKINS et al., 2010
				Oreochromis mossambicus		
				Oreochromis niloticus		
				Xiphophorus hellerii		
27	Dvina Bay	65,006508	39,571289	*Leuciscus aspius*		NOVOSELOV, 2018
				Ballerus sapa		

28	Ebro Delta	40,728666	0,868965	*Sander lucioperca*		
				Fundulus heteroclitus	Aquaculture	GISBERT; LÓPEZ, 2007
				Gambusia holbrooki	Biological control	VIDAL et al., 2010
				Pseudorasbora parva	Aquaculture	CAIOLA; SOSTOA, 2002
29	Edremidsk Bay	39,482814	26,722235	*Champsodon nudivittis*	Ballast water	TORCU KOC et al., 2015
30	Ekincik Bay	36,830509	28,551861	*Champsodon nudivittis*	Ballast water	FILIZ et al., 2014
31	El Bibane	33,253214	11,229185	*Upeneus pori*		AMOR et al., 2019
32	Elbe Estuary	53,945438	8,784568	*Neogobius melanostomus*	Sport fishing	HEMPEL; THIEL, 2013
33	Evros Estuary	40,795143	26,002471	*Acipenser gueldenstaedtii*	Aquaculture	CORSINI-FOKA; ECONOMIDIS, 2007
				Acipenser stellatus		
				Acipenser sturio		
				Huso huso		
				Chelon carinatus		
				Planiliza haematocheilus		
34	Fethiye Bay	36,649886	29,109414	*Champsodon nudivittis*	Ballast water	FILIZ et al., 2014
35	Finike Bay	36,300257	30,151138	*Champsodon nudivittis*	Ballast water	ERGUDEN; TURAN, 2011
36	Florianópolis Bay	-27,612511	-48,567851	*Odontesthes bonariensis*		CATTANI, 2015
				Oreochromis niloticus		
37	Florida Keys	25,172204	-80,522507	*Mayaheros urophthalmus*		HARRISON et al., 2013
				Belonesox belizanus		HARMS; TURINGAN, 2012; KERFOOT et al., 2011
				Gambusia holbrooki		VIDAL et al., 2010
38	Gokova Bay	36,886046	27,71748	*Lagocephalus*	Range expansion	AKYOL et al., 2005

				sceleratus	through a man-made canal	
				Platax teira		BILECENOGLU; KAYA, 2006
39	Great Fish Estuary	-33,490995	27,127988	*Cyprinus carpio*		WHITFIELD et al., 1994
40	Groenvlei	-34,030851	22,853692	*Cyprinus carpio*	Sport fishing	PHAIR et al., 2015
				Gambusia affinis	Sport fishing; Commercial fishing	DE MOOR; BRUTON, 1988
				Lepomis macrochirus		
				Micropterus floridanus	Sport fishing	JUBB, 1973; HARGROVE et al., 2019
				Micropterus salmoides	Sport fishing; Commercial fishing	HARGROVE et al., 2019
				Oreochromis mossambicus		DE MOOR; BRUTON, 1988
41	Guadalquivir Estuary	36,789889	-6,365232	*Carassius auratus*		BRAVO-UTRERA, 2010
				Carassius sp.		MORENO-VALCÁRCEL et al., 2013
				Cyprinus carpio		MORENO-VALCÁRCEL et al., 2013; BRAVO-UTRERA, 2010
				Fundulus heteroclitus		MORENO-VALCÁRCEL et al., 2013; BRAVO-UTRERA, 2010
				Gambusia holbrooki		MORENO-VALCÁRCEL et al., 2013; BRAVO-UTRERA, 2010
				Lepomis gibbosus		MORENO-VALCÁRCEL et al., 2013
				Micropterus salmoides		MORENO-VALCÁRCEL et al., 2013
				Ameiurus melas	Sport fishing	GARCIA-DE-LOMAS et al., 2009
				Cynoscion regalis	Ballast water	BAÑON et al., 2017
				Gambusia affinis	Biological control	FERNANDÉZ-DELGADO, 1989
42	Guadiana Estuary	37,171884	-7,400294	*Cynoscion regalis*		MORAIS; TEODÓSIO, 2016
43	Guanabara Bay	-22,827366	-43,156152	*Omobranchus punctatus*		CASTRO, 2008
				Trichopodus trichopterus	Aquarium trade	CAVALCANTI; LOPES, 2017

44	Guldborgsund	54,629138	11,803067	*Neogobius melanostomus*	Ballast water	BEHRENS et al., 2017; AZOUR et al., 2015; HERLEVI et al., 2017; SCHWARTZBACH et al., 2019
45	Gulf of Antalya	36,460577	31,110756	*Saurida undosquamis*		MUTLU, 2015
46	Gulf of Ob	68,863295	73,498623	*Abramis brama*	Aquaculture	INTERESOVA, 2016
				Sander lucioperca		
47	Gulf of Riga	57,693051	23,877674	*Carassius gibelio*	Aquaculture	OLENIN, 2005
				Cyprinus carpio		
				Neogobius melanostomus	Ballast water	
48	Hawke's Bay	-39,287406	177,270267	*Gambusia affinis*		PURCELL; STOCKWELL, 2015
49	Hudson Estuary	40,712475	-74,024539	*Cyprinus carpio*		STRAYER et al., 2005
				Micropterus dolomieu	Sport fishing	SCHMIDT; STILLMAN, 1998
50	Huleia Estuary	21,949882	-159,357064	*Gambusia affinis*		MACKENZIE; BRULAND, 2012
51	Igarapé Fortaleza	-0,121608	-49,959746	*Oreochromis niloticus*	Commercial fishing	BITTENCOURT et al., 2014
52	Ilog-Hilabangan Estuary	10,020549	122,723542	*Clarias batrachus*		OÑATE-PACALIOGA; PERALTA, 2016
				Oreochromis niloticus		
				Trichopodus trichopterus		
53	Irigoyen Estuary	-53,804295	-67,688663	*Oncorhynchus tshawytscha*	Aquaculture	NARDI et al., 2019
54	Iskenderun Bay	36,638847	35,889098	*Callionymus filamentosus*		ERGUDEN et al., 2016
				Champsodon nudivittis	Ballast water	CICEK; BILECENOGLU, 2009
				Jaydia queketti		ERYILMAZ; DALYAN, 2006
				Pelates quadrilineatus	Range expansion through a man-made canal	ERGUDEN et al., 2018
				Plotosus lineatus		DOGDU et al., 2016

				Pterois volitans		GURLEK et al., 2016
				Trypauchen vagina		AKAMCA et al., 2011
				Tylerius spinosissimus		TURAN; YAGLIOGLU, 2011
55	Ismarída	40,981981	25,317336	*Planiliza haematocheilus*		KOUTRAKIS; ECONODIMIS, 2000
56	Izmir Bay	38,434259	27,075954	*Etrumeus golanii*	Range expansion through a man-made canal	AKYOL; ULAS, 2016
57	Jounieh Bay	33,986269	35,632001	*Champsodon vorax*	Ballast water	BARICHE, 2010
58	Kaelepulu	21,395654	-157,728337	*Gambusia affinis*		MACKENZIE; BRULAND, 2012
				Mugilogobius cavifrons		
59	Kahana Estuary	21,555917	-157,869059	*Lutjanus fulvus*		FITZSIMONS et al., 2005
				Osteomugil engeli		
				Poecilia mexicana		
				Sarotherodon melanotheron		
60	Kakahai'a Fishpond	21,062901	-156,949074	*Gambusia affinis*		MACKENZIE; BRULAND, 2012
61	Kaloko	21,078897	-157,00106	*Gambusia affinis*		MACKENZIE; BRULAND, 2012
				Osteomugil engeli		
62	Kaneohe Bay	21,43482	-157,768625	*Gambusia affinis*		ENGLUND, 1999
				Poecilia latipinna		
				Poecilia mexicana		
				Poecilia reticulata		
				Poecilia vittata		
				Sarotherodon melanotheron		
				Xiphophorus hellerii		
				Xiphophorus maculatus		

63	Karrebaek Fjord	55,190038	11,673314	*Neogobius melanostomus*		BEHRENS et al., 2017; SCHWARTZBACH et al., 2019
64	Kayamkulam	9,128392	76,472517	*Poecilia mexicana*	Biological control; Aquarium trade	REMYA; AMINA, 2018
65	Klaipeda Port	55,665019	21,139251	*Neogobius melanostomus*	Ballast water	OLENIN, 2005; SKABEIKIS; LESUTIENE, 2015; HERLEVI et al., 2017
66	Kleinriviersvlei	-34,416713	19,348297	*Cyprinus carpio*		CLARK; NIEKERK, 2015
				Micropterus dolomieu		
				Micropterus punctulatus		
				Micropterus salmoides		
				Oreochromis mossambicus		
67	Kowie Estuary	-33,603743	26,902672	*Tilapia sparrmanii*		
				Micropterus salmoides	Commercial fishing; Sport fishing	MAGORO, 2014; WEYL; LEWIS, 2006; MURRAY et al., 2015; MAGORO et al., 2015
				Oreochromis mossambicus		WHITFIELD et al., 1994
68	Kundu Estuary	36,856184	30,899988	*Gambusia affinis*	Biological control	INNAL; AVENANT-OLDEWAGE, 2012
69	La Rogera	42,219505	3,112862	*Gambusia holbrooki*		ALCARAZ; GARCÍA-BERTHOU, 2007
70	Lagoa dos Patos e Lagoa Mirim	-31,829869	-52,143224	*Acestrorhynchus pantaneiro*	-	QUINTELA et al., 2018
				Clarias gariepinus	Aquaculture	BRAUN et al., 2003
				Cyprinus carpio	Aquaculture; Aquarium trade	TROCA et al., 2012
71	Laguna La Torrecilla	18,442147	-65,986024	*Pterois volitans*	Aquarium trade	OTERO; GONZÁLEZ, 2017
72	Lake Albert and Alexandrina	-35,506449	139,07296	*Carassius auratus*		HALLIDAY et al., 2018; WEDDERBURN et al., 2014; WEDDERBURN; BARNES, 2011; WEDDERBURN; BARNES, 2013; WEDDERBURN; BARNES, 2014; WEDDERBURN et al., 2012; S. WEDDERBURN; BARNES, 2016

				Cyprinus carpio		SMITH, 2006
				Perca fluviatilis		HALLIDAY et al., 2018; WEDDERBURN et al., 2014; WEDDERBURN; BARNES, 2011; WEDDERBURN; BARNES, 2013; WEDDERBURN; BARNES, 2014; WEDDERBURN et al., 2012; S. WEDDERBURN; BARNES, 2016
				Tinca tinca		WEDDERBURN et al., 2014; WEDDERBURN; BARNES, 2011; WEDDERBURN; BARNES, 2013; WEDDERBURN; BARNES, 2014;
				Gambusia holbrooki		WEDDERBURN et al., 2014; WEDDERBURN; BARNES, 2011; WEDDERBURN; BARNES, 2013; WEDDERBURN; BARNES, 2014; WEDDERBURN et al., 2012; S. WEDDERBURN; BARNES, 2016
73	Lake Kawahara-oike	32,623709	129,832758	*Carassius cuvieri*	Sport fishing	HOSSAIN et al., 2013
				Lepomis macrochirus		
				Micropterus salmoides	Biological control	
74	Lake Los Cipreses	-50,252701	-74,770572	*Oncorhynchus kisutch*	Aquaculture	GÓRSKI et al., 2017
75	Lake Pontchartrain	30,18834	-90,080715	*Herichthys cyanoguttatus*	Aquarium trade	LORENZ, 2008
76	Lake Skadar	42,156869	19,276431	*Perca fluviatilis*		MRDAK et al., 2018
77	Lambert Bay	-32,038214	18,295249	*Cyprinus carpio*	Commercial fishing; Sport fishing	MEAD et al., 2011
78	Lanoka Harbor	39,865967	-74,130177	*Gambusia affinis*	Biological control	VIDAL et al., 2010
79	Lapataia	-54,874898	-68,692122	*Oncorhynchus tshawytscha*	Aquaculture	NARDI et al., 2019
80	Lawai Kai	21,887979	-159,502958	*Mugilogobius cavifrons*		MACKENZIE; BRULAND, 2012
				Oreochromis mossambicus		
				Osteomugil engeli		
				Poecilia reticulata		

				Sarotherodon melanotheron		
81	L'Estartit	42,045656	3,194855	*Gambusia holbrooki*	Biological control	ALCARAZ; GARCÍA-BERTHOU, 2007
82	Loire Estuary	47,287546	-2,12544	*Gambusia holbrooki*	Biological control	VIDAL et al., 2010
83	Loobu	59,581039	25,83498	*Neogobius melanostomus*		VERLIIN et al., 2017
84	Lysakerelva Estuary	59,911579	10,641769	*Oncorhynchus gorbuscha*	Commercial fishing	GARGAN et al., 2019
85	Maketu Estuary	-37,758404	176,436028	*Gambusia affinis*		PURCELL; STOCKWELL, 2015
86	Maravilla River Estuary	-51,917991	-73,652008	*Oncorhynchus tshawytscha*	Aquaculture	GÓRSKI et al., 2017
87	Mariehamn Bay	60,085693	19,927106	*Neogobius melanostomus*	Ballast water	HERLEVI et al., 2017
88	Marina Bay	43,50927	16,141234	*Paranthias furcifer*	Oil plataform	DULCÍC; DRAGICEVIC, 2013
89	Matsalu Bay	58,759828	23,636886	*Carassius gibelio*		OJAVEER et la., 2011
90	Mersin Bay	36,783183	34,621247	*Cyclichthys spilostylus*		ERGUDEN et al., 2012
91	Molochny Estuary	46,551084	35,336479	*Carassius gibelio* *Lepomis gibbosus* *Planiliza haematocheilus*		DEMCHENKO; DEMCHENKO, 2015
92	Mosqueiro Estuary	-11,121783	-37,163568	*Butis koilomatodon*		MACIEIRA et al., 2012
93	Mucuri Estuary	-18,092643	-39,547001	*Butis koilomatodon*		MACIEIRA et al., 2012
94	Muga River Estuary	42,23757	3,122618	*Gambusia holbrooki*	Biological control	ALCARAZ; GARCÍA-BERTHOU, 2007
95	Mustoja Estuary	59,585044	26,167388	*Neogobius melanostomus*		VERLIIN et al., 2017
96	Muuga Bay	59,50568933	24,95093133	*Neogobius melanostomus*	Ballast water	JARV et al., 2011; OJAVEER et al., 2011; HERLEVI et al., 2017
97	Noetsieriver Estuary	-34,078835	23,128905	*Gambusia affinis*		SMITH et al., 2018
98	Paldiski Bay	59,302782	23,9978	*Neogobius*		VERLIIN et al., 2017

				melanostomus	
99	Panyu Estuary	22,867568	113,558132	*Clarias gariepinus*	RADHAKRISHNAN et al., 2011
				Cirrhinus mrigala	ZHOU et al., 2019
				Micropterus salmoides	
				Oreochromis aureus	
				Piaractus brachypomus	
				Pterygoplichthys multiradiatus	
				Sciaenops ocellatus	
100	Paranaguá Bay	-25,453226	-48,359258	*Odontesthes bonariensis*	SPACH et al., 2004
				Opsanus beta	IGNÁCIO; SPACH, 2010; PICHLER, 2010; NAGATA, 2013
				Oreochromis niloticus	CONTENTE et al., 2011
				Pterois volitans	BUMBEER et al., 2018
101	Pearl Harbor	21,341884	-157,969264	*Gambusia affinis*	ENGLUND, 1998; MACKENZIE; BRULAND, 2012
				Poecilia latipinna	
				Poecilia mexicana	
				Poecilia reticulata	
				Poecilia vittata	
				Sarotherodon melanotheron	
				Xiphophorus hellerii	
				Xiphophorus maculatus	
				Oreochromis mossambicus	
				Mugilogobius cavifrons	

				Osteomugil engeli		
102	Pelican Lagoon	-35,818115	137,772885	*Carassius auratus*		SMITH, 2006
				Cyprinus carpio		
				Gambusia holbrooki		
				Perca fluviatilis		
103	Peter the Great Bay	43,054608	132,158325	*Abbottina rivularis*	Aquaculture	KOLPAKOV et a;., 2010
				Acheilognathus chankaensis		
				Channa argus		
				Ctenopharyngodon idella		
				Culter alburnus		
				Hemiculter leucisculus		
				Hypophthalmichthys molitrix		
				Hypophthalmichthys nobilis		
				Sander lucioperca		
				Sarcocheilichthys czerskii		
				Sarcocheilichthys sinensis		
				Silurus soldatovi		
104	Piraquê-Açu Estuary	-19,950505	-40,145262	*Butis koilomatodon*		MACIEIRA et al., 2012
105	Pomeranian Bay	53,938829	14,335009	*Acipenser gueldenstaedtii*		GESSNER et al., 1999
106	Port Phillip Bay	-38,115541	144,858473	*Forsterygion lapillum*		HICKEY et al., 2004
107	Port Waikato	-37,364344	174,695618	*Gambusia affinis*	Biological control	PURCELL; STOCKWELL, 2015
108	Puck Bay	54,560026	18,567649	*Acipenser gueldenstaedtii*	Sport fishing; Aquaculture	SKÓRA; ARCISZEWSKI, 2013

				Neogobius melanostomus	Ballast water	SAPOTA; SKÓRA, 2005
109	Puma Estuary	-50,252701	-74,770572	*Oncorhynchus kisutch*	Aquaculture	GÓRSKI et al., 2017
110	Rio Escuro	-23,492079	-45,164574	*Butis koilomatodon*	-	MACIEIRA et al., 2012
111	Saint Lawrence Estuary	47,962227	-69,666847	*Oncorhynchus mykiss*	Commercial fishing; Sport fishing	THIBAULT et al., 2010; THIBAULT et al., 2009
112	San Francisco Bay	37,852166	-122,353579	*Acanthogobius flavimanus*	Ballast water	WORKMAN; MERZ, 2007; GEWANT; BOLLENS, 2012; BROWN et al., 2006; FEYRER, 2004; BROWN; MICHNIUK, 2007; MOYLE; BENNETT, 2008; SCHREIER et al., 2016; COHEN; CARLTON, 1995; BRITTAN; HOPKIRK, 1970; GIBBLE; HARVEY, 2015; MOYLE et al., 2012; NEILSON; WILSON JR, 2005; FEYRER et al., 2003; O'REAR et al., 2019
				Alosa sapidissima	Commercial fishing; Sport fishing	GANSSLE, 1966; FEYRER, 2004; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; MOYLE et al., 2012; FEYRER et al., 2003
				Ameiurus catus		BROWN et al., 2006; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014;
				Ameiurus melas		BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008
				Ameiurus natalis		COHEN; CARLTON, 1995
				Ameiurus nebulosus	Commercial fishing	GANSSLE, 1966; BROWN; MICHNIUK, 2007; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014;
				Carassius auratus	Aquarium trade	GANSSLE, 1966; BROWN et al., 2006; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; MOYLE et al., 2012
				Cyprinella lutrensis		BROWN et al., 2006; BROWN; MICHNIUK, 2007
				Cyprinus carpio	Commercial fishing; Aquarium trade	GANSSLE, 1966; BROWN et al., 2006; GRIMALDO et al., 2003; BROWN AND MICHNIUK, 2007; MOYLE et

		al., 2012; MOYLE; BENNETT, 2008; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; FEYRER et al., 2003
Dorosoma petenense	Commercial fishing	BROWN et al., 2006; FEYRER, 2004; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016
Gambusia affinis	Biological control	BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; MOYLE et al., 2012
Hypomesus nipponensis		BROWN et al., 2006; GRIMALDO et al., 2003; MOYLE; BENNETT, 2008
Ictalurus furcatus	Commercial fishing	COHEN; CARLTON, 1995
Ictalurus punctatus		BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012;
Lepomis cyanellus		BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012;
Lepomis gibbosus	Commercial fishing	COHEN; CARLTON, 1995; BROWN; MICHNIUK, 2007
Lepomis gulosus		BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012;
Lepomis macrochirus		BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014;
Lepomis microlophus		BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016
Lepomis sp.		GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007
Lucania parva	Ballast water	COHEN; CARLTON, 1995; HUBBS; MILLER, 1965; QUIÑONES; MOYLE, 2014; MOYLE et al., 2012;
Menidia audens	Biological control; Commercial fishing	MAHARDJA et al., 2016; MOYLE et al., 2012; SCHREIER et al., 2016; QUIÑONES; MOYLE, 2014; MOYLE et al., 2012
Menidia beryllina		COHEN; CARLTON, 1995; BROWN et al., 2006; FEYRER, 2004; GRIMALDO et al., 2003; BROWN;

		MICHNIUK, 2007; MOYLE; BENNETT, 2008
Micropterus dolomieu	Commercial fishing	COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; BROWN; MICHNIUK, 2007
Micropterus punctulatus		BROWN; MICHNIUK, 2007; MOYLE et al., 2012; SCHREIER et al., 2016
Micropterus salmoides		BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016
Micropterus sp.		GRIMALDO et al., 2003
Misgurnus dabryanus	Aquaculture; Aquarium trade	KIRSCH, et al., 2018
Morone saxatilis	Commercial fishing; Sport fishing	GANSLEE, 1966; BROWN et al., 2006; FEYRER, 2004; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; MOYLE et al., 2012; FEYRER et al., 2003
Notemigonus crysoleucas		COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; BROWN et al., 2006; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016
Percina macrolepida		COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; BROWN et al., 2006; FEYRER, 2004; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008
Pimephales promelas	Commercial fishing	BROWN et al., 2006
Pomoxis annularis		COHEN; CARLTON, 1995; BROWN et al., 2006; BROWN; MICHNIUK, 2007;
Pomoxis nigromaculatus		COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; GANSSLE, 1966; BROWN et al., 2006; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; SCHREIER et al., 2016
Pomoxis sp.		GRIMALDO et al., 2003
Salmo trutta		QUIÑONES; MOYLE, 2014

				Spirinchus thaleichthys		FEYRER et al., 2003
				Tridentiger barbatus		
				Tridentiger bifasciatus	Ballast water	BROWN et al., 2006; FEYRER, 2004; GRIMALDO et al., 2003; BROWN; MICHNIUK, 2007; MOYLE et al., 2012; MOYLE; BENNETT, 2008; SCHREIER et al., 2016; MATERN, 2001; COHEN; CARLTON, 1995; QUIÑONES; MOYLE, 2014; MATERN; BROWN, 2005
				Tridentiger trigonocephalus	Ballast water; Ship fouling	RADECKI, 2011; COHEN; CARLTON, 1995; GIBBLE; HARVEY, 2015; MOYLE et al., 2012
113	Santos Estuary	-23,968486	-46,294768	*Opsanus beta*	Ballast water	TOMÁS et al., 2012; SOUZA, 2017
114	São Marcos e Arraial Bay	-2,593105	-44,424289	*Colossoma macropomum*	Aquaculture	MORAES, 2016
				Megaleporinus macrocephalus		
115	Schelde Estuary	51,37939	3,692806	*Acipenser baerii*	-	BREINE, 2009
				Ameiurus nebulosus		
				Carassius gibelio		
				Ctenopharyngodon idella		
				Cyprinus carpio		
				Lepomis gibbosus		
				Oncorhynchus mykiss		
				Pseudorasbora parva		
				Salmo salar		
				Sander lucioperca		
116	Sepetiba Bay	-23,005367	-43,791332	*Coptodon rendalli*		ARAÚJO et al., 2015
117	Sevastopol Bay	44,622881	33,549479	*Syngnathus acus*		BOLTACHEV; KARPOVA, 2014
				Tridentiger trigonocephalus	Aquarium trade	
118	Shannon Estuary	52,595602	-9,256691	*Leuciscus leuciscus*	Sport fishing	KELLY et al., 2014 ; HARRINGTON, 2017

				Perca fluviatilis		
				Phoxinus phoxinus		
				Salmo trutta		
119	Shatt Al-Arab Estuary	30,831628	47,557906	*Carassius auratus*	-	MOHAMED et al., 2015; MOHAMED et al., 2012
				Coptodon zillii		MOHAMED et al., 2015
				Ctenopharyngodon idella		
				Cyprinus carpio		MOHAMED et al., 2015; MOHAMED et al., 2012
				Gambusia holbrooki		MOHAMED et al., 2015
				Hemiculter leucisculus		
				Heteropneustes fossilis		
				Hypophthalmichthys molitrix		
				Poecilia latipinna		MOHAMED et al., 2015; MOHAMED et al., 2012
120	Skælskør	55,247356	11,281519	*Neogobius melanostomus*		AZOUR et al., 2015
121	Soledade	-5,0814	-36,706331	*Butis koilomatodon*		MACIEIRA et al., 2012
122	Songkhla Lake	7,197169	100,463513	*Oreochromis mossambicus*		CHESOH, 2009
				Oreochromis niloticus		
				Poecilia velifera	Aquarium trade; Biological control	SA-NGUANSIL; LHEKNIM, 2010; SA-NGUANSIL, 2009
123	Still Bay	-34,378765	21,423682	*Cyprinus carpio*	Commercial fishing; Sport fishing	MEAD et al., 2011
124	Strait of Georgia - Sturgeon Bank	49,315762	-123,27453	*Alosa sapidissima*		LEVINGS et al., 2002
				Ameiurus nebulosus		
				Cyprinus carpio	Aquarium trade	
				Pomoxis nigromaculatus		

				Salmo salar	Aquaculture	
125	Strait of Johor	1,463504	103,787484	*Etroplus suratensis* *Mayaheros urophthalmus* *Oreochromis* spp. *Mugil cephalus*		THENG et al., 2016
126	Sundays Estuary	-33,70624	25,840286	*Clarias gariepinus* *Cyprinus carpio* *Gambusia affinis* *Oreochromis mossambicus* *Tilapia sparrmanii*		KIMBERG et al., 2014
127	Tabaru Estuary	24,46978	122,999232	*Oreochromis niloticus*		ISHIKAWA et al., 2013
128	Tamar Estuary	-41,382183	147,082886	*Gambusia holbrooki*	Biological control	KEANE; NEIRA, 2004
129	Tampa Bay	27,771806	-82,538754	*Belonesox belizanus*	Aquaculture	GREENWOOD, 2017
130	Tavoro Falls	-16,826251	-179,873232	*Gambusia affinis* *Oreochromis mossambicus* *Oreochromis niloticus* *Xiphophorus hellerii*		JENKINS et al., 2010
131	Tendrovsky Bay	46,239039	31,880815	*Syngnathus abaster*		MOVCHAN, 1988
132	Todos os Santos Bay	-12,863852	-38,637968	*Microphis brachyurus* *Omobranchus punctatus*		BARBALHO, 2007 REIS-FILHO et al., 2016
133	Toolse	59,53489	26,45733	*Neogobius melanostomus*		VERLIIN et al., 2017
134	Tote Estuary	-50,252701	-74,770572	*Oncorhynchus kisutch*	Aquaculture	GÓRSKI et al., 2017
135	Tripa Estuary	3,84871	96,38642	*Oreochromis*	Aquaculture	MUCHLISIN et al., 2015

				niloticus		
136	Utlyuk Estuary	46,155685	34,967738	*Carassius gibelio*	Aquaculture	DEMCHENKO; DEMCHENKO, 2015
				Hypophthalmichthys molitrix		
				Hypophthalmichthys nobilis		
				Lepomis gibbosus	Range expansion through a man-made canal	
				Planiliza haematocheilus	Aquaculture	
137	Varela Bay	-54,87341	-67,281174	*Oncorhynchus tshawytscha*	Aquaculture	NARDI et al., 2019
138	Varna Bay	43,180254	27,919366	*Pomatoschistus marmoratus*		APOSTOLOU et al., 2011
139	Vasse Estuary	-33,643956	115,393269	*Carassius auratus*	Aquarium trade	TWEEDLEY et al., 2012; TWEEDLEY et al., 2017; BEATTY et al., 2016
				Gambusia holbrooki		TWEEDLEY et al., 2012; TWEEDLEY et al., 2017
140	Veli-Akkulam Lake	8,510092	76,888337	*Pterygoplichthys sp.*	Aquarium trade	KUMAR et al., 2018
				Clarias gariepinus		REGI; BIJUKUMAR, 2012
				Oreochromis mossambicus		
141	Verlorenvlei	-32,33532	18,417828	*Cyprinus carpio*		SINCLAIR et al., 1986
				Micropterus dolomieu		
				Micropterus salmoides		
				Oreochromis mossambicus		
				Tinca tinca		
142	Vistula Lagoon	54,491341	19,736386	*Acipenser gueldenstaedtii*	Aquaculture; Aquarium trade; Sport fishing	SAPOTA, 2004

				Neogobius fluviatilis	Range expansion through a man-made canal	LEJK et al., 2013
				Neogobius melanostomus	Ballast water	BARTEL, 1968
143	Waimea	21,640313	-158,066392	*Hemichromis elongatus*		MACKENZIE; BRULAND, 2012
				Oreochromis mossambicus		
144	Wilderness LS	-33,99176	22,621431	*Micropterus salmoides*		HALL et al., 1987
				Oreochromis mossambicus	Aquaculture; Commercial fishing; Sport fishing	HALL et al., 1987; OLDS et al., 2011; OLDS et al., 2016
				Cyprinus carpio		OLDS et al., 2016
				Gambusia affinis	Biological control	OLDS et al., 2011; SLOTERDJIK et al., 2015; OLDS et al., 2016
145	Yaquina Bay	44,615318	-124,021709	*Lucania parva*		HUBBS; MILLER, 1965
146	Zandvlei	-34,082338	18,467794	*Clarias gariepinus*	-	QUICK; BENNETT, 1989
				Cyprinus carpio	-	SHELTON, 1975; BEGG, 1976; GAIGHER; THORNE, 1979; QUICK; BENNETT, 1989; CLARK et al., 1994; GIBBS et al., 2007
				Gambusia affinis	Biological control	CLARK et al., 1994; GIBBS et al., 2008
				Micropterus salmoides	Aquaculture	CLARK et al., 1994; GIBBS et al., 2009
				Oreochromis mossambicus	-	SHELTON, 1975; BEGG, 1976; GAIGHER; THORNE, 1979; QUICK; BENNETT, 1989; CLARK et al., 1994; GIBBS et al., 2007
				Tilapia sparrmanii	-	CLARK et al., 1994; GIBBS et al., 2011