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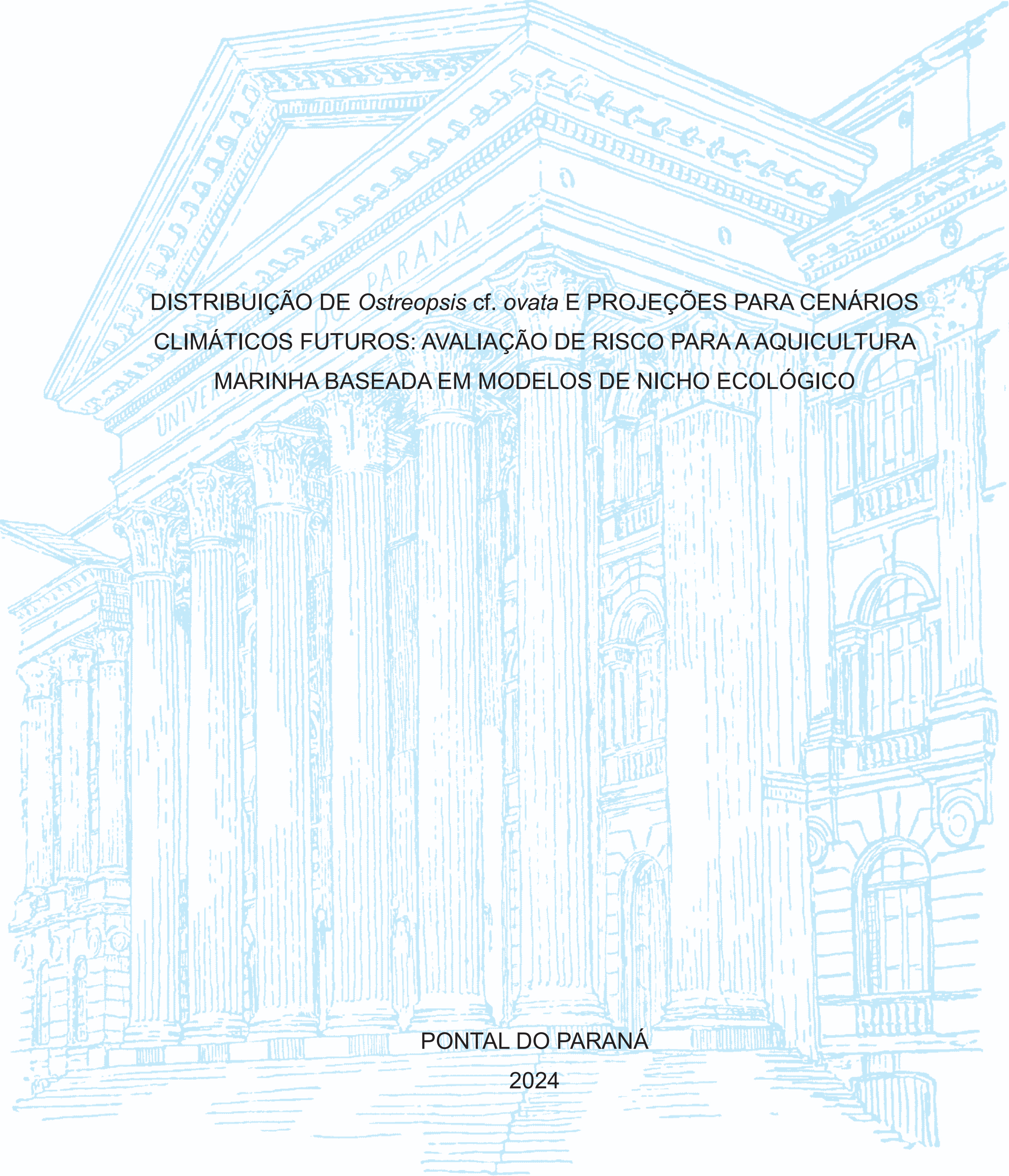

DISTRIBUIÇÃO DE *Ostreopsis* cf. *ovata* E PROJEÇÕES PARA CENÁRIOS CLIMÁTICOS FUTUROS: AVALIAÇÃO DE RISCO PARA A AQUICULTURA MARINHA BASEADA EM MODELOS DE NICHO ECOLÓGICO

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Orientador: Prof. Dr. Luiz Laureno Mafra Jr.

Coorientador: Dr. André Menegotto Domingos

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação SISTEMAS COSTEIROS E OCEÂNICOS da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **KAIANAN MAUÊ SANTOS ROSA** intitulada: **"Distribuição de *Ostreopsis* cf. *ovata* e Projeções para Cenários Climáticos Futuros: Avaliação de Risco para a Aquicultura Marinha Baseada em Modelos de Nicho Ecológico"**, sob orientação do Prof. Dr. LUIZ LAURENO MAFRA JÚNIOR, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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RESUMO

As microalgas marinhas são fundamentais para os ciclos biogeoquímicos e a sustentação da vida no planeta, porém, diversas espécies são formadoras de florações nocivas, com potencial de gerar danos ecossistêmicos, à saúde humana e às atividades aquícolas. Florações do dinoflagelado bêntico *O.* cf. *ovata*, produtor de substâncias altamente tóxicas, têm-se expandido globalmente nos últimos anos, gerando quadros graves de intoxicação em seres humanos, além da mortalidade massiva de animais cultiváveis pela aquicultura marinha. Este trabalho utilizou a modelagem de nicho ecológico para avaliar a distribuição atual desta microalga no ambiente marinho e projetar seus deslocamentos perante possíveis cenários climáticos de aquecimento do planeta, que variam de ~2 °C a >4 °C. Segundo o modelo gerado, 2.759.632 km² de áreas rasas marinhas globais possuem condições ambientais atualmente propensas à ocorrência da espécie, principalmente nas zonas tropicais e temperadas, ao passo que, nas latitudes polares, não há habitats suficientemente adequados para *O.* cf. *ovata*. Há uma distribuição heterogênea do risco associado à presença desta microalga ao longo dos locais de produção aquícola marinha, variando entre risco moderado e nulo. O modelo projeta, para um cenário de aquecimento climático de 2 °C, uma tendência de expansão global da distribuição da espécie em 30%, o que deve resultar na sua presença mais frequente em zonas temperadas e pode levar, inclusive, ao surgimento de habitats suficientemente adequados para ocorrência de *O.* cf. *ovata* nas latitudes polares. Contudo, cenários de maior aquecimento tendem a culminar em contração da distribuição global da espécie entre 11% e 63%, além da diminuição de 49% a 80% no número de locais de produção aquícola com presença potencial deste dinoflagelado tóxico. Apesar da tendência global de diminuição, projetam-se para vários locais, inclusive importantes regiões de produção aquícola marinha, tendências de aumento do risco perante todos os cenários de aquecimento analisados, indicando diferenças contrastantes a depender da escala espacial de análise. Trata-se, pois, de algo preocupante no contexto de mudanças climáticas e de projeções de aumento populacional pelos próximos anos, que demandará uma produção maior e mais diversa de alimentos, tendo a aquicultura marinha como uma das fontes mais promissoras. Portanto, para lidar com a tendência projetada de aumento do risco associado à presença de *O.* cf. *ovata*, determinados locais precisarão se preocupar com o monitoramento de microalgas nocivas e ficotoxinas na água, além de incorporar aos seus planos espaciais marinhos estratégias de enfretamento, a fim de prevenir possíveis danos ecossistêmicos, à saúde humana e às atividades aquícolas.

Palavras-chave: Microalgas Nocivas. Biogeografia Marinha. Produção Aquícola Marinha. Ameaças Ambientais Emergentes.

ABSTRACT

Marine microalgae are fundamental to biogeochemical cycles and the sustenance of life on Earth. However, several species are responsible for harmful algal blooms (HABs), with the potential to cause ecosystem damage, human health issues, and massive mortality of potentially farmable organisms via aquaculture. Blooms of the benthic dinoflagellate *Ostreopsis* cf. *ovata*, a producer of highly toxic substances, have expanded globally in recent years, resulting in severe cases of human intoxication and mass mortality of marine aquaculture organisms. This study employed ecological niche modeling to assess the current distribution of this microalga in marine environments and project its shifts under potential climate warming scenarios ranging from ~2°C to >4°C. According to the generated model, 2,759,632 km² of global shallow marine areas currently exhibit environmental conditions favorable for the occurrence of the species, primarily in tropical and temperate zones, whereas polar latitudes lack sufficiently suitable habitats for *O.* cf. *ovata* at the present. The associated risk for the presence of this microalga is heterogeneously distributed across marine aquaculture sites, ranging from moderate to negligible. Under a 2°C warming scenario, the model projects a 30% global expansion in the species' distribution, likely increasing its occurrence frequency in temperate zones and potentially emerging suitable habitats in polar latitudes. However, scenarios of more intense warming are projected to lead to a 11% to 63% global contraction in the species' distribution, and a reduction by 49% to 80% in the number of aquaculture production sites with potential presence of this toxic dinoflagellate. Despite the decreasing global trend, several locations, including key regions of marine aquaculture production, are projected to experience increased risk under all warming scenarios analyzed, highlighting contrasting outcomes depending on the spatial scale. This is particularly concerning in the context of climate change and projected population growth in the coming years, which will demand greater and more diversified food production, with marine aquaculture serving as one of the most promising sources. Therefore, to address the projected increase in risk associated with the presence of *O.* cf. *ovata*, certain locations will need to focus on monitoring harmful microalgae and phycotoxins in water, as well as incorporating coping strategies into their marine spatial planning to prevent potential ecosystem damage, human health risks, and disruptions to aquaculture activities.

Keywords: Harmful Microalgae. Marine Biogeography. Marine Aquaculture Production. Emerging Environmental Threats.

SUMÁRIO

1 INTRODUÇÃO

O oceano é um componente fundamental do sistema climático global, com grande capacidade de armazenar gases e calor (GALLAND, HARROULD-KOLIEB e HERR, 2012) e cuja produtividade primária dá suporte à biodiversidade marinha e promove importantes ciclos químicos, como o do oxigênio (SIGMAN & HAIN, 20212). Ademais, as atividades econômicas relacionadas com o oceano geram centenas de milhões de empregos e, aproximadamente, 2,5 trilhões de dólares para a economia global anualmente (HOEGH-GULDBERG 2015; IPCC, 2019). Todavia, além da grande importância para a economia global, os serviços e benefícios não mercantis ofertados pelo oceano também são fundamentais para o bem estar, a saúde, os modos de vida e a sobrevivência humana (COSTANZA et al. 2014; GAINES, 2023). As mudanças climáticas antropogênicas, resultantes do aumento exponencial das emissões de gases de efeito estufa desde a revolução industrial, representam uma fonte de risco que afeta o oceano de diversas maneiras, tais como suas características biológicas, químicas e físicas. Os aspectos dessas mudanças manifestam-se criticamente sobre os habitats, a produtividade biológica e as assembleias de espécies marinhas, comprometendo os benefícios econômicos que se extraem do mar. Assim, os impactos sobre os serviços ecossistêmicos, a economia oceânica e o bem estar humano poderão aumentar consideravelmente até o final deste século, a depender da trajetória global de emissão de gases de efeito estufa - GEE (IPCC, 2018; 2019; GAINES, 2023).

Sabe-se que as mudanças nos processos e no funcionamento do oceano impactam fortemente a economia global. Portanto, estratégias de adaptação e mitigação são necessárias para garantir a sustentabilidade da economia no contexto de mudanças climáticas. A pesca, a aquicultura marinha e o turismo costeiro são os setores da economia oceânica que mais exigem estratégias de adaptação para garantir que se mantenham sustentáveis conforme o clima muda (GAINES, 2023). Desta forma, este trabalho busca avaliar os efeitos das mudanças climáticas sobre a distribuição de uma espécie de microalga marinha formadora de florações tóxicas, que afetam os sistemas biológicos, sociais e econômicos: o dinoflagelado bêntico *Ostreopsis* cf. *ovata*. O objetivo é quantificar as possíveis mudanças na distribuição geográfica desta espécie e as regiões com maiores tendências de aumentou ou diminuição de ocorrência da microalga sob diferentes cenários previstos de mudanças climáticas. Por fim, considerando o potencial impacto à saúde ambiental e humana decorrente de florações de *O*. cf. *ovata*, e assumindo que os riscos associados à ocorrência desta microalga deverão variar geograficamente conforme o planeta se aquece e as características físico-químicas do oceano mudam, este estudo fará uma análise mais refinada em regiões com tradição no cultivo de organismos marinhos, particularmente de moluscos bivalves suspensívoros.

1.1 Mudanças climáticas e riscos para os sistemas biológicos, sociais e a economia

Há aproximadamente 20 mil anos, o planeta passava pelo pico da última era glacial, com um clima cerca de 7 a 9 ºC mais frio do que este dos dias atuais (DESSLER, 2021). Reconstruções paleoclimáticas feitas a partir de amostras de sedimentos e gelo demonstram que, desde então, o clima do planeta vem passando pelo aquecimento mais acelerado de sua história. A temperatura média do planeta nunca esteve tão quente desde o Plioceno (cerca de 3 milhões de anos atrás), o que torna a adaptação da biota terrestre muito mais difícil (RAHMSTORF, 2024). Neste contexto, o Acordo de Paris estabeleceu um limite máximo de 1,5 ºC para o aquecimento global em relação ao final do Século XIX. Porém, neste momento, o clima da Terra já se encontra 1,1 ºC mais quente que os registros daquele período (IPCC, 2021).

O aumento da temperatura afeta não apenas a atmosfera terrestre, mas também a água do mar, pois o oceano absorve a maior parte do calor adicional decorrente da mudança do clima. Desde 1900, a temperatura da superfície marinha aumentou, em média, 0,7 ºC (BARANGE et al., 2018; JEWETT e ROMANOU, 2017). Conforme o oceano aquece, a tendência é que a distribuição geográfica de muitas espécies marinhas se desloque rumo às altas latitudes. Aquelas capazes de se dispersar tenderão a mudar sua distribuição para habitats mais adequados em locais com águas menos aquecidas (BARANGE et al., 2018; CHEUNG et al., 2016; IPCC, 2019; PINSKY et al., 2018). As demais, que não conseguirem se dispersar, precisarão se adaptar às novas condições decorrentes das mudanças climáticas ou irão perecer. Um oceano mais aquecido tende também a aumentar a frequência e intensidade de eventos como o El Niño - Oscilação Sul (ENOS; BARANGE et al., 2018 ; CAI et al., 2015; IPCC, 2019 ; WANG et al., 2017), que podem impactar ainda mais a pesca, a aquicultura marinha e o turismo costeiro (RAHMSTORF, 2024).

O aquecimento do planeta não vai aumentar apenas a frequência e intensidade do ENOS, ele também irá gerar um aumento na ocorrência de eventos atmosféricos extremos. Isso porque, a cada grau de aumento na temperatura, a quantidade de água que uma massa de ar precisa para se tornar saturada aumenta em 7%. Além disso, cada incremento de um 1 ºC aumenta em 2-3% a taxa de evaporação do oceano (RAHMSTORF, 2024). Assim, massas de ar, quando saturam, possuem muito mais vapor d'água e, ao precipitar, geram fortes tempestades, fazendo com que várias regiões do planeta já apresentem um aumento nas precipitações extremas (e.g., regiões norte e central da Europa; RAHMSTORF, 2024). Ademais, o aumento na taxa de evaporação da água do oceano é menor que o aumento na capacidade das massas de ar suportarem vapor d'água, gerando massas de ar menos saturadas, que por sua vez provocam maiores períodos de secas (RAHMSTORF, 2024).

O aquecimento do planeta também causa outras mudanças nas dinâmicas atmosféricas. O clima polar ártico aqueceu quatro vezes mais que o resto do mundo nos últimos 40 anos (VOOSSEN, 2021). Isso faz com que o gradiente de temperatura entre a região polar e a região tropical se torne menor e, dessa forma, o padrão de circulação das massas de ar acabe sendo afetado. A diminuição da velocidade de circulação dos ventos, então, tende a gerar ondas de calor e secas prolongadas. Tais eventos de longas secas geram queda nas atividades agropecuárias, o que, consequentemente, aumenta os preços dos alimentos e a insegurança alimentar, podendo gerar ou aumentar as crises sociais e afetar até mesmo a política global (RAHMSTORF, 2024). Um clima mais quente também tende a gerar ciclones mais destrutivos, pois estes obtêm energia do calor armazenado na superfície do oceano. De fato, já se observa atualmente um aumento na proporção de tempestades tropicais classificadas como fortes. As estimativas são de que, nos próximos anos, tempestades tropicais possam se intensificar ainda mais rapidamente, deslocar-se mais lentamente e mover-se para maiores latitudes. Dessa maneira, os impactos sobre as áreas atingidas se tornarão ainda mais severos (RAHMSTORF, 2024).

As atuais massas de gelo continentais, presentes principalmente na Antártica e na Groenlândia, são capazes de prover água suficiente para elevar o nível global do mar em vários metros. Desde o final do século XIX, o nível médio do mar já subiu cerca de 20 cm. O aumento do nível do mar coloca em risco principalmente a população que atualmente vive na zona costeira, uma faixa onde existem mais de 130 cidades com mais de um milhão de habitantes em todo o mundo. Além disso, é nessa região onde se encontram instaladas várias obras de infraestrutura, como portos, aeroportos e mais de 200 usinas de energia nuclear que utilizam água do mar em seus sistemas de resfriamento (RAHMSTORF, 2024).

Como a velocidade do degelo cresce com a temperatura, o aumento do nível do mar vem ocorrendo de modo acelerado. Segundo o último relatório do IPCC (IPCC, 2021), até o final deste século, o nível do mar deve ficar 70 cm acima do valor médio registrado no final do século XIX, considerando-se um clima 3 ºC mais quente. Posteriormente, entre 2100 e 2150, a marca de 1 m de aumento do nível do mar poderá ser atingida. Todavia, para cenários de altas emissões de gases do efeito estufa, o nível do mar pode aumentar mais de 2 m já por volta de 2100 e até 5 mpor volta de 2150. Mesmo após a temperatura do planeta se estabilizar, o nível do mar continuará subindo por milênios. Caso o planeta atinja o aumento médio de 3 ºC com relação ao final do século XIX, o nível do mar continuará a subir a uma taxa de 1 m por século. A elevação do nível do mar e outras mudanças oceanográficas provocadas pela mudança do clima deverão provocar o deslocamento de milhões de pessoas no mundo, principalmente os mais pobres (IPCC, 2019). As economias e as populações de algumas nações-ilha, tais como Maldivas, Ilhas Marshall, Tuvalu e Nauru encontram-se sob maiores riscos de sofrer os efeitos do aumento do nível do mar (IPCC, 2019). Em altas latitudes, embora a redução do gelo marinho tenha aberto novas rotas para a navegação internacional, ela tem também prejudicado as atividades turísticas baseadas no gelo e colocado em risco os modos de vida tradicionais baseados na pesca e na caça de espécies polares (IPCC, 2019).

A atual taxa de elevação do nível do mar está ocorrendo de maneira heterogênea entre as regiões do planeta, i.e., cerca de três vezes mais rapidamente no Pacífico oeste do que a média global, ao passo que, no Pacífico leste, essa variação tem sido nula ou negativa (BARANGE et al, 2018; DANGENDORF et al., 2017). Portanto, os impactos econômicos dessa elevação também tendem a ocorrer de maneira bastante heterogênea. Esses possíveis impactos incluem, por exemplo, modificações das linhas de costa, redução da produtividade costeira – conforme os recifes e as gramas marinhas tornam-se mais submersos – e aumento das inundações (BARANGE et al., 2018; IPCC, 2019). Os efeitos combinados da elevação do nível do mar e do aumento da frequência e da intensidade das tempestades devem também impactar gravemente as infraestruturas costeiras e oceânicas, tais como áreas aquícolas, portos e empreendimento de produção de energia offshore, além de impor riscos à navegação (IPCC, 2019).

Conforme o clima se aquece e o degelo e a precipitação continental aumentam, o aporte fluvial e as inundações também se tornam mais intensos. Estes processos impactam as águas costeiras reduzindo a salinidade, aumentando a sedimentação e afetando a produtividade biológica (IPCC, 2019; JHA et al., 2006; PERVEZ e HENEBRY, 2015; SIDERIUS, et al., 2013; LOO et al., 2015). Devido às conexões dos processos climáticos, o colapso do gelo do Ártico pode culminar no colapso do gelo na Groenlândia, das florestas boreais na América do Norte, da *permafrost* na Europa Oriental e da circulação termohalina no Oceano Atlântico (RAHMSTORF, 2024). A circulação termohalina é fundamental para a redistribuição de calor e de água doce, determinando climas locais, a produtividade biológica e a química marinha. É importante, também, para definir a capacidade de sequestro de carbono pelo oceano. O aumento do fluxo de água doce e quente para o oceano compromete o processo de afundamento da água, que precisa estar salgada e fria para descender e, dessa forma, desacelera a circulação termohalina (BARANGE et al., 2018; IPCC, 2019; LIU et al., 2017). A Circulação Meridional do Atlântico e a Corrente do Golfo, por exemplo, já demonstram estar enfraquecendo (CAESAR et al., 2018; IPCC, 2019; THORNALLEY et al., 2018; BARANGE et al., 2018). Contudo, excetuando-se a Corrente do Golfo, todas as correntes de contorno oeste deverão se intensificar devido às mudanças atmosféricas nas latitudes tropicais e aos deslocamentos dos padrões de ventos decorrentes das mudanças do clima, o que tende a gerar tempestades costeiras mais destrutivas (BARANGE et al., 2018; YANG et al., 2016).

As mudanças climáticas também estão afetando a quantidade de oxigênio dissolvido no oceano, devido à maior estratificação da coluna d’água decorrente do aquecimento superficial somada a outros processos físicos e biogeoquímicos (BARANGE et al., 2018; BREITBURG et al., 2018; GATTUSO et al., 2018; IPCC, 2019; JACOX e EDWARDS, 2011; OSCHLIES et al., 2018). Assim, as zonas de concentração mínima de oxigênio têm se expandido, principalmente nas regiões tropicais. Nestas áreas, o consumo de oxigênio pelas bactérias do sedimento excede a quantidade disponível desta substância (BARANGE et al., 2018; BREITBURG et al., 2018; IPCC, 2019; OSCHLIES et al., 2018; STRAMMA et al., 2010; LEVIN, 2002).

A tendência de diminuição da concentração de oxigênio na água deverá provocar perdas de habitats, deslocamentos na distribuição e redução da abundância de várias espécies (i.e., perdas da biodiversidade) (BREITBURG et al., 2018; STRAMMA et al., 2010; LEVIN, 2002). Portanto, os impactos futuros sobre as espécies marinhas dependerão também da sua tolerância aos baixos níveis de oxigênio (GAINES et al., 2023).

As ressurgências – fenômeno oceanográfico de afloramento de águas mais frias e ricas e nutrientes vindas de fundo devido à ação do vento sobre a camada superficial, aumentando a produtividade primária – podem se intensificar devido a padrões de vento mais favoráveis, conforme o continente e o oceano se aquecem a diferentes taxas. Contudo, o aumento da estratificação termal da coluna d’água pode restringir a profundidade em que as águas afloram, o que, por sua vez, pode prejudicar a ascensão das águas de fundo para a superfície (BAKUN, 1990; BARANGE et al., 2018; JACOX e EDWARDS, 2011; RYKACZEWSKI et al., 2015; SYDEMAN et al., 2014; WANG et al., 2017). Uma eventual intensificação das ressurgências pelas mudanças climáticas pode resultar em aumento do aporte de nutrientes para a superfície e, consequentemente, da produtividade primária ou, alternativamente, numa plataforma continental com águas mais ácidas e com menos oxigênio dissolvido (BAKUN et al., 2015; BARANGE et al., 2018). As mudanças nos padrões de ressurgência deverão ter grande impacto sobre a pesca, uma das atividades econômicas mais importantes associadas a essas zonas de afloramento das águas profundas (GAINES et al., 2023).

Por fim, a acidez do oceano já aumentou 26% desde a revolução industrial, com variações regionais de intensidade, devido à absorção da grande quantidade de CO_2 emitido na atmosfera (BARANGE et al., 2018; GATTUSO et al., 2018; IPCC, 2019; JEWETT e ROMANOU, 2017). Um oceano mais ácido pode prejudicar diversos organismos marinhos, principalmente aqueles que se encontram nas fases iniciais de vida. Corais e outros organismos com estruturas carbonáticas são especialmente sensíveis a meios ácidos (BARANGE et al., 2018; FAO, 2018; PÖRTNER et al., 2014). Quando o meio se torna muito ácido, atinge-se o ponto de saturação a partir do qual torna-se impossível a produção das estruturas carbonáticas por parte dos organismos calcificadores. O aumento mais acentuado da acidez marinha deverá ocorrer nas latitudes tropicais, justamente onde predominam os recifes de corais (BARANGE et al., 2018; HARRIS et al., 2013).

As mudanças das características físicas, químicas e biológicas dos oceanos estão aumentando a vulnerabilidade dos organismos marinhos (PINSKY et al., 2019) e afetando a composição dos ecossistemas, especialmente sua estrutura espacial e o seu funcionamento (IPCC, 2019). Ainda que se alcance o cenário mais otimista de emissões de gases do efeito estufa - o que parece pouco provável, haja vista que as emissões continuam crescendo - o planeta, especialmente o oceano, experimentará mudanças consideráveis. Dessa forma, os benefícios obtidos a partir do oceano serão impactados, da mesma forma que as populações humanas que dependem do acesso aos recursos marinhos (CRAIG, 2012; PECL et al., 2017), o que ameaça o bem estar, a subsistência e a prosperidade da humanidade (MOONEY et al., 2009; GATTUSO et al., 2015; RILOV et al., 2020), que vive majoritariamente nas zonas costeiras. Todavia, poucos planejamentos espaciais marinhos incorporam questões de mudanças climáticas e ações de adaptação e mitigação necessárias diante de tais mudanças (GISSI, FRASCHETTI e MICHELI, 2019; RILOV et al, 2020).

Para embasar as estratégias de adaptação do planejamento espacial marinho, têm-se considerado as análises de cenários futuros como a abordagem mais promissora (GISSI, FRASCHETTI e MICHELI, 2019; FRAZÃO SANTOS, 2020). As projeções informam como deverão ser as condições de uma área de interesse para os próximos anos e, consequentemente, quais estratégias de gestão deverão ser adotadas (LUKIC et al., 2018; EHLER, ZAUCHA e GEE, 2019). Com essa abordagem, é possível projetar vários cenários futuros alternativos com base nas possíveis trajetórias de emissões de gases estufa, trajetórias essas que dependem das decisões sócio-políticas que venham a ser adotadas pelas lideranças mundiais. Tais projeções nos permitem avaliar como os usos humanos, a exemplo da pesca e da aquicultura, poderão ser impactados e redistribuídos no espaço e no tempo (EHLER e DOUVERE, 2009; GISSI, FRASCHETTI e MICHELI, 2019; FRAZÃO SANTOS, 2020).

Análises de modelos, mapas e linhas do tempo ajudam a vislumbrar como diferentes escolhas de planejamento e gestão, bem como trajetórias de desenvolvimento são determinantes para o clima, para os usos do mar (e.g., pesca, aquicultura e navegação) e, consequentemente, para o bem estar humano futuros. Processos de construção de cenários ajudam a vislumbrar qual a situação mais provável de ocorrer e a encontrar soluções quanto ao que se pode e ao que se deve fazer. As análises de cenários projetados fazem-se, portanto, fundamentais para integrar os impactos das mudanças do clima ao planejamento espacial marinho (FRAZÃO SANTOS, 2020).

A avaliação espacial do risco, da exposição e da vulnerabilidade precisa ser incorporada ao planejamento espacial marinho, de modo que se possa dar atenção especial aos locais onde as consequências das mudanças demonstram ser mais significantes (UNESCO, 2017; SALE et al., 2014; OKEY et al., 2014). Para que se identifiquem as áreas-chave problemáticas e se fomentem as ações necessárias, é preciso conhecer onde os sistemas socioecológicos marinhos estejam mais vulneráveis (i.e., suscetíveis e predispostos a danos), expostos (i.e., presentes em locais que possam sofrer efeitos danosos) e sob maior probabilidade de incidência de eventos prejudiciais (FRAZÃO SANTOS, 2020).

1.2 Sobre a espécie-foco do estudo: *Ostreopsis* cf. *ovata*

Florações de microalgas bênticas nocivas são um foco de preocupação devido aos seus possíveis impactos sobre os ecossistemas marinhos, a saúde humana e as atividades econômicas da pesca, aquicultura e turismo. Trata-se de um problema que tem recebido atenção da comunidade científica e de alguns tomadores de decisões, porém, ainda é preciso conhecer melhor a ecologia, a fisiologia e a toxinologia desses microrganismos causadores (MAFRA et al., 2023a), de modo que permita à sociedade pensar e implementar estratégias de prevenção e mitigação.

Muitas espécies de microalgas bênticas são produtoras de uma variedade de compostos bioativos que podem intoxicar os seres humanos e os organismos marinhos (LEE et al., 2020). No Brasil, já se reportou a ocorrência de 24 espécies de dinoflagelados bênticos tóxicos marinhos e estuarinos, principalmente na costa nordeste do país (MAFRA et al., 2023a). Entre tais espécies, está o dinoflagelado marinho *Ostreopsis* cf. *ovata*. Esta espécie é o foco deste trabalho, que investiga sua ecologia e biogeografia a fim de subsidiar as estratégias de mitigação e de adaptação para os riscos impostos por esta microalga à saúde humana, aos ecossistemas marinhos e à economia oceânica, no presente e em possíveis cenários futuros de mudanças climáticas.

Espécies do gênero *Ostreopsis* são predominantemente bênticas e formadoras de florações, que, nos casos mais intensos, costumam formar uma película amarronzada fracamente anexada ao substrato (ACCORONI, 2016). No entanto, algumas vezes as células destes organismos podem ser encontradas em suspensão, integrando a assembleia planctônica (MAFRA et al., 2023). As espécies deste gênero produzem palitoxinas, e outras substâncias análogas, que estão associadas a episódios de irritação respiratória e dermatites em seres humanos devido à inalação e ao contato cutâneo, respectivamente (DURANDO et al., 2007; VILA et al., 2016), além de casos esporádicos, porém graves, de intoxicação alimentar por ingestão de pescados contaminados, a palitoxicose (RAMOS e VASCONCELOS, 2010; TUBARO et al., 2011). Os quadros clínicos de envenenamento humano mais comumente reportados incluem a rabdomiólise (OKANO et al., 1998; KODAMA et al., 1989; TANIYAMA et al., 2002), que afeta os músculos esqueléticos e culmina em colapsos musculares e no derramamento de grande quantidade de conteúdo intracelular (miócito) no plasma sanguíneo (DEEDS e SCHWARTZ, 2010). Envenenamentos em seres humanos por palitoxinas (PlTX), usualmente identificados pelo gosto metálico ou azedo no pescado contaminado, manifestam-se, ainda, sob a forma de cólicas abdominais, náusea, vômito, diarreia, parestesia, bradicardia, falha dos rins, cianose e disfunção respiratória (ALCALA et al., 1988; KODAMA, 1989; TANIYAMA et al., 2002). Os casos fatais costumam ser precedidos pelas duas últimas complicações (MUNDAY, 2008; RAMOS e VASCONCELOS, 2010). Além de causar a palitoxicose (ALCALA et al., 1988; DURANDO et al., 2007; TANIYAMA, 2008), acredita-se que PlTX possa ser a causa do clupeotoxismo, uma síndrome de intoxicação severa associada ao consumo do peixe clupeídeos (DEEDS e SCHWARTZ, 2010). Sabe-se que nove espécies do gênero *Ostreopsis* são produtoras de palitoxinas (ACCORONI e TOTTI, 2016) e que estas substâncias podem ser transferidas ao longo da cadeia trófica (ALIGIZAKI et al., 2011). Assim, episódios de letalidade humana já foram reportados nas Filipinas (ALCALA et al., 1988) e em Madagascar (ONUMA et al., 1999), associados ao consumo de caranguejo *Demania reynaudii* e de sardinha *Herklotsichthys quadrimaculatus*, respectivamente.

Já se reportaram episódios graves com centenas de casos de síndromes respiratórias em seres humanos associados a florações de *Ostreopsis* spp. nas costas da Itália (CASAVOLA et al., 2005; BRESCIANINI et al., 2006; CIMINIELLO et al., 2006; FAIMALI et al., 2012) e da Espanha (ALVAREZ et al., 2005; BARROSO GARCIA et al., 2008; VILA et al., 2008). A intoxicação respiratória, aparentemente, ocorre devido à inalação de *spray* marinho contendo células de *Ostreopsis* spp. ou fragmentos de células e toxinas em estado livre (MANGIALAJO et al., 2011).Além de afetar a saúde humana, os efeitos nocivos de *Ostreopsis* spp. para os organismos marinhos já foram reportados em artêmias (RHODES et al., 2000; NEVES et al., 2017; MAGRO, 2021; SILVA, 2023), crustáceos (RAMOS & VASCONCELOS, 2010; FAIMALI, 2012), peixes juvenis (FAIMALI, 2012), poliquetas (SIMONINI, ORLANDI & ABBATE, 2011), ouriços-do-mar (VALE e ARES, 2007; SHEARS e ROSS, 2009; PRIVITERA, 2012; NEVES, CONTINS & NASCIMENTO, 2018; NEVES et al., 2018), vieiras (RHODES et al., 2002), ostras (FAUSTINO et al., 2021), mexilhões, cirrípedes, lapas e cefalópodes (CIMINIELLO et al., 2006; VALE e ARES, 2007; MALAGOLI et al., 2008; TOTTI et al., 2010). Vários episódios de mortalidade massiva de animais marinhos já foram reportados na Itália (CIMINIELLO et al., 2006; VALE e ARES, 2007; TOTTI et al., 2010), no Brasil (FERREIRA et al., 2006), na Nova Zelândia (PEARCE, MARSHALL e HALLEGRAEFF, 2000; SHEARS e ROSS, 2009) e no Japão (HASHIMOTO et al., 1969). Desta forma, além dos efeitos nocivos das toxinas produzidas por *Ostreopsis* spp. se manifestarem em nível populacional (FAIMALI et al., 2012), eles podem ser substancialmente agravados ao escalonar para o nível de ecossistema (SHEARS & ROSS, 2009; TOTTI et al., 2010).

As primeiras ocorrências de *Ostreopsis* spp. foram reportadas em águas tropicais. Contudo, posteriormente passaram a se observar florações nas costas subtropicais e temperadas dos hemisférios norte e sul (RHODES, 2011; ACCORONI e TOTTI, 2016). Em águas subtropicais e temperadas, ocorrem altas concentrações principalmente de *Ostreopsis* cf. *ovata* e *Ostreopsis* cf. *siamensis*, sobretudo no verão (ACCORONI e TOTTI, 2016). Nestas zonas latitudinais, a ocorrência de *Ostreopsis* spp. já foi reportada no Mar da China (FUKUYO, 1981), no Oceano Pacífico (FUKUYO, 1981; PEARCE et al., 2001; RHODES et al., 2002; TANIYAMA et al., 2003;), no Mar da Tasmânia (PEARCE, MARSHALL e HALLEGRAEFF., 2000), no Oceano Índico (LENOIR et al., 2004), no Oceano Atlântico (GRANÉLI et al., 2002; RIOBÓ, PAZ e FRANCO, 2006; TIBIRIÇÁ et al., 2019), no Golfo do México (BALLANTINE, TOSTESON e BARDALES, 1988; FAUST, 1999) e no Mar Mediterrâneo (PENNA et al., 2005; ALIGIZAKI e NIKOLAIDIS, 2006; CIMINIELLO et al., 2006; TOTTI et al., 2010).

Ostreopsis cf. *ovata* é uma das espécies mais associadas às florações de microalgas bênticas nocivas na América do Sul (MAFRA et al., 2023). Ocorrências de *O.* cf. *ovata* têm sido reportadas ao longo da costa brasileira desde 1998 (FERREIRA, 2006), quando uma floração foi detectada em Arraial do Cabo, RJ. Nesse episódio, houve uma mortalidade massiva de ouriços-do-mar, que culminou em uma redução expressiva da abundância destes animais (FERREIRA, 2006). Em 2001, ocorreu outra floração na mesma área (GRANÉLI et al., 2002). Florações da espécie têm sido detectadas em Armação de Búzios, RJ, desde 2006 (NASCIMENTO, 2016). No arquipélago de Currais, PR, detectaram-se florações em 2017 e 2018, que culminaram na contaminação de mexilhões (TIBIRIÇÁ et al., 2019).

Nos últimos anos também ocorreram florações intensas de *Ostreopsis* cf. *ovata* e *O.* cf. *siamensis* em diversas praias rochosas do Mediterrâneo, especialmente durante o verão e o final do verão (ACCORONI e TOTTI, 2016). Essa expansão de *Ostreopsis* spp. para as regiões temperadas tem ocorrido, possivelmente, devido à água de lastro dos navios de carga e às mudanças nas condições climáticas (SHEARS e ROSS, 2009). Tais eventos de floração em altas latitudes, cada vez mais frequentes e intensos (TOGNETTO et al., 1995; VILA et al., 2001; PENNA et al., 2005; MANGIALAJO et al., 2008; TOTTI et al., 2010; CHOMÉRAT et al., 2022), estão associados com episódios de mortalidade de organismos bênticos e problemas de saúde em seres humanos (FAIMALI et al., 2012).

1.3 Mecanismo de ação tóxica da palitoxina e de seus análogos

A PlTX e seus análogos (e.g., palitoxina isobárica, ostreocinas, mascarenotoxinas e ovatoxinas) são produzidos pela maioria das espécies do gênero *Ostreopsis* (USAMI et al., 1995; UKENA et al., 2001; LENOIR et al., 2004; ROSSI et al., 2010). Essa molécula grande e complexa, que pode apresentar mais de 10^{21} estereoisômeros (KATIKOU, 2007; RAMOS e VASCONCELOS, 2010), foi encontrada pela primeira vez em corais moles (*soft corals*) do gênero *Palythoa* no Oceano Pacífico (RAMOS e VASCONCELOS, 2010). Em sua longa cadeia de carbono, encontram-se regiões lipofílicas e outras hidrofílicas, conferindo a natureza anfipática da molécula (WANG, 2008; INUZUKA, UEMURA e ARIMOTO, 2008). De modo geral, a palitoxina e seus análogos permanecem estáveis mesmo após aquecidos. Porém, decompõem-se rapidamente em soluções aquosas ácidas ou alcalinas, reduzindo, assim, sua toxicidade (KATIKOU, 2007).

A PITX age na célula animal sobre a Na^+/K^+-ATPase, uma bomba na membrana plasmática que carrega cátions e, assim, mantém o gradiente iônico transmembrana (SÁEZ, LOZANO e ZALDÍVAR-RIVERÓN, 2009; WU, 2009; ROSSINI e BIGIANI, 2011; TUBARO et al. 2011, FAIMALI et al., 2012). Esta proteína transmembrana normalmente transporta três cátions Na^+ para fora da célula e dois K^+ para dentro dela. Estabelece, dessa forma, um gradiente eletroquímico fundamental para a homeostase celular (WU, 2019). Esse gradiente eletroquímico é necessário para a manutenção do balanço osmótico, o favorecimento do transporte de nutrientes e aminoácidos para o interior das células, a regulação do volume celular e a manutenção e recuperação do potencial da membrana em células nervosas excitáveis (THERIEN e BLOSTEIN, 2000; CEREIJIDO, CONTRERAS e SHOSHANI, 2004; KÜHLBRANDT 2004). A PITX, por ter como marcador celular a Na^+/K^+-ATPase, provoca distúrbios no equilíbrio iônico nos sistemas biológicos (ROSSINI e BIGIANI, 2011). Ela adere à porção extracelular alfa desta proteína da membrana plasmática e a transforma em canais de cátions não seletivos, o que culmina no fluxo passivo de íons no sentido do gradiente de concentração (ARYSTARKHOVA et al., 1999). Além disso, a PITX também interfere no acoplamento entre os portais interno e externo da bomba Na/K e, assim, faz com que estes portais fiquem simultaneamente abertos, o que afeta o fluxo de íons (ROSSINI e BIGIANI, 2011). A despolarização da membrana provoca um aumento expressivo de Ca^{2+} no citosol e essa variação na concentração intracelular de cátions afeta diversas funções vitais, o que, geralmente, culmina na morte celular (SATOH, ISHII e NISHIMURA, 2003; VALVERDE et al., 2008; RAMOS e VASCONCELOS, 2010, FAIMALI et al., 2012).

A PITX apresenta significativa atividade biológica mesmo sob baixas concentrações (MOORE e SCHEUER, 1971). Trata-se de uma das moléculas mais tóxicas que ocorrem na natureza e, por isso, é capaz de provocar quadros severos de envenenamento nos seres humanos, com os casos mais graves podendo ser letais (FAIMALI et al., 2012). Ela também causa diversos efeitos farmacológicos secundários, como contrações violentas dos músculos lisos, esqueléticos e cardíacos, assim como efeitos cardiovasculares, hemólise, histamina, prostaglandina e lançamento de norepineferina, agregação de plaquetas, reabsorção óssea e inibição da mobilidade dos espermatozoides (WU, 2009; HILGEMANN, 2003; MORTON et al., 1982; LAZZARO et al., 1987; NAGASE e KARAKI , 1987; NAGASE et al., 1987). Assim, por ser altamente tóxica, o Painel sobre Contaminantes na Cadeia Alimentar da Autoridade Europeia para a Segurança Alimentar (EFSA, 2009) recomendou que a PITX seja regulamentada, com um limite máximo de 30 mg kg^{-1} em tecidos de pescados contaminados (MUNDAY, 2011).

1.4 Ecologia de *O*. cf. *ovata*

As várias espécies de microalgas bênticas marinhas nocivas distribuem-se por uma ampla gama de habitats. Elas possuem forte associação com substratos bióticos e abióticos, tais como tapetes de algas, macrófitas, grama marinha, corais, destroços de corais desnudos, rochas e sedimentos (BOMBER & AIKMAN, 1989; BOMBER, RUBIO e NORRIS, 1989; FAUST e MORTON, 1995; MAFRA et al., 2023a). Esses substratos, juntamente com fatores abióticos como luz, temperatura e salinidade influenciam a distribuição das espécies de microalgas bênticas nocivas. Assim, conforme certas espécies são mais favorecidas, os tipos e quantidades de toxinas que entram na cadeia trófica marinha também são modificados.

O gênero *Ostreopsis* é comumente descrito habitando superfícies de macroalgas, gramas marinhas, fragmentos de corais ou sobre a areia (FAIMALI et al., 2012; MAFRA et al., 2023a). Nas Ilhas Perhentian, Malásia, as maiores abundâncias de *Ostreopsis* spp. encontram-se associadas a corais rígidos, tapetes de algas microfilamentosas e macroalgas verdes, marrons e vermelhas (LEE et al., 2020). No Mediterrâneo, onde não há recifes de corais tão extensos e desenvolvidos como em outros lugares, a ocorrência de *Ostreopsis* spp. está fortemente associada a substratos consolidados, principalmente rochas e estruturas construídas por seres humanos, além de densos tapetes de macroalgas e tapetes de algas microfilamentosas. (LEE et al., 2020). Na América do Sul, elas ocorrem predominantemente associadas a macroalgas (MAFRA et al., 2023). No Mar Adriático norte, *O*. cf. *ovata* pode ser encontrada assumindo modos de vida epifítico, epilítico e epizooico, porém, as maiores abundâncias ocorrem sobre substratos consolidados, ao passo que, as menores, sobre conchas de moluscos (TOTTI et al., 2010). Diversos estudos apontam que as maiores abundâncias de dinoflagelados bênticos ocorrem em áreas com condições hidrodinâmicas baixas (SANSONI et al., 2003; SIMONI et al., 2004; BARONE e PRISINZANO, 2006; CONGESTRI et al., 2006; ZINGONE et al., 2006; SHEARS e ROSS, 2009) ou moderadas (VILA et al., 2001). TOTTI et al. (2010), por exemplo, verificaram que o hidrodinamismo exerce um papel importante para *O*. cf. *ovata*, uma vez que as áreas abrigadas apresentaram maiores abundâncias que as áreas expostas no Mar Adriático norte. Possivelmente, isso ocorre porque *O*. cf. *ovata* não possui estruturas que garantam forte adesão ao substrato e, assim, as células são facilmente ressuspendidas na coluna d’água. É possível, inclusive, que o padrão verificado de maiores abundâncias de *O*. cf. *ovata* sobre os talos mais ramificados de macrófitas seja uma consequência do hidrodinamismo, que torna esses dinoflagelados mais facilmente removíveis dos talos menos ramificados pela ação das ondas e das correntes (TOTTI et al., 2010).

Nas Ilhas Perhentian, Malásia, as maiores abundâncias de *Ostreopsis* spp. foram verificadas a 1,2 m de profundidade, com células ocorrendo até a profundidade máxima de 16 m (LEE et al., 2020), demonstrando-se a associação positiva da espécie com luz (LEE et al., 2020). No Mar Adriático norte, a abundância de *O.* cf. *ovata*, para todos os tipos de substratos, também decresce com a profundidade, devido, possivelmente, à diminuição da intensidade de luz. Assim, as florações foram detectadas em locais com profundidade entre 1 e 2 m. Em profundidades >3m, registraram-se os menores valores de abundância (TOTTI et al., 2010). Tibiriçá et al. (2019) verificaram, no Arquipélago de Currais, PR - Brasil, uma floração de *O*. cf *ovata* com extensão pelo leito marinho em profundidades entre 0 e 8 metros, com maiores densidades celulares em áreas mais rasas (1.5 m), decrescendo exponencialmente em áreas menos iluminadas em maiores profundidades.

Florações de *O*. cf. *ovata* aparentam ser impulsionadas por uma combinação ótima de temperatura e concentração de nutrientes no meio. Os cistos parecem germinar apenas quando a temperatura da água atinge um limiar mais elevado e a proliferação celular se dá quando a razão N:P encontra-se em torno do valor de Redfield (ACCORONI, 2016). Em laboratório, os cistos (que são produzidos, temporariamente, durante as fases de descanso), após germinarem, conseguem sobreviver por até cinco meses em meio com temperatura de 25 ºC, mas não sob 21 ºC (ACCORONI et al, 2014). Da mesma forma, em ensaio laboratorial, *O.* cf. *ovata* apresentou aumento da toxicidade celular em meios com maiores temperaturas da água (FAIMALI et al., 2011). Granéli et al. (2008) verificaram aumento da toxicidade perante temperatura >20 °C, enquanto que Manganelli et al. (2007) demonstraram que a toxicidade em meio com temperatura de 28 ºC é maior que em meio a 24 °C.

1.5 Aquicultura marinha sob risco

A aquicultura é o sistema de produção alimentar que cresceu mais rapidamente nos últimos anos (FAO, 2018). Parte dessa produção ocorre em ambientes marinhos, como fiordes, águas costeiras e abertas, mares fechados ou instalações fechadas, o que configura a maricultura, ou aquicultura marinha (CLAWSON ET AL., 2022). Desde os anos 1990, a produção da aquicultura marinha aumentou cerca de cinco vezes. Assim, em 2018, essa atividade alcançou um total de 30,8 milhões de toneladas (em peso vivo). A produção de moluscos totalizou 17,3 milhões de toneladas, correspondente a 56,3% da produção aquícola total marinha e costeira. A produção de peixes marinhos totalizou 7,3 milhões de toneladas e de crustáceos, outras 5,7 milhões de toneladas (FAO, 2020).

Pelas próximas décadas, juntamente com as projeções de crescimento da população mundial, a demanda por alimento também deve aumentar. Portanto, será preciso conciliar o suprimento de alimentos com a sustentabilidade ambiental (UN, 2019; OYINLOLA et al., 2020). Nesse sentido, a maricultura demonstra um menor potencial de impacto ambiental quando comparada com a produção animal terrestre (TILMAN e CLARK, 2014; HALL et al., 2011; POORE e NEMECEK, 2018). Ademais, os pescados possuem alta composição proteica e baixas quantidades de ácidos graxos trans-insaturados, oferecendo, assim, vários benefícios à saúde. Dessa forma, a aquicultura marinha se destaca como uma promissora fonte de alimento nutritivo e sustentável, especialmente num contexto de demanda crescente por proteína (CLAWSON et al., 2022). Contudo, as mudanças climáticas poderão comprometer a produção da aquicultura marinha e, consequentemente, o suprimento de alimentos a partir desta atividade (OYINLOLA et al., 2020). O aumento da temperatura e da acidez da água, as mudanças na salinidade, a elevação do nível do mar, as alterações da ação das ondas, a maior variabilidade das condições do tempo, o aumento da intensidade e da frequência das tempestades e outros eventos extremos irão alterar a adequabilidade dos habitats marinhos, afetando também o cultivo de frutos do mar (BARANGE & PERRY, 2009; CHEUNG et al., 2009; GATTUSO et al., 2015; HARLEY et al., 2006; FAO, 2020; REID et al., 2019). O aumento da temperatura e da acidez da água do mar, em especial, devem impactar diretamente as espécies cultivadas (COCHRANE et al., 2009), afetando as taxas de crescimento e de sobrevivência desses organismos, sua suscetibilidade a doenças e parasitas e sua reprodução, além de prejudicarem particularmente a qualidade das conchas dos bivalves (HANDISYDE et al., 2006; GAZEAU et al., 2013; GREEN et al., 2013; ROSA et al., 2014; BARANGE et al., 2018; FROEHLICH et al., 2018). As mudanças climáticas, portanto, demonstram potencial para afetar negativamente a quantidade e a qualidade da produção de frutos do mar a partir da maricultura (OYINLOLA et al., 2020), comprometendo, por consequência, os lucros deste setor econômico e a oferta de alimento de qualidade à população (LI et al., 2016).

Diferentemente da maior parte das atividades pesqueiras, as operações envolvidas na aquicultura marinha exigem uma quantidade expressiva de infraestruturas para que se possa cultivar as espécies em seus diferentes estágios de vida. Essas infraestruturas são vulneráveis a tempestades, as quais devem aumentar em frequência e intensidade devido às mudanças climáticas (DE SILVA, 2012; IPCC, 2019; GAINES et al., 2023). Tais infraestruturas serão, ainda, comprometidas pelo aumento do nível do mar, que deverá modificar a morfologia das linhas de costa, além de reduzir a disponibilidade de habitats para bivalves, peixes e crustáceos (OYINLOLA et al., 2020).

Outro problema que já se percebe é o aumento dos impactos das florações de algas nocivas (FANs) sobre a aquicultura (TRAINER et al., 2020b), que deve se intensificar com as mudanças do clima (BARANGE et al., 2018; FROEHLICH et al., 2018). A aquicultura é mais afetada pelas FANS do que a pesca (TRAINER et al., 2020a), pois as espécies cultivadas não podem se mover para longe das áreas de ocorrência destes eventos. Assim, os organismos cultivados podem morrer devido à desoxigenação da água ou pelos efeitos diretos das toxinas e de outros mecanismos nocivos, como a obstrução e lesões nas brânquias de peixes (LENZEN, LI e MURRAY, 2021). O aumento das chuvas tenderá a aumentar o aporte continental de nutrientes e, consequentemente, tornará mais prováveis os eventos de FANs em diferentes regiões do globo (HIMES-CORNELL et al., 2013; ROSA et al., 2014). Ademais, as florações costumam ocorrer em águas estuarinas e costeiras, onde se concentram as atividades de maricultura (LENZEN, LI e MURRAY, 2021). Nos Fiordes da Patagônia chilena, em 2016, por exemplo, um episódio de floração culminou na morte de 40 mil toneladas de peixes e uma perda econômica avaliada em US$ 800 M (DÍAZ et al., 2019). Na China, em 2012, uma floração de *Karenia mikimotoi* gerou um prejuízo de US$ 330 M (GUO et al., 2014). Globalmente, estimase um impacto anual das FANs na ordem de US$ 8 B (BROWN et al., 2020). Esses prejuízos compreendem os custos da suspensão das atividades de cultivo quando da presença de biotoxinas, dos custos humanos com serviços e bens de saúde, monitoramento da qualidade dos alimentos marinhos, seguros, além dos impactos sobre as atividades de turismo (SANSEVERINO et al., 2016a; KOUAKOU e PODER, 2019).

Moluscos bivalves podem acumular ficotoxinas mais rapidamente que outros organismos e, por isso, tendem a sofrer mais os efeitos das interdições das áreas de cultivos (BRICELJ e SHUMWAY, 1998; FARRELL et al., 2015; REIZOPOULOU et al., 2008; ROURKE et al., 2021). Países cuja produção da aquicultura marinha e estuarina estejam mais focadas no mercado externo precisarão de assistência para implementar programas de monitoramento de florações e de outros parâmetros de qualidade da água, de modo a garantir a sanidade aquícola dos alimentos marinhos. Esses países podem vir a requerer assistência de agências internacionais, através de treinamentos e infraestrutura necessários aos programas de monitoramento (LENZEN, LI e MURRAY, 2021). Alguns países já possuem programas de monitoramento de toxinas em frutos do mar implementados há décadas (e.g., Japão, EUA, Canadá, Nova Zelândia, Reino Unido e parte da União Europeia). Contudo, em várias regiões, ainda não há medidas oficiais de proteção, deixando os consumidores de pescados desprotegidos. Os principais motivos dessa ausência regulatória nos países são: territórios extensos, prevalência de indústria de frutos do mar em pequena escala e o alto custo para implementar e manter técnicas analíticas efetivas. No Brasil, há programas oficiais de monitoramento das toxinas e das florações de algas nocivas apenas no estado de Santa Catarina e em algumas áreas dos estados de São Paulo e Rio Grande do Norte (MAFRA et al., 2023b). Nesse sentido, a insuficiência de recursos destinados â pesquisa, treinamento e monitoramento voltados às microalgas nocivas intensificam os impactos provocados por esses microrganismos (MAFRA et al., 2023a).

Considerando-se cenários climáticos futuros de aquecimento do planeta, são esperados ganhos de riqueza potencial para a maricultura nas altas latitudes e perdas ao longo dos trópicos (FROEHLICH, GENTRY e HALPERN, 2018; HANDISYDE et al., 2006; PORTER et al., 2014; KLINGER, LEVIN e WATSON, 2017; OYINLOLA et al., 2020), entendendo-se riqueza potencial como o número total de espécies que podem ser cultivadas dado o conjunto de condições ambientais específicas (OYINLOLA et al., 2020). Percebe-se, dessa forma, a ameaça que as mudanças climáticas representam para áreas atualmente importantes para a produção aquícola marinha e seus aspectos associados à geração de empregos, investimentos e segurança alimentar (OYINLOLA et al., 2020). No entanto, ainda faz-se necessário investigar como os diferentes eventos associados ao aquecimento médio do planeta, tais como as mudanças na distribuição de espécies nocivas e o aumento de eventos de FANs, podem impactar essa atividade ao redor do globo.

1.6 Modelando os impactos das mudanças climáticas sobre as microalgas nocivas marinhas

É esperado que as mudanças climáticas afetem a magnitude, a frequência, a toxicidade, a biogeografia e a fenologia dos eventos de FANs (MOORE et al., 2008; HALLEGRAEFF, 2010; ANDERSON et al., 2015; WELLS et al., 2015). Como há uma grande diversidade de táxons de microalgas nocivas, a resposta desses táxons às mudanças climáticas possivelmente também ocorrerá de maneira diversa. De modo geral, climas futuros poderão impactar as espécies desses microrganismos marinhos devido ao aquecimento da água, aumento da estratificação, alteração na disponibilidade de nutrientes, variações de intensidade luminosa e de acidez do oceano (MOORE et al., 2008; HALLEGRAEFF, 2010; ANDERSON et al., 2015; WELLS et al., 2015). As mudanças climáticas também poderão afetar essas espécies indiretamente, através de impactos sobre o zooplâncton herbívoro e organismos patógenos, que afetam tanto o fito quanto o zooplâncton (WELLS et al., 2015, RALSTON & MOORE, 2020). Nesse sentido, o desenvolvimento de modelos de distribuição de espécies pode ser muito útil para embasar as decisões de mitigação e adaptação a eventos de FANs frente às mudanças do clima (RALSTON & MOORE, 2020).

A modelagem estatística tem sido uma das abordagens mais utilizadas para encontrar a relação entre a ocorrência de espécies de microalgas nocivas marinhas e as características do ambiente. Através desta técnica, Moore et al. (2011) projetaram, para o fim deste século, tendência de aumento da duração anual das condições ambientais sazonais propensas para florações de *Alexandrium catenella* em um estuário do Estado de Washington (EUA). Townhill et al. (2018) projetaram, ao longo do mar do noroeste Europeu, tendências de deslocamento latitudinal de

Dinophysis acuta e *Gymnodinium catanatum* rumo ao norte, ao passo que *Alexandrium ostenfeldii*, *Alexandrium minutum e Pseudo-nitzschia australis* devem ter suas distribuições deslocadas para o sul. Jacobs et al. (2015) verificaram que a temporada anual de florações de *Alexandrium fundyense,* no mar de Puget Sound (oeste dos EUA), tenderá a ocorrer mais cedo (antecipação de 2 meses) e persistir por 2 meses a mais no final deste século. Glibert et al. (2014) projetaram tendência de expansão da distribuição *Prorocentrum* spp. e *Karenia* spp. no sistema de plataforma do Mar Báltico para o final do século. Fabri-Ruiz et al. (2024), utilizando modelos de nicho ecológico, verificaram que os preditores ambientais mais importantes para mapear abundância de *O*. cf. *ovata* na região do Mar Mediterrâneo são temperatura da água, taxa de variação da temperatura da água e taxa de variação de clorofila-*a*. Verificaram que a temporada anual de florações da espécie deve iniciar mais cedo e findar mais tarde, com tendência de aumento da abundância celular em algumas regiões. Trabalhos desse tipo, portanto, são valiosos para avaliar possíveis mudanças na vulnerabilidade das zonas costeiras aos eventos de florações nocivas e os consequentes riscos para a saúde humana e ecossistêmica, as atividades pesqueiras e a aquicultura.

Existem diferentes algoritmos desenvolvidos para modelar a distribuição de espécies, mas, de modo geral, todos buscam encontrar a lógica de associação entre as variáveis dependentes (presença e ausência da espécie) e as variáveis preditoras (parâmetros ambientais). Com isso, esses algoritmos geram representações do nicho de uma espécie e da distribuição geográfica desta. Assim, pode-se usar essa técnica para predizer a distribuição geográfica da espécie no presente, bem como fazer projeções para cenários climáticos futuros (GUISAN & ZIMMERMANN, 2000; FRANKLIN, 2010; PETERSON et al., 2011; NAIMI & ARAÚJO, 2016, GUISAN et al., 2017). Em um contexto de FANs no ambiente marinho, modelos preditivos como estes podem ser utilizados para a gestão governamental de áreas costeiras, com vistas a proteger a população e as atividades aquícolas dos riscos ambientais, econômicos e à saúde provocados por esses eventos (DAVIDSON et al., 2016; FRANKS, 2018). Neste trabalho, modelou-se o nicho ecológico da microalga nociva *O*. cf. *ovata* com o fim de identificar os habitats mais adequados para ocorrência desta espécie e a sua distribuição potencial ao longo do ambiente marinho em diferentes cenários climáticos.

2 OBJETIVOS, PERGUNTAS E HIPÓTESES DO TRABALHO

Este trabalho teve por objetivo geral: *elucidar quais regiões marinhas estão mais sujeitas à ocorrência da microalga tóxica* O. *cf.* ovata *e avaliar como mudanças climáticas deverão impactar a distribuição futura desta espécie.* Com isso, o estudo contribuirá para que ações de mitigação dos riscos à saúde humana, aos ecossistemas marinhos e à sustentabilidade das atividades aquícolas possam ser tomadas nas áreas com presença potencial desta microalga em cenário presente e futuro.

Nesse sentido, os objetivos específicos desta dissertação consistem em:

1. Mapear, em escala global, as regiões marinhas mais suscetíveis à ocorrência do dinoflagelado toxigênico *O.* cf. *ovata*;
2. Verificar as tendências de magnitude e direção no deslocamento das áreas propensas à ocorrência da espécie no contexto de mudanças climáticas; e
3. Avaliar áreas de risco para a aquicultura marinha no presente e em possíveis cenários climáticos futuros frente às mudanças na distribuição potencial desta espécie.

Esta pesquisa, portanto, guiou-se pelas seguintes perguntas norteadoras:

i. Quais regiões marinhas estão mais propensas à ocorrência de *O.* cf. *ovata*, considerando suas características ambientais?

ii. Em quais regiões marinhas deverão ocorrer expansão ou contração de ocorrência desta espécie diante dos possíveis cenários climáticos futuros? Qual a magnitude e a direção esperadas desses deslocamentos?

iii. Como as mudanças climáticas afetarão a adequabilidade ambiental desta microalga tóxica nas áreas de aquicultura marinha distribuídas ao longo do planeta?

Esta pesquisa partiu da seguinte hipótese: se a distribuição geográfica de *O.* cf. *ovata* é dependente da concentração de nutrientes, incidência de radiação fotossinteticamente ativa, além de pH, temperatura e salinidade dentro das faixas de tolerância da espécie, entre outros fatores, e sabendo-se que muitas dessas variáveis estão sofrendo alterações em decorrência das mudanças climáticas, especialmente o aquecimento dos oceanos, então espera-se que suas áreas de ocorrência sejam deslocadas em direção a latitudes maiores em cenários de continuada emissão de gases do efeito estufa, já que migrar para águas mais profundas, como projetado para outras espécies marinhas, não é uma opção viável para microalgas devido à limitada penetração de luz nesses ambientes.

A pesquisa será apresentada na forma de um artigo científico, a ser submetido à revista *Science of the Total Environment*, com Fator de Impacto 8.2 e classificação A1 na área de Biodiversidade no sistema Qualis da CAPES.

3 ARTIGO: *Ostreopsis* cf. *ovata* as an emerging threat to marine aquaculture: shifting risks under future climate warming

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ABSTRACT

Blooms of the toxigenic marine microalga *Ostreopsis* cf. *ovata* have recently expanded, emerging as a significant threat due to their potential impacts to the aquatic biota, human health, and economic activities such as aquaculture. In this study, ecological niche modeling was employed to assess the current distribution of this species and its potential shifts under four warming scenarios, ranging from ~2 to >4 °C. According to model predictions, 2,759,632 km² of global shallow waters are now environmentally suitable for the species' presence, especially in tropical and temperate zones, while polar regions lack the minimum environmental conditions required for the species. The risk associated with the presence of this microalga for aquaculture is heterogeneously distributed, with some aquaculture-producing regions at higher risk and others classified as risk-free. Under warming climates, a 2 °C increase is expected to drive a ~30% global expansion of this microalga, which may reach polar latitudes then. However, high-emission scenarios may lead to a 11–63% contraction in the species' global distribution, and a 49–80% reduction in the number of aquaculture sites with potential presence of *Ostreopsis* cf. *ovata* worldwide.

Nonetheless, projections indicate an increased occurrence and associated risks in various locations, including major marine aquaculture producing areas, across all climate scenarios, indicating contrasting trends depending on the spatial scale of analysis. This is particularly critical in the context of climate change and projected growth of global population, which will demand increased and diversified food production, with marine aquaculture being one of the most promising sources.

Keywords: species distribution shifts, marine provinces, harmful algae, aquaculture production, environmental threats

INTRODUCTION

Global warming is driving significant changes in the biological, chemical and physical characteristics of the ocean, including alterations in salinity, acidity, dissolved oxygen levels, water column stratification, mixing processes and circulation (Rahmstorf, 2024). These changes threaten key processes in marine habitats, affecting their biological productivity, spatial structure, and ecosystem functioning (IPCC, 2018, 2019; Pinsky et al., 2019; Gaines, 2023). Consequently, vital ocean-related services and benefits, essential to the global economy, human prosperity, and well-being, are at risk (Mooney et al., 2009; Craig, 2012; Costanza et al., 2014; Gattuso et al., 2015; Pecl et al., 2017; Rilov et al., 2020; Gaines, 2023). Certain ocean-based industries/activities—such as fisheries, marine aquaculture, and coastal tourism—are particularly vulnerable to climate change. These sectors of the global ocean economy will require adaptive strategies designed for regional needs to remain sustainable as climate conditions continue to evolve (Gaines, 2023). Marine aquaculture, in particular, is considered a promising source of nutritious and sustainable food in light of the projected global population growth over the coming decades (Clawson et al., 2022). However, climate change may compromise this strategic economic activity and its associated food supply (Oyinlola et al., 2020).

Aquaculture is already being impacted by the increasing occurrence of harmful algal blooms (HABs) (Trainer et al., 2020b), a phenomenon that is expected to intensify with climate change (Barange et al., 2018; Froehlich et al., 2018). This increased occurrence of HABs have occurred especially in estuarine and coastal waters, where most marine organisms are cultivated (Lenzen, Li, & Murray, 2021).

Farmed species, which cannot move away from affected areas, are particularly vulnerable to mass mortality events caused by water deoxygenation or exposure to toxic compounds (Lenzen, Li, & Murray, 2021). Furthermore, organisms like suspension-feeding bivalve molluscs and finfishes, the main taxa used in farming activities, may accumulate unsafe levels of algal toxins and pose a health risk to human consumers when exposed to such events (Hallegraeff et al., 2021; Mafra et al., 2023a), compromising directly the regional economy. Globally, HABs are estimated to cause an annual economic impact of approximately $US 8 billion (Brown et al., 2020). These losses include the costs associated with suspending cultivation activities following the detection of biotoxins, healthcare expenses, monitoring of seafood quality, and the impacts on tourism (Sanseverino et al., 2016a; Kouakou & Poder, 2019).

Approximately 140 species of microalgae are currently listed as responsible for noxious events in the marine environment (Moestrup et al., 2009). Among these, the marine benthic dinoflagellate *Ostreopsis* cf. *ovata* stands out for producing palytoxins (PlTX) and other analogous substances, such as ovatoxins (Pavaux et al., 2020). These are some of the most toxic naturally occurring molecules, capable of causing severe poisoning and, in some cases, fatal consequences in humans (Faimali et al., 2012). Palytoxin and its analogs can bioaccumulate and biomagnify through the food chain, leading to severe health issues in humans consuming contaminated seafood. These health conditions include clupeotoxism (Deeds & Schwartz, 2010; Onuma et al., 1999; Aligizaki et al., 2011), palytoxicosis (Alcala et al., 1988; Durando et al., 2007; Taniyama, 2008), and rhabdomyolysis (Deeds & Schwartz, 2010). There is a hypothesis that Haff disease, which causes rhabdomyolysis in humans in various regions worldwide, is associated with PlTX-analogous molecules (CARDOSO et al., 2022). The presence of PlTX-like compounds in seafood may add a metallic or sour taste, while human poisoning symptoms may include abdominal cramps, nausea, vomiting, diarrhea, paresthesia, bradycardia, kidney failure, cyanosis, and respiratory dysfunction (Alcala et al., 1988; Kodama, 1989; Taniyama et al., 2002). Additionally, direct contact with aerosolized *Ostreopsis* spp. cells or inhalation of these cells may lead to respiratory irritation and dermatitis (Durando et al., 2007; Vila et al., 2016). Besides human health impacts, PlTX and its analogs have been reported to cause mass mortality events among wild marine organisms (Ferreira, 2006; Ramos & Vasconcelos, 2010), and negatively affect commonly farmed animals, such as crustaceans (Ramos and Vasconcelos, 2010; Faimali, 2012), juvenile fish (Faimali, 2012), scallops (Rhodes et al., 2002), mussels (Malagoli et al., 2008), and oysters (Faustino et al., 2021).

Considering the importance of *O.* cf. *ovata* for the global economy and population health, this study employed ecological niche modeling (ENM) to map environmental suitability for this species across the coastal ocean. ENMs utilize algorithms that apply correlative techniques to capture the statistical relationship between the species and its environment. These algorithms cross-reference georeferenced occurrence data with corresponding environmental variable values at those locations, allowing for the capture of the macro-ecological preferences of the target species (Elith & Leathwick, 2009; Tyberghein et al., 2012; Assis et al., 2018). When well-calibrated, these models provide valuable insights into the species' environmental tolerances and habitat preferences, enabling the identification of areas likely to support the target species under current conditions and alternative climate scenarios. Based on these ENMs, species distribution models are generated for a specific study area (Guisan & Zimmermann, 2000; Franklin, 2010; Peterson et al., 2011; Naimi & Araújo, 2016; Guisan et al., 2017; Booth et al., 1988; Peterson et al., 2011; Barbosa et al., 2012; Aiello-Lammens et al., 2015). These models assume that the species-environment relationship remains constant across space and time and that the species has colonized most of its suitable habitats within the study area (Guisan et al., 2014). The application of ENMs to marine species has been increasingly adopted, supported by the growing availability of marine environmental predictors derived from remote sensing data and *in situ* observations, as well as advancements in marine geographic information systems (Franklin, 2010; Tyberghein et al., 2012; Assis et al., 2017). Thus, the ENM approach has become a highly valued tool for conservation and environmental management (Franklin, 2010).

Given the anticipated effects of climate change on the magnitude, frequency, toxicity, biogeography, and phenology of HABs (Moore et al., 2008; Hallegraeff, 2010; Anderson et al., 2015; Wells et al., 2015; Gobler, 2020), this study aims to evaluate how climate-induced alterations in the marine environment may affect the future distribution of *Ostreopsis* cf. *ovata*. Records of *Ostreopsis* spp. were initially reported in tropical latitudes (Meroni et al., 2018), but in recent decades, they have also been observed in temperate latitudes, possibly due to ballast water from cargo ships and marginal changes in climatic conditions (Shears & Ross, 2009; Faimali et al., 2012).

Using species distribution modeling, we identify here regions with the highest potential for expansion or contraction of this species, which is associated with noxious events worldwide (Pavaux et al., 2020; Mafra et al., 2023b). These projections provide insights into how *O.* cf. *ovata* hotspots, particularly those related to marine aquaculture areas, may vary spatially as the planet's climate continues to change.

METHODS

Species distribution data

Global occurrence data for *Ostreopsis* cf. *ovata* were retrieved from the Global Biodiversity Information Facility (GBIF, 2024), the Ocean Biodiversity Information System (OBIS, 2004), and Leite et al. (2022), which compiles occurrence data extracted from scientific literature. Initially, there were 485 records for the target species worldwide. The occurrence data were filtered to maintain a minimum spacing of 6 km between records (since the environmental rasters used further have a spatial resolution of 0.05 degrees, i.e., approximately 5.5 km at the equator) using the *spThin* package (Aiello-Lammens et al., 2015), a crucial step for correcting geographic sampling bias and ensuring model quality (Aiello-Lammens et al., 2015). Additionally, occurrence records located erroneously on land due to localization errors were either excluded if they were more than 20 km from the ocean or manually repositioned to the nearest oceanic grid cell. Occurrence records located in deeper ocean regions (depths greater than 100 m) underwent the same process, being excluded if they were more than 20 km from a shallow area or repositioned to the nearest shallow location. This depth criterion was adopted because the target species is a benthic microalga that requires light to reach the seabed for photosynthesis. After this filtering procedure and the exclusion of duplicates, 166 occurrence records remained in our data set.

Environmental predictors

Marine environmental predictor data representing key factors for the target species were obtained from Bio-ORACLE for both present and projected climate conditions (Tyberghein et al., 2012; Assis et al., 2018, 2024). These data are provided as spatial grids (rasters) with a resolution of 0.05° (~5.5 km at the equator). Environmental data corresponding to the present climate (2000-2020) was used to model the ecological niche of the species and predict its current geographic distribution. To project changes in the distribution of *O.* cf. *ovata* under warmer climate scenarios, we used the projections based on alternative CO_2 emission pathways, which reflect different global socioeconomic development strategies and climate policies that may be adopted in the coming years (Assis et al., 2024). Specifically, we used the SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 emission scenarios (IPCC, 2021) for the end of the century (2080-2100), which are projected to result in a warmer global climate by up to 1.8 °C (1.3–2.4 °C), 2.7 °C (2.2–3.5 °C), 3.6 °C (2.8–4.6 °C), and 4.4 °C (3.3–5.7 °C), respectively, relative to the pre-industrial 1850–1900 period (IPCC, 2021). These scenarios indicate a likelihood greater than 50% of limiting global warming to temperature thresholds of 2°C, 3°C, 4°C, and above 4°C, respectively, by the end of the century (IPCC, 2023). Henceforth, these thresholds will be used as references to denote the corresponding warmer scenarios.

The initial set of marine environmental variables considered for the models included mean and range values of temperature, salinity, current velocity, light at the seabed, pH, and concentrations of nitrate, iron, and phosphate, considering that these are parameters of recognized importance for marine dinoflagellates. After collinearity tests, which are essential for correlative models, 10 predictors with Pearson's correlation coefficient below 0.7 were selected, including mean values for light at the seabed, current velocity, nitrate and iron, as well as mean and range values for salinity, temperature and pH. Among these, only mean light at the seabed variable is not directly provided by Bio-ORACLE, so it was obtained indirectly by multiplying mean photosynthetically available radiation (PAR) at surface by the exponential of the product between mean diffuse attenuation (DA) and minimum bathymetry (BAT), following the equation $PAR \times \exp(DA \times BAT)$.

Unfortunately, the variables required to calculate the mean light at the seabed are not available for projected scenarios. Therefore, the same layer corresponding to light at the seabed at present conditions was used for future projections, assuming it could remain constant. Preliminary tests revealed that under present conditions, the mean PAR variable has a strong negative correlation with mean cloud cover (r = -0.88), and that mean cloud cover shows minimal differences (mean difference: -0.01667 [-0.01671; -0.016663], 95% CI) between present conditions and the most pessimistic future scenario (SSP5-8.5), suggesting potential temporal consistency in the light variable. All ten variables were cropped to include only the study area, namely the continental shelf, considering that these are the shallowest locations, where sunlight can reach the seabed and enable photosynthesis, which is essential for the survival of the target species in this study. All procedures were performed in the R software environment (R Development Core Team, 2022) using the *terra* package (HIJMANS, 2024).

Species distribution modeling

The modeling in this study was conducted in three stages: (1) development of ecological niche model to capture the environmental conditions favorable for the occurrence of *O.* cf. *ovata* in large scale; (2) generation of the species distribution model, highlighting regions of potential occurrence of the species due to their environmental conditions; and (3) projections of the species' potential distribution under different possible oceanographic conditions resulting from climate change.

Ecological niche modeling was performed using correlative statistical techniques implemented by different types of algorithms. Most algorithms used for model construction require either absence or background data to inform the environmental conditions where the target species is not present. Thus, algorithms can capture the whole set of environmental conditions along the study area and the values that can make the specie thrive or not. Since true absence data is rare, pseudo-absence data is typically generated (Hijmans et al., 2005; Elith et al., 2006). Pseudo-absences and background points (10,000 records) were randomly sampled within the area defined as accessible to the species (i.e., global shallow sea with a minimum depth of less than 200 m), excepting locations with *O*. cf. *ovata* occurrence data. Then, the dataset of occurrence and pseudo-absence/background points was partitioned, at each replication, using the bootstrap method (i.e., with reposition of sampled data), allowing a random fraction of the data to be used for model training and the remaining for model testing.

A total of six different algorithms were employed to model the ecological niche and the potential distribution of *O.* cf. *ovata*, including those built upon envelope models (Bioclim), distance models (Domain), regression-based models (GLM), and machine learning algorithms (Maxent, GLM, and Random Forest). This variety allowed different perspectives to capture the associations between the species' occurrence and the environmental variables. Two replicates per algorithm were generated, totaling 12 niche models, which quantify environmental suitability for the species' occurrence across the study area. The subset of occurrence and pseudo-absence/background data reserved for testing was then used to calculate evaluation metrics, including specificity (absence prediction accuracy), sensitivity (presence prediction accuracy), and, from these, the True Skill Statistics (TSS). Another evaluation metric used was the Area Under the Curve (AUC), which also provides information on the model's ability to correctly distinguish between presences and absences. Subsequently, models with good performance (TSS > 0.5 and AUC > 0.7) were combined using weighted ensemble modeling, with TSS as the weighting parameter. This approach ensures that better-performing models contribute more to the generation of the final ecological niche model. The final ecological niche model was then used to project environmental suitability for the species across the study area under possible future scenarios where climate change is expected to alter oceanographic conditions. From each ensembled niche model (i.e., present conditions and project warmer scenarios), a binary species distribution model was generated using the maximum [specificity + sensitivity] threshold. In this approach, suitability values above the threshold are classified as potential species presence, while values below indicate absence. This provides valuable estimates of the trends in the species’ potential occurrence under the uncertain conditions in the years to come. Ecological niche models and species distribution models for *O.* cf. *ovata* were developed using the R software environment (R Development Core Team, 2022), with the package *sdm* (Naimi and Araújo, 2016).

Analysis of Spatial Patterns, Climatic Trends, and Risk Assessments for Aquaculture

Polygons from the Marine Ecoregions of the World (Spalding et al., 2007) were used to assess the zonal patterns of suitability and potential presence of the species across the different scenarios. These polygons encompass the global costal zones where the study area is included, and they can be used to indicate both the marine provinces and latitudinal zones. For each climate scenario, polygons were used to average the habitat suitability within each province and latitudinal zone, as well as calculate the total area potentially occupied by the target species, allowing us to assess present patterns and projected trends.

Georeferenced data for global marine aquaculture farms (n = 95,422) (Clawson et al., 2022) were used to assess how many farms are located in areas with potential presence of the target species and which marine aquaculture production regions are at higher risk of co-occurring with the target species, both under current conditions and in projected warmer climate scenarios. The marine aquaculture farms are divided into six cultivation categories: bivalve molluscs, salmonidae fish, bluefin tuna, general marine fish, shrimps and prawns, and non-shrimp crustaceans. Together, these categories account for 96% of global fish and invertebrate mariculture production in 2017 (Clawson et al., 2022). Given the spatial clustering of many aquaculture farms, 100 km² plots were created to define the aquaculture sites and assess their potential risk to the presence of the toxic microalga. Using these plots, rather than individual farms, ensures data independence and helps avoid underestimating or overestimating the risk.

Although a farm may not be directly at risk due to the presence of the species in its exact location, the species may still occur in relatively nearby areas. Thus, the greater the area potentially occupied by the species in the surroundings of aquaculture farms, the higher the associated risk to these farms. In regions with a high farm density, this interaction between potential risk and farms concentration increases the potential for impact. To quantify this potential impact, we measured the area with potential species occurrence within 10,000 km² plots and counted the number of farms within each plot. Both variables were normalized, and an impact potential score was created by multiplying these variables. In this way, the potential risk is higher when both the species' potential coverage and the number of farms are high. Given that the number of farms per plot is generally small, but a few plots exhibit extremely high values, a logarithmic transformation (base 10) was applied to this variable to reduce skewness. Furthermore, recognizing that the impact of the interaction between the microalga's potential distribution and the number of farms may not be linear but rather increase more steeply in scenarios of strong interaction, we raised the product of these variables to the power of 0.5. Thus, our impact score was calculated as:

$$(\text{CPsp} \times \log_{10}(\text{NFA}))^{0.5}$$

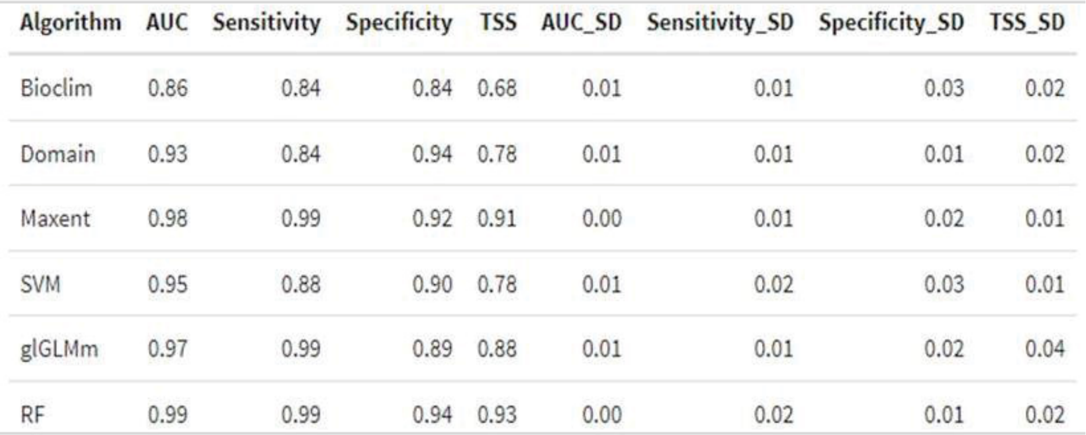
where CPsp represents the species' potential coverage and $\log_{10}$(NFA) is the number of aquaculture farms, both normalized to range between 0 and 1.

RESULTS

Model performance and best environmental predictors

All six algorithms used in our study demonstrated good performance, as evidenced by high specificity (mean ± standard deviation = 0.90 ± 0.04) and sensitivity (0.92 ± 0.07) values. This resulted in high TSS (0.83 ± 0.09) and AUC values (0.95 ± 0.04; Table 1), which indicates good model fit, and that a high proportion of presences and absences were predicted correctly by all the models (values close to 1 indicate good performance for all of these evaluation metrics). Thus, the six algorithms' models were ensembled to generate the final ecological niche model, and consequently, the distribution model for *O.* cf. *ovata*. Among the variables used to build these models, mean light and mean temperature at the bottom were the best predictors of *O.* cf. *ovata* distribution (Pearson-based: 63.8% and 34.2%; AUC-based: 27.7% and 29.6%, respectively), followed by average values of nitrate concentration (19.1% and 12.4%; Tables S1 and S2, Supplementary Material). This result was consistent across both metrics used to estimate the relative importance of the variables, although single most important predictor fluctuated between mean light and mean temperature according to the metric used.

Table 1. Performance of the models that were ensembled to generate the final ecological niche and distribution models for *O.* cf. *ovata*. AUC = Area Under the Curve; TSS = True Skill Statistic; SD = Standard Deviation.



Algorithm	AUC	Sensitivity	Specificity	TSS	AUC_SD	Sensitivity_SD	Specificity_SD	TSS_SD
Bioclim	0.86	0.84	0.84	0.68	0.01	0.01	0.03	0.02
Domain	0.93	0.84	0.94	0.78	0.01	0.01	0.01	0.02
Maxent	0.98	0.99	0.92	0.91	0.00	0.01	0.02	0.01
SVM	0.95	0.88	0.90	0.78	0.01	0.02	0.03	0.01
glGLMm	0.97	0.99	0.89	0.88	0.01	0.01	0.02	0.04
RF	0.99	0.99	0.94	0.93	0.00	0.02	0.01	0.02

Modeled distribution and predicted spatial changes

The current environmental suitability for *O.* cf. *ovata* in shallow marine waters ranged from 0 to 0.693, with a mean of 0.031 (±0.066). Considering only cells with environmental suitability above 0.11357 – the threshold for potential presence of *O.* cf. *ovata* in the final model – the total area potentially occupied by this species in global coastal waters was estimated in 2,759,632 km². Both environmental suitability values and the area of potential presence are highest in the tropical zone, followed closely by temperate zones, and are minimal or negligible in the polar zones (Figures 1A and 1B).

Under a 2 °C warming scenario, the average value of environmental suitability for *O.* cf. *ovata* presented a slight (3%) increase, attaining a mean value of 0.032 (±0.054). This resulted in a 29% expansion in the total area potentially occupied by this harmful microalga (3,556,094 km²). This expansion is observed across all zones but becomes more pronounced with increasing latitude (Figures 1A and 1B). Whereas the area of potential presence of *O.* cf. *ovata* is projected to expand by 24% in the tropical zone, temperate latitudes are expected to experience a 60% increase. Polar waters, which show no evidence of its presence under current conditions, are projected to support 2970 km² of potentially inhabitable area (Figure 1B; Table S3, Supplementary Material).

Beyond the 2 °C warming scenario, average suitability of *O.* cf. *ovata* begins to decline, attaining mean values of 0.026 (±0.044) under 3 °C, 0.013 (±0.030) under

4 °C, and 0.013 (±0.028) under the >4 °C warming (Figure 1A). Globally, the area potentially occupied by this microalga decreases by 11% to 63% compared to the current potential distribution, covering from 2,445,808 km² under 3 °C warming to 1,018,815 km² under >4 °C warming. However, this reduction varies spatially, and is more pronounced at tropical latitudes. In the temperate zone, the area potentially occupied remains 21% higher than current levels under 3 °C warming, and only drops below these values at more extreme warming scenarios (4 °C warming: -31.4%; >4 °C warming: -49%). In polar waters, areas potentially occupied by *O.* cf. *ovata* do not return to the presently observed zero levels in any warming scenario (Figure 1B; Table S3, Supplementary Material).

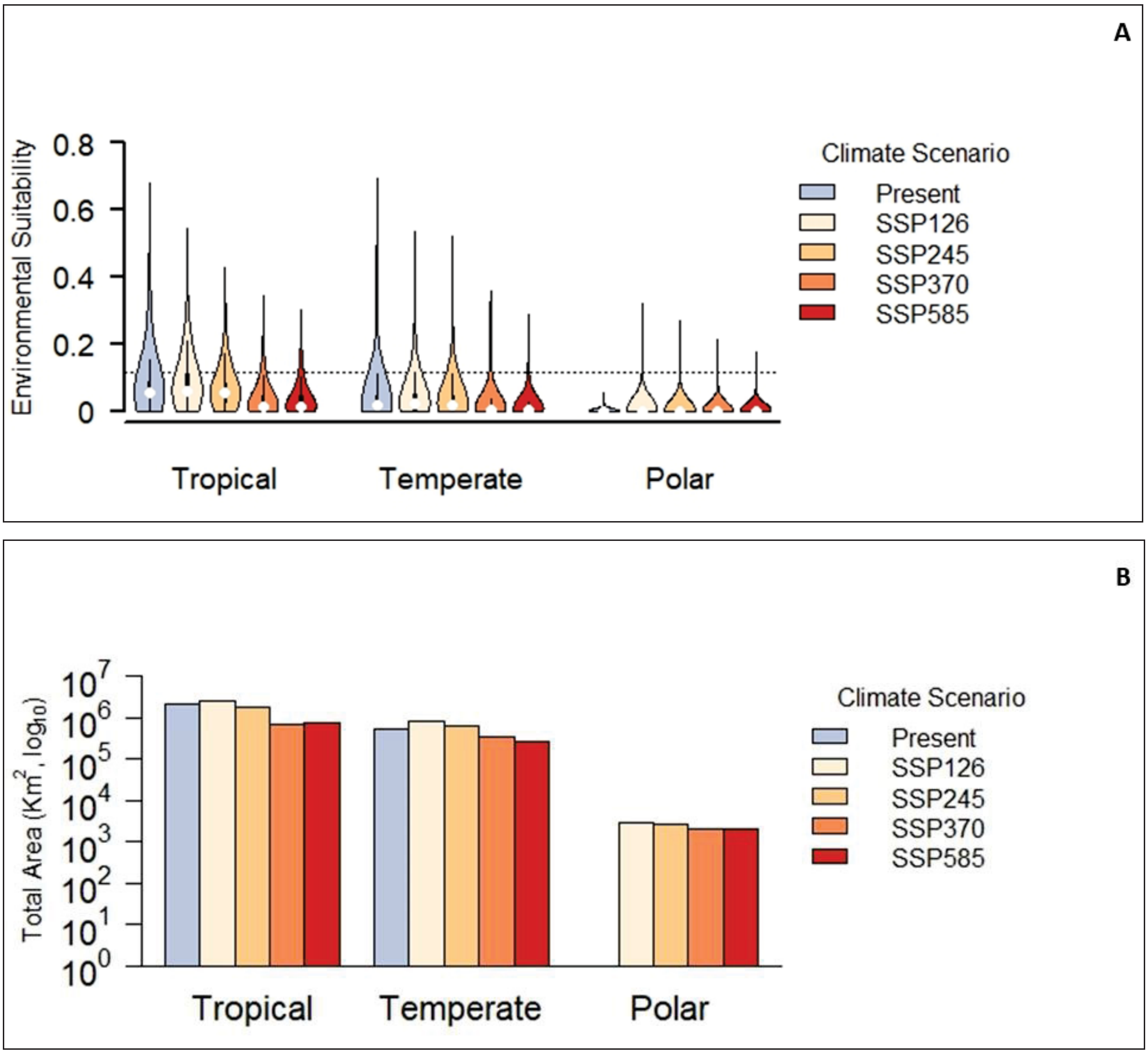


Figure 1. (A) Distribution of environmental suitability values for *O. cf. ovata* in coastal waters across latitudinal zones and climate scenarios. Dashed line = threshold (0.11357) for classification of suitability values as potential presence for *O. cf. ovata*. White circles inside "violin plots" represent median values, while vertical lines represent the interquartile range, indicating the central dispersion of the data. Wider sections = higher density of values. (B) Total area with potential presence of *O.* cf. *ovata* across latitudinal zones and climate scenarios.

At a finer scale and under current conditions, the “Northeast Australian Shelf” is the marine province with the highest proportion of areas where *O.* cf. *ovata* may potentially be present (43.4%), followed by the “Red Sea and Gulf of Aden” province (10.8%; Figure S1, Supplementary Material). However, the presence of this species is expected to shift significantly across marine provinces under warmer climate scenarios. Under a 2 °C warmer climate, 47% of the marine provinces are expected to experience a 0–50% increase in the area with potential presence of *O.* cf. *ovata*, with some marine provinces (30%) experiencing even more remarkable increases (up to 1219% in the “Cold Temperate Northeast Pacific” province). Under 3 °C warming, however, provinces generally exhibit decreased proportions of this area, although a few provinces like the “Bay of Bengal” (+981%) are still projected to experience substantial increases. At 4 °C and >4 °C warming scenarios, most (61% and 72%, respectively) provinces are projected to experience reductions of 50% to 100% compared to the area estimated in current conditions, with only a minority of them (<20%) showing slight increases (Figures 2 and 3). The largest decreases are projected in “Amsterdam-St. Paul” (-100%, under 2 °C warming) and “Magellanic” provinces (-100%, under 4 °C and >4 °C warming scenarios). At this scale, it becomes evident the greatest increases in both temperate and polar zones located in the Northern Hemisphere, whereas several provinces in the Southern Hemisphere, such as the “Continental High Antarctic”, “Scotia Sea”, “Subantarctic Islands”, and “Subantarctic New Zealand”, show no signal of *O.* cf. *ovata* presence under any scenario analyzed (Figure 2). Additionally, although a reduced area is expected in tropical waters (Figure 1B), it can be noted that some tropical provinces, such as the “North Brazil Shelf” and “Bay of Bengal”, are still projected to experience an increase in the presence of this harmful species under all warming scenarios (Figure 2).

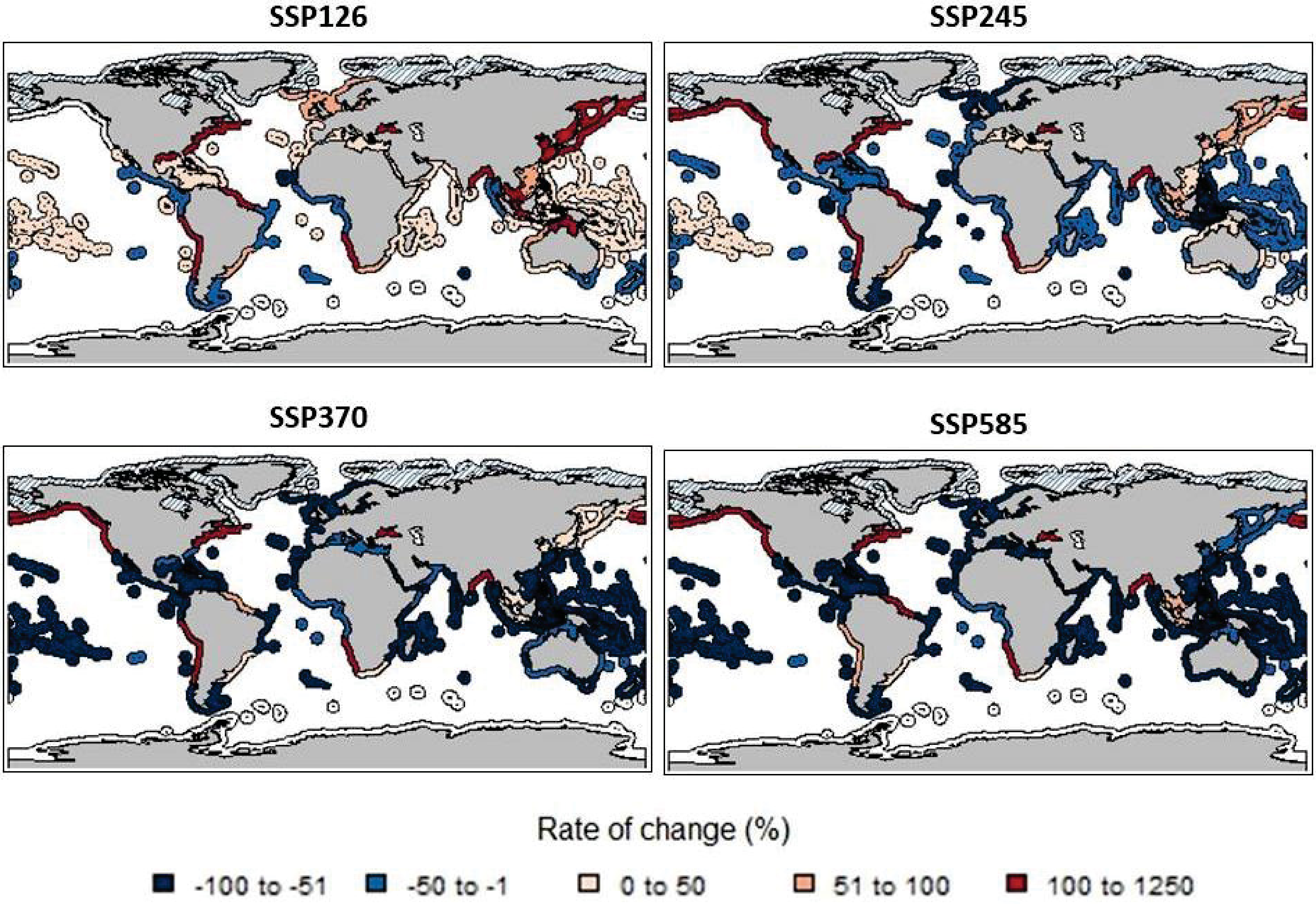


Figure 2. Percent rate of change in total area with potential *O.* cf. *ovata* presence across global marine provinces under each warming climate scenario. Hatched areas denote polar provinces where potential presence areas are currently zero, and thus the percent changes could not be calculated. Uncolored areas denote provinces where potential presence is and remains zero. Note that the provinces surrounding the Antarctic continent are uncolored because they lack potential presence of *O.* cf. *ovata* in any scenario.

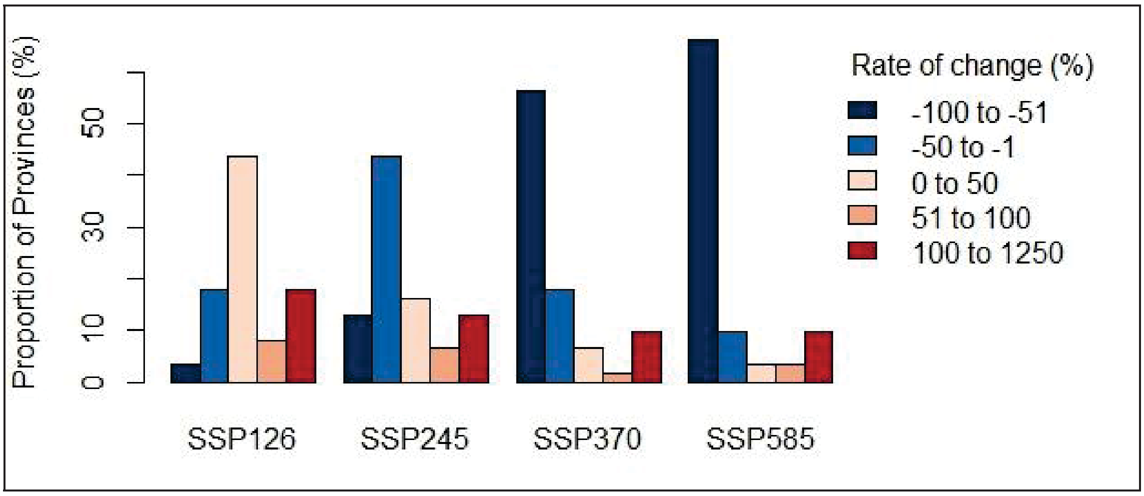


Figure 3. Proportions of global marine provinces (n = 62) experiencing different percent rates of change in the total area with potential occurrence of *O*. cf. *ovata* under each warming climate scenario.

Potential presence of O. cf. ovata *in marine aquaculture farming areas*

The analyzed marine aquaculture farms grow a wide range of organisms: bluefin tuna (0.2%), salmonids (4.1%), general marine fish (6.2%), non-shrimp crustaceans (1.3%), shrimps and prawns (16.3%), and – predominantly – unfed or algal-fed bivalve mollusks (72.1%).

Currently, 57% of the 100 km² marine plots containing one or more aquaculture farms are potentially subjected to the presence of *O.* cf. *ovata*, encompassing almost half (47%) of all analyzed farming areas. The proportion of plots with aquaculture farms at risk for the *O.* cf. *ovata* occurrence is projected to decrease as global temperatures rise, reaching 51%, 38%, 23%, and 20% of the plots under warming scenarios of 2 °C, 3 °C, 4 °C, and >4 °C, respectively. Most plots projected to become potentially “free” of the toxic microalga presence are located in the Northern Hemisphere (Figure 4A), largely because this region already contains the highest number of plots at risk. Even with up to 400 plots per 5° latitude expected to become less vulnerable to *O.* cf. *ovata* worldwide under extreme warming scenarios (>4 °C warming), the proportion of plots under potential risk remains higher in the Northern Hemisphere, particularly at temperate mid-latitudes (Figure S2, Supplementary Material).

At the 10,000 km² scale, there is no significant trend of change in the number of plots with potential *O. cf. ovata* presence in the Southern Hemisphere, except at latitudes near 45ºS, where the trend shows a decline. In the Northern Hemisphere, however, milder warming scenarios tend to increase the number of plots with potential presence of the dinoflagellate, especially in temperate latitudes, with the most notable increase around 45ºN. Only in climate warming scenarios ≥ 4ºC there is a significant declining trend in the number of plots with potential presence near the equator and up to tropical latitudes. At higher latitudes (>40ºN, approximately), even scenarios of greater warming tend to increase the number of plots with potential presence of *O*. cf. *ovata* (Figure 4B). As a result, the vulnerability of marine plots in tropical and temperate latitudes of the Northern Hemisphere remains consistently high across all the considered climate scenarios (Figure S3, Supplementary Material).

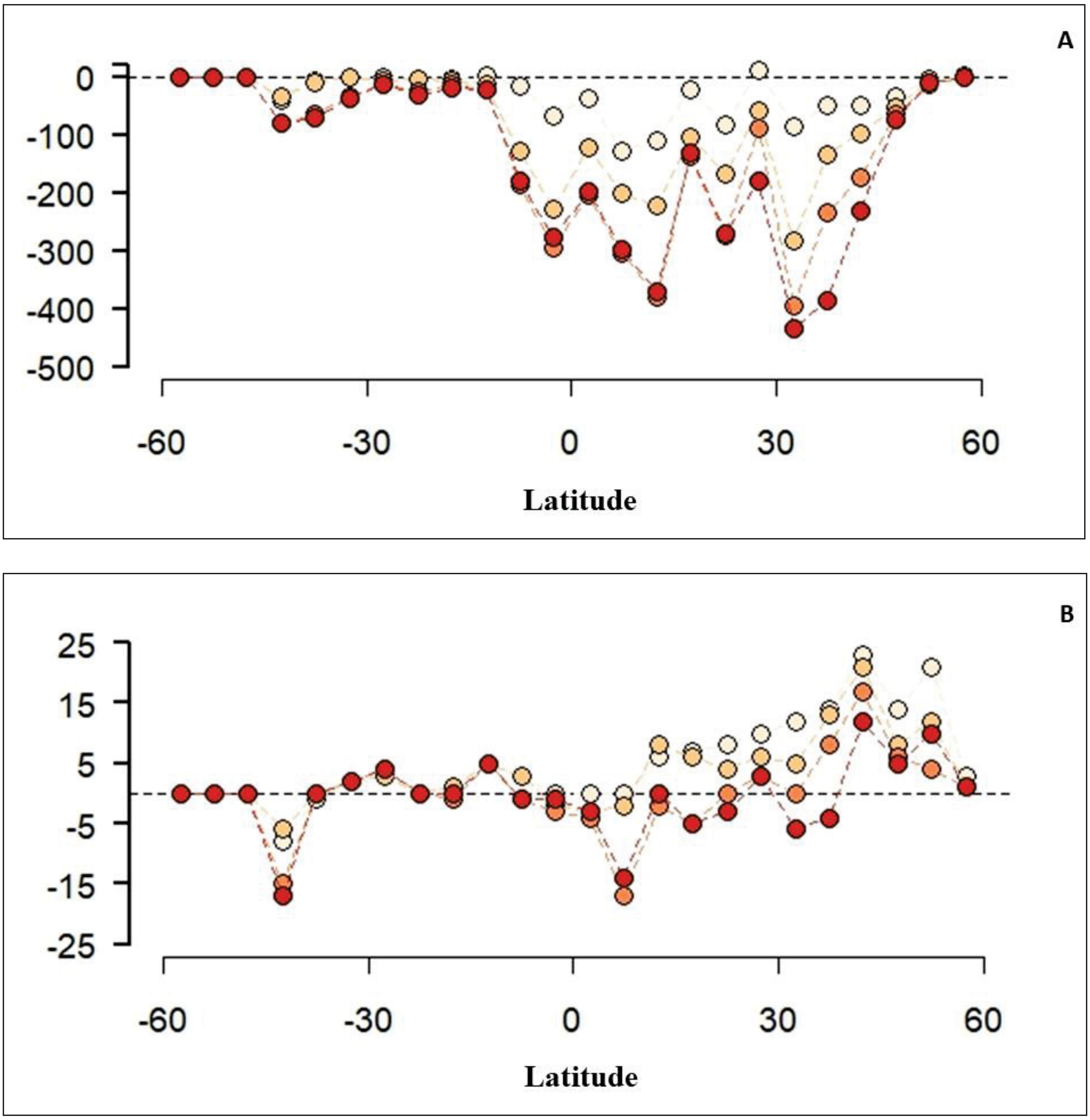


Figure 4. Expected changes in the number of plots (A: 100 km²; B: 10,000 km²) containing one or more aquaculture farms with the potential presence of *O.* cf. *ovata* across latitudes and climate warming scenarios (darker dots = warmer scenario, from SSP1-2.6 to SSP5-8.5). Negative latitude values denote Southern Hemisphere locations.

Important marine aquaculture regions and the potential presence of O. *cf.* ovata

Considering the 100 km² plots with one or more marine aquaculture farms, globally important marine aquaculture regions vary in their risk for the potential presence of *O.* cf. *ovata* due to their specific environmental characteristics. Currently, regions such as Setúbal, Algarve, and the Estuary of Sado River (Portugal), the Ebro Delta and Rías Baixas (Spain), Provence-Alpes-Côte d'Azur, Normandy, and Brittany (France), Hauraki Gulf, Tasman Bay, and Marlborough Sounds (New Zealand), Seto

Inland Sea (Japan), and the coasts of São Paulo, Paraná, and Santa Catarina (Brazil) have all or nearly all of their plots prone to *O*. cf. *ovata* occurrence. Under a warmer climate, some of these regions could become largely or entirely uninhabitable for this microalga. For instance, Pays de la Loire (France) lose suitability under a 2 °C warming scenario, followed by Normandy and Brittany (France) at 3 °C, and regions such as Funka Bay (Japan), Tasman Bay and Marlborough Sounds (New Zealand), and the northern coast of Santa Catarina (Brazil) starting at 4 °C warming and beyond (Figures S4 A-Z, Supplementary Material). Conversely, aquaculture regions like Shandong, the Pearl River Delta, and the Yangtze River Delta (China), British Columbia (Canada), and Lake Saroma (Japan) have their plots, or the majority of them, without the potential presence of *O.* cf. *ovata* (Figures S4: A-Z, Supplementary Material). Although, among these, only British Columbia and Lake Saroma are projected to remain free of the potential presence of this toxic microalga under warming scenarios. Regions such as Shandong and the deltas of the Pearl and Yangtze Rivers (China), in contrast, exhibit increasing risk for the potential presence of *O.* cf. *ovata* under warmer scenarios (Figures S4: A-Z, Supplementary Material).

Different from the analysis at 100 km² plots, when we focused only in the potential presence or absence of the toxic microalga, at the 10,000 km² scale we assessed the Potential Impact Score (PIS). This index considers the number of farms and the proportion of the area with the potential presence of *O*. cf. *ovata*. Currently, PIS values show great heterogeneity throughout the study area. No plot are under high or very high risk, with only moderate risk levels being reached (Figure 5). Moderate-risk plots (9% of total plots globally) are particularly concentrated in the Indo-Pacific region, centered in the Coral Triangle (Indonesia, Malaysia, and the Philippines), as well as in South and Southeast Asia, the Mediterranean Sea, the Red Sea, the Persian Gulf, Eastern and Southwestern USA, Central America, and northwestern South America. New Zealand also emerges as a hotspot for moderate-risk plots. Low-risk plots (53% of the total plots, globally) are specially distributed throughout the Atlantic coast of European countries, the Northern and Southeastern Australia, the whole Brazilian and South African coasts. The Pacific coast of South America is almost entirely characterized by low- and no-risk plots, especially south from the Equator. Similarly, low- and no-risk plots dominate the southern portion of the African continent. Furthermore, only "no-risk" plots are observed along the

Atlantic and Pacific coasts of northern Canada, as well as along the shores of northern European countries.

In a 2 °C warmer climate scenario, some plots are expected to transition from low risk to moderate risk in Eastern Asia, according to the PIS values. A similar shift may occur in part of the Brazilian coast. Thus, moderate risk plots reaches 14% of the total globally. On the Pacific coast of South America, numerous plots are projected to move from "no risk" to low risk, a trend also expected along the northern Canadian coastline, particularly on its Atlantic shore and in parts of its Pacific coast, and the northwestern USA coast. Under a 3°C warmer scenario, the most noticeable change involves plots transitioning from moderate risk to low risk globally, thus moderate risk plots falls to only 3% of the total globally. When facing a 4°C warmer climate, moderate-risk plots become increasingly scarce, reaching 1.3%, with the Mediterranean Sea emerging as the global hotspot in terms of PIS for *O.* cf. *ovata*. Under an even warmer scenario, it is projected that moderate-risk plots (0.3% globally) will persist only in Southeast Asia, while the rest of the world will predominantly experience low-risk plots, with no-risk plots mostly restricted to higher latitudes (Figure 5).

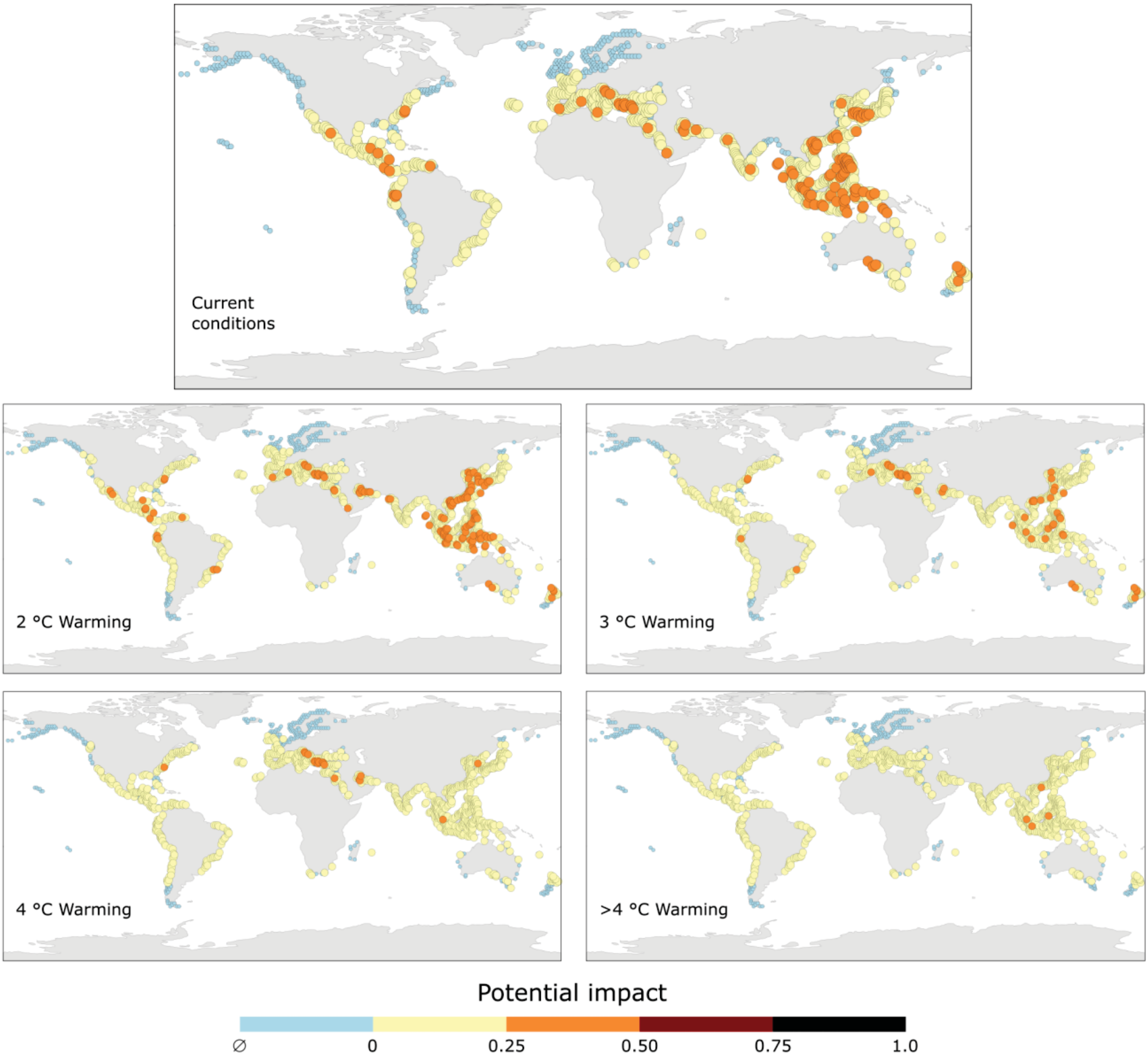


Figure 5: Potential Impact Score for *Ostreopsis* cf. *ovata* occurrence throughout 10,000 km² plots with aquaculture farms under different climate scenarios.

DISCUSSION

The modeled distribution of Ostreopsis cf. *ovata*

The niche and species distribution models applied in this study revealed the potential occurrence of the benthic dinoflagellate O*streopsis* cf. *ovata* in global coastal waters. On a finer scale, the models also identified key aquaculture regions at greater risk for the presence of this harmful species. Furthermore, our projections suggest how the species distribution – and the associated risks to aquaculture – are expected to shift under different climate change scenarios. Modeled projections are valuable tools for analyzing future scenarios, providing insights into the expected conditions for a given area over the coming years. These insights contribute to the formulation of management strategies, supporting alternative planning decisions and guiding sustainable development pathways (Lukic et al., 2018; Ehler, Zaucha, & Gee, 2019). In the context of marine environment modelling, decisions derived from projected conditions will significantly influence the use of natural resources (e.g., fishing, aquaculture, tourism and navigation), the redistribution of these uses, and future human well-being. Thus, scenario-based analyses are essential for integrating the impacts of climate change into marine spatial planning (Ehler & Douvere, 2009; Gissi, Fraschetti, & Micheli, 2019; Frazão Santos, 2020) and, ultimately, for urging preventive measures.

The ecological modeling approach has been widely adopted by various researchers studying harmful marine microalgae to better understand the relationship between these organisms and their environment. Considering the substantial diversity of harmful microalgae taxa, their responses to climate change are also expected to be diverse (Ralston & Moore, 2020). Moore et al. (2011) applied statistical model based on air temperature, water temperature, current velocity, wind shear, and tidal variability to predict the occurrence of *Alexandrium catenella* blooms in an estuary in Washington State (WA), USA. Their projections indicated an extended seasonal period of favorable environmental conditions for blooms by the end of the 21st century. Similarly, Jacobs et al. (2015) also used statistical models to map the distribution of *Alexandrium fundyense* in Puget Sound, WA, and projected an extension of two months in the expected bloom season by the end of the century. Together, this would lead to an increased risk of seafood contamination by paralytic shellfish toxins (PST) due to *A. catenella* and *A. fundyense* blooms in the region. Other studies used multiple environmental predictors to model habitat suitability and project the present and future distribution of several species causative of HABs, including the dinoflagellates *Prorocentrum* spp., *Karenia* spp., *Dinophysis acuta*, *Gymnodinium catenatum*, *Alexandrium ostenfeldii*, *A. minutum* and *A. catenella* (Glibert et al., 2014; Townhill et al., 2018; Borges et al., 2022b), as well as the diatoms *Pseudo-nitzschia australis, P. seriata,* and *P. fraudulenta* (Borges et al., 2022a).

Contrary to most HAB species assessed in previous investigation, the present study modelled the environmental niche and large-scale distribution of a benthic species, whose set of habitat conditions would differ from those affecting planktonic microalgae. Indeed, our models indicated mean bottom light intensity as the variable with the highest relative importance in defining the niche and distribution of the microalga *Ostreopsis* cf. *ovata* in coastal waters, followed by mean temperature and mean nitrate concentration. Microalgal growth and population dynamics are directly influenced by abiotic factors such as light intensity, temperature and nutrient availability, being ultimately shaped by direct and indirect biotic interactions (Vila et al., 2001; Totti et al., 2010; Larsson et al., 2019; Grigoriyan et al., 2024). Incident light is of paramount importance for photoautotrophic algae (Metsoviti et al., 2019), as it drives the intensity of photosynthetic activity and may regulate cell development and respiration rates (Masojídek et al., 2013). Light availability varies both latitudinally and seasonally. In the ocean, it is strongly influenced by the local atmospheric conditions, as well as by factors such as depth, water color, and turbidity – the latter ones relatively more relevant for benthic species. In addition, microalgal growth and survival are critically influenced by temperature (Raven & Geider, 1988), which plays a decisive role in important physiological processes such as cell motility, cyst germination, nutrient uptake, and photosynthesis (Beardall & Raven, 2004; Toseland et al., 2013; Wells et al., 2015; Zhang et al., 2022). The optimal temperature range for survival and growth varies according to the algal species (Wells et al., 2020). However, capturing the direct effects of temperature on algal physiology is a challenging task, as it also induces changes in key environmental parameters, such as the physical structure of the water column (i.e., stratification), light penetration, and nutrient availability (Wells et al., 2020). Finally, nutrients are essential resources that regulate the growth, metabolism and, therefore, the abundance and composition of microalgal assemblages (Pezzolesi et al., 2016; Wells et al., 2020; Grigoriyan et al., 2024). Like temperature, the nutrient concentrations required for growth vary significantly among different microalgal species (Grigoriyan et al., 2024).

In contrast to what the present models indicate, a recent study that compiled growth rate data from laboratory-cultivated strains of *O.* cf. *ovata* suggested that both light intensity and photoperiod had only mild effects on cell growth (Grigoriyan et al., 2024). However, the relationship between light intensity and growth rate was widely variable in that compilation, probably because strains were isolated from differentially adapted populations inhabiting different locations and latitudes. Furthermore, the majority of their data (>70%) were derived from studies that tested 12:12 h or 14:10 h (light: dark) photoperiods and light intensities >50 µmol photon m^{-2} s^{-1} – unlikely growth-limiting conditions or near saturation for the species. When considering single-strain/population studies, conversely, light intensity appears to be rather relevant in regulating *O.* cf. *ovata* growth and distribution. For instance, during natural blooms, *O.* cf. *ovata* usually attains the highest cell abundances at shallower depths (e.g., Tibiriçá et al., 2019), where light is more intense and polychromatic. Instead of light, temperature and salinity were the most significant factors influencing *O.* cf. *ovata* growth when analyzing multiple laboratory trials together (Grigoriyan et al., 2024). As opposed to temperature, which was the second most important environmental variable defining *O.* cf. *ovata* distribution in the present study, salinity did not rank among the top three predictors. Indeed, germination of *O*. cf. *ovata* cyst occurs only when water temperature exceeds a certain threshold, and blooms of this species appear to be driven by the optimal combination of temperature and nutrient concentrations (Accoroni & Totti, 2016), the third most relevant variable in the present niche and distribution models. In general, our models are based on the main abiotic factors affecting *O.* cf. *ovata* growth. Partial discrepancies among models, isolated field studies and assembled laboratory cultures suggests that the species' relationship with its environment must occur on a fine scale, but the relative importance of specific environmental variables may shift when the scale of analysis is broadened.

Marine organisms are directly influenced by their environment, and within the marine ecosystem, there are areas that are more suitable for them, creating spatial refuges for certain species (Lima et al., 2016; Smith et al., 2017; Pinsky, Selden & Kitchel, 2020). Conversely, areas where local populations fail to sustain positive growth rates under less suitable conditions may lead to Extirpation episodes (Cahill et al., 2014; Louthan et al., 2015). Moreover, marine species tend to be more sensitive to environmental variations than their terrestrial counterparts, and more prone to colonize new territories (Pinsky, Selden & Kitchel, 2020). Thus, rapid shifts in distribution across large spatial scales are a key mechanism through which marine species can adapt to climate change, as already documented for several organisms (Pinsky, Selden & Kitchel, 2020). Greenhouse gas (GHG) emissions have raised sea surface temperature (SST) by 0.7°C and increased partial pressure of carbon dioxide (pCO_2) since the end of the 19th century, triggering cascading effects on important ocean characteristics and processes, such as pH, primary productivity, water column stratification, and circulation (Hartmann et al., 2013; Rhein et al., 2013). Our models suggest that a 2°C global atmospheric warming scenario is likely to make shallow marine areas, on average, slightly more suitable for the occurrence of *O.* cf. *ovata* than at present. Since our projections assumes constant light incidence at the bottom, we cannot assess its potential influence on the species' distribution under future scenarios. Therefore, the observed results indicate that temperature and nutrient concentrations in these areas will probably approach the species' optimal levels. Consequently, scenarios of decreased overall suitability for *O.* cf. *ovata* are projected to lead to a reduction in the total area with its potential presence in the future.

The dinoflagellate *O.* cf. *ovata* can thrive across a broad temperature range (Carnicer et al., 2016), which is likely a key factor enabling its presence in both tropical and temperate areas (Tanimoto et al., 2013; Carnicer et al., 2016). Laboratory studies confirm that *O.* cf. *ovata* can grow in temperatures ranging from 16°C to 30°C (Graneli et al., 2011; Scalco et al., 2012; Gémin et al., 2021). Additionally, warmer waters favor the growth of *O.* cf. *ovata* along the Japanese coast (Yamaguchi et al., 2012). Accordingly, based on our models' estimates, the total area with potential presence of *Ostreopsis* cf. *ovata* is currently four times larger in tropical latitudes than in temperate zones. In polar latitudes, in turn, the models did not detect any areas with potential presence of the species under current conditions. This aligns with findings by Carnicer et al. (2016), who, through a multi-factorial experiment, reported that *O. cf. ovata* growth is inhibited at 19°C, with maximum growth rates observed at 24°C. Thus, tropical regions currently provide more suitable habitats for this benthic dinoflagellate, likely due to higher solar radiation and warmer waters. Conversely, the colder waters and less illuminated seafloor in coastal polar regions should inhibit the growth of this species. It is no coincidence that the first recorded occurrences of *Ostreopsis* spp. blooms were in tropical waters, with blooms in temperate coasts being only reported more recently, in both southern and northern hemispheres (Rhodes, 2011; Accoroni & Totti, 2016). Furthermore, according to the models, the marine provinces exhibiting the highest proportion of total area with potential presence are situated in tropical latitudes: the “Northeast Australian Shelf” (43.4%) and the “Red Sea and Gulf of Aden” (10.8%) provinces. Even though, provinces within the same latitudinal zones show significant variability in environmental suitability and the proportion of total area with potential presence of *O.* cf. *ovata*. This discrepancy highlights the environmental regional differences throughout the ocean space.

Climate warming scenarios are likely to result in the emergence of more suitable areas with the potential presence of *O* cf. *ovata* in polar latitudes. This suggests that water temperatures in some regions will eventually exceed the species’ lower growth limiting threshold. The poleward expansion in the geographic distribution of marine species is currently estimated at an average rate of 72 km per year, and is significantly faster than what is observed for terrestrial species (Pinsky, Selden & Kitchel, 2020). Another adaptive behavior noted in hundreds of marine species is their shift to greater depths as ocean temperature rises (Poloczanska et al., 2013; Poloczanska et al., 2016; Pinsky, Selden & Kitchel, 2020). However, for the target species of this study, this latter strategy is unfeasible as *O.* cf. *ovata* is a benthic photosynthetic organism, restricted to relatively shallow depths where sunlight penetrates. Potential poleward redistributions are predicted for several toxigenic species, including *D. acuta* and *G. catenatum* in the Northwest European seas (Townhill et al., 2018), *Karenia* spp. in the Baltic Sea (Glibert et al., 2014) and *Pseudo-nitzschia* spp. globally (Borges et al., 2022a), for instance. According to our models, warming scenarios of 2°C and 3°C are expected to lead to the expansion of the species’ distribution boundaries into polar latitudinal zones, without any noticeable contraction of its distribution range in tropical and temperate latitudes. This pattern aligns with observations for marine species in general, where the range contraction for a given species occurs at rates approximately five times slower than the respective range expansion (Poloczanska et al., 2013). Consequently, many species are expanding poleward without a corresponding contraction at the equator, and the proportion of range limits currently expanding is therefore much greater than those contracting (Alarcón-Muñoz et al., 2008; Zeidberg & Robison, 2007).

It is important to emphasize that substrate plays a fundamental role in the ecology of the dinoflagellate *Ostreopsis* cf. *ovata* (Vila et al., 2001; Aligizaki & Nikolaidis, 2006; Barone & Prisinzano, 2006; Totti et al., 2010; Lee et al., 2020). This species is capable of colonizing a wide variety of substrates, exhibiting epiphytic, epilithic, and epizoic lifestyles (Totti et al., 2010). Field studies have reported higher abundances on consolidated substrates, such as rocks and mollusk shells, particularly the former (Totti et al., 2010). This microalga also grows on macrophytes—including rhodophytes, phaeophytes, ulvophytes, and seagrasses (Vila et al., 2001; Aligizaki & Nikolaidis, 2006; Totti et al., 2010), especially on branched-thalli seaweeds (Barone & Prisinzano, 2006; Totti et al., 2010). High abundances have also been observed in association with scleractinian corals (Lee et al., 2020). The type of substrate, together with abiotic factors such as light, temperature, and salinity, influence the distribution of harmful benthic microalgae species (Lee et al., 2020). However, in the present study, it was not possible to incorporate the first variable into the species distribution and niche models. This limitation stems from the current lack of a global georeferenced database on marine substrate types—particularly one that distinguishes at least between consolidated and unconsolidated substrates—which would be essential for generating more spatially refined models and maps.

Implications for marine aquaculture

In 2022, global aquaculture production surpassed that of capture fisheries (FAO, 2024). Since the 1990s, marine aquaculture production has increased nearly fivefold. By 2018, it reached a total of 30.8 million tons live weight. The contribution of marine aquaculture to total aquaculture production rose significantly, from 14% in 2000 to 37% in 2016 (FAO, 2018), becoming an important source of animal protein for feeding the growing global population (Poore & Nemecek, 2018; Tilman & Clark, 2014). By 2018, mollusk production accounted for 17.3 million tons, representing 56.3% of total marine and coastal aquaculture production, while finfish production totaled 7.3 million tons, and crustaceans 5.7 million tons (FAO, 2020). Invertebrate farming (bivalve mollusks, shrimps and prawns, and non-shrimp crustaceans) occupies nearly 90% of the coastal area dedicated to marine aquaculture worldwide. The models developed in this study predict that nearly half of these marine aquaculture sites (100 km² areas) overlap with regions of potential *Ostreopsis* cf. *ovata* presence. Notably, more than 70% of the marine aquaculture areas analyzed focus on cultivating bivalve mollusks, which are known to accumulate phycotoxins more quickly and in higher concentrations than other organisms. Consequently, these areas are more prone to periodic harvesting closure during harmful algal blooms (Bricelj & Shumway, 1998; Farrell et al., 2015; Reizopoulou et al., 2008; Rourke et al., 2021).

The current coastal waters used for aquaculture are distributed across a wide latitudinal range. However, those located in areas with potential *O.* cf. *ovata* presence are primarily concentrated in tropical and subtropical latitudes, followed by temperate latitudes. These regions currently offer the most suitable habitats for the species, primarily due to higher average light intensity, temperature, and nitrate concentrations. According to the modeled projections, as global temperatures rise, the number of aquaculture sites subjected to the potential presence of *O.* cf. *ovata* is expected to decrease mainly in tropical and subtropical zones. In contrast, temperate latitudes tend to show the smallest decreases in the number of aquaculture sites with potential *O*. cf. *ovata* presence, where environmental conditions are expected to experience the least decrease in suitability for the occurrence of this toxic microalga.

Climate change may impact marine aquaculture in various ways, including the loss or reduction of suitable farming areas due to rising sea levels, increased frequency of extreme events, changes in ocean productivity, ocean acidification, and rising surface temperatures (Reid et al., 2019; FAO, 2020; Clawson et al., 2022). In this study, the global trend indicates a reduction in the number of aquaculture areas with potential presence of *O.* cf. *ovata* under warmer climate scenarios, which could alleviate at least this specific risk for the aquaculture sector on a global scale. However, the impacts of climate change on aquaculture are expected to vary across locations, species, and production methods (Soto et al., 2018). Indeed, shifting the analysis from global to smaller scales, the projections indicate a different trend for certain regions, including areas of intense aquaculture production and/or where *Ostreopsis* spp. has negatively affected human and animal health.

In the Mediterranean, the models project that nearly all aquaculture sites in the Ebro Delta region of Catalonia will remain within areas under the potential presence of *O.* cf. *ovata*. That region, along with neighboring coastal areas in Spain and Italy, has historically experienced massive *O*. cf. *ovata* blooms (Brescianini et al., 2006; Ciminiello et al., 2006; Faimali et al., 2012; Casavola et al., 2005; Alvarez et al., 2005; Barroso Garcia et al., 2008; Vila et al., 2008). These events have led to benthic organism mortality and health issues in humans (Faimali et al., 2012). In Italy, for instance, hundreds of individuals who came into contact with marine aerosols during recreational activities required medical care for respiratory symptoms in 2000 (Brescianini et al., 2006; Ciminiello et al., 2006; Faimali et al., 2012). Similar incidents occurred in 2001 in Italy, (Casavola et al., 2005) and in 2004 and 2006 in Spain, affecting more than 200 people in each episode (Alvarez et al., 2005; Barroso Garcia et al., 2008; Vila et al., 2008; Faimali et al., 2012). The mussel *Mytilus galloprovincialis* and the clam *Ruditapes philippinarum* are the two most extensively farmed bivalve mollusk species in the Mediterranean (Tičina, Katavić & Grubišić, 2020). In the Adriatic-Ionian subregion, where mussel, clam and oyster farming has grown significantly in recent years (Tičina, Katavić & Grubišić, 2020), aquaculture areas under potential risk for the presence of *O.* cf. *ovata* are notably concentrated. In North African Mediterranean countries such as Egypt and Israel, where potential risk areas have been also identified, aquaculture serves as the primary source of seafood (Carvalho & Guillen, 2021). Blooms of *Ostreopsis* spp. have also been reported in recent years along the Atlantic coasts of France (Drouet et al., 2021; Chomérat et al., 2022), and the presence of the species has likewise been detected along the Atlantic Iberian Peninsula, spanning the coasts of Portugal and Spain (David et al., 2013), thereby becoming an emerging threat in these regions.

The Asia-Pacific region accounts for approximately 90% of the global marine aquaculture production (Phillips & Pérez-Ramírez, 2017), predominantly concentrated in Chinese, North Korean, and Japanese waters (Botta et al., 2020). The macroregion can be currently considered the main hotspot for the potential impact risk associated with the presence of O. cf. ovata, particularly in its southern, southeastern, and eastern portions. This region, moreover, is expected to remain a risk hotspot under all analyzed warming scenarios. This may compromise food supply and pose a risk to human health in densely populated areas, where seafood serves as an important source of livelihood (Dey & Ahmed, 2005; Suzuki, 2021) and is a significant component of traditional diets (Suzuki, 2021). Indeed, cases of human fatality have been already linked to the consumption of potentially contaminated crabs in the Philippines (Alcala et al., 1988). In New Zealand, where the aquaculture industry is valued at nearly USD 0.5 billion (Rolton et al., 2022), primarily from bivalves (*Perna canaliculus* and *Crassostrea gigas*) and king salmon (*Oncorhynchus tschawytscha*) production, episodes of massive faunal mortality have been associated to *Ostreopsis* blooms (Pearce, Marshall & Hallegraeff, 2000; Shears & Ross, 2009).

In the American continent, the main aquaculture producers face varying risk levels for the potential presence of *O.* cf. *ovata*. In Brazil, despite the frequent *O.* cf. *ovata* blooms (Mafra et al., 2023) including episodes of associated faunal mortality (Ferreira, 2006), the potential impact risk for marine aquaculture is generally low along the Brazilian coastline. Whereas *O.* cf. *ovata* blooms are more frequent in the tropical central and northeastern regions, shellfish farming is concentrated in the subtropical southern Brazilian coast, where 14.2 thousand tonnes of oysters, scallops and mussels were produced in 2018 (IBGE, 2018; Marques et al., 2020; Souto Cavalli et al., 2021). Chile presents a low impact risk, which is a relief for one of the leading exporting countries in the aquaculture sector (Salazar et al., 2018). Finally, Canada produces salmon, other finfish and bivalve mollusks (Neis & Knott, 2019; Ochs et al., 2021), mostly in British Columbia (Pacific) and in the Atlantic provinces of New Brunswick, Newfoundland and Labrador, Nova Scotia, and Prince Edward Island (DFO, 2019; Ochs et al., 2021). Canada is mostly considered a "no risk" region for the potential presence of *O.* cf. *ovata*. In Europe, Norway, which represents another major salmon producer located in temperate and polar regions (Espinasse et al., 2023), is also classified as having "no risk" for the potential impact from *O.* cf. *ovata*.

The sustainable use and conservation of oceans and their resources is one of the goals outlined in the United Nations 2030 Agenda for Sustainable Development (United Nations, 2015). Shifts in species distribution caused by a warming climate may disrupt food chains, alter ecological network structures, and cause regions that historically lacked the potential presence of a toxic microalga species to experience significant ecosystem changes. Studies like this, which project the possible impacts of climate change, are invaluable for fostering strategies aimed at supporting the ocean economy and promoting human well-being. Marine spatial plans (MSPs) have become increasingly prominent globally, and he trend indicates further expansion of these plans in the coming years, particularly in countries in Africa and South America (Frazão Santos et al., 2020). Countries whose marine and estuarine aquaculture production are heavily focused on export markets will require assistance in implementing monitoring programs for harmful algal blooms (HABs) and other water quality parameters to ensure the safety of aquaculture products. Evaluating the potential impacts of activities such as marine aquaculture is fundamental to ensuring access to human nutrition. Nevertheless, few MSPs currently incorporate climate change-related issues and the necessary adaptation and mitigation actions (Gissi, Fraschetti & Micheli, 2019; Rilov et al., 2020). To address the risks associated with HABs caused by toxic marine microalgae, some countries have implemented seafood toxin monitoring programs for decades (e.g., Japan, the USA, Canada, New Zealand, the United Kingdom, and parts of the European Union). However, many other regions lack official protective measures, leaving seafood consumers unprotected. In Brazil, for instance, official monitoring programs for toxins and harmful algal blooms are currently limited to the state of Santa Catarina and parts of São Paulo, Rio Grande do Norte and Paraná (Mafra et al., 2023b). Thus, there is a pressing need to expand monitoring programs and develop mitigation and prevention strategies to address the harmful effects of toxic microalgae such as *O.* cf. *ovata*, whose occurrence is expected to increase in specific locations under warmer climate scenarios.

CONCLUSION

The large-scale spatial distribution of the toxigenic marine microalga *O.* cf. *ovata* was modeled satisfactorily in this study, using predictors such as average light at the bottom, temperature, and nitrate concentration. Tropical zones provide more suitable habitats for *O.* cf. *ovata*, resulting in a larger area where the species is potentially present. Polar latitudes, on the other hand, lack the minimum environmental conditions at present for the species' occurrence.

Currently, most marine aquaculture production sites are located within areas of potential *O.* cf. *ovata* presence, encompassing nearly half of all aquaculture farms. Regions of global importance for marine aquaculture production vary widely concerning their potential presence of *O.* cf. *ovata* in aquaculture sites. Some of them exhibit all or nearly all sites with potential microalga presence, while others are potentially free from it. The Potential Impact Score (PIS), which accounts for the number of farms and the proportion of area with potential presence within an aquaculture site, reveals that the risk levels are heterogeneously distributed among aquaculture sites. The highest observed PIS values fall within the moderate-risk class. Areas with relatively higher PIS values are located in southern, southeastern, and eastern Asia and in the Mediterranean Sea. Most aquaculture sites worldwide exhibit low potential risk, such as those situated along the subtropical Brazilian and South African coasts. In higher latitudes, no-risk sites predominate.

In the future, a 2°C warmer climate is expected to slightly increase the global average suitability for *O.* cf. *ovata*. This will be likely sufficient to expand its potential presence area, especially in temperate regions, and to allow the species to reach polar latitudes. Thus, some aquaculture sites are expected to shift from “low-risk” to “moderate-risk” of *O.* cf. *ovata* presence, increasing the global proportion of areas classified as such. Additionally, many sites are projected to transition from “no-risk” to “low-risk”. However, warming scenarios exceeding 3°C are projected to make oceanographic conditions progressively less favorable for the species compared to the current situation, leading to a general contraction in the species' global distribution. A projected trend indicates that many locations currently used for marine aquaculture will decrease in risk level at that point, moving from moderate-risk to low-risk. In even higher warming scenarios (i.e., 4°C and beyond), most marine provinces are projected to reduce their areas potentially subjected to *O.* cf. *ovata* occurrence by ≥50% compared to today. The proportion of aquaculture sites with potential *O*. cf. *ovata* presence is thus expected to decline progressively under climate warming scenarios. Certain regions are projected to become entirely or nearly free of this toxigenic dinoflagellate, particularly in higher latitudes. Aquaculture sites under “moderate-risk” are expected to remain primarily in Asia.

Therefore, despite the global trend of reduced risk associated with the presence of *O.* cf. *ovata* under more dramatic warming scenarios, marine spatial planning should incorporate strategies at both regional and local levels to address the projected increasing risk in specific locations. Furthermore, in a more optimistic view, a less warm future would lead to larger areas under the potential risk for the harmful effects of *O.* cf. *ovata*. In these regions, taking into consideration the projections from this study, it is essential for marine spatial plans to ensure the provision of food, which is expected to be increasingly demanded in the coming years, supporting the ocean economy and promoting human well-being.

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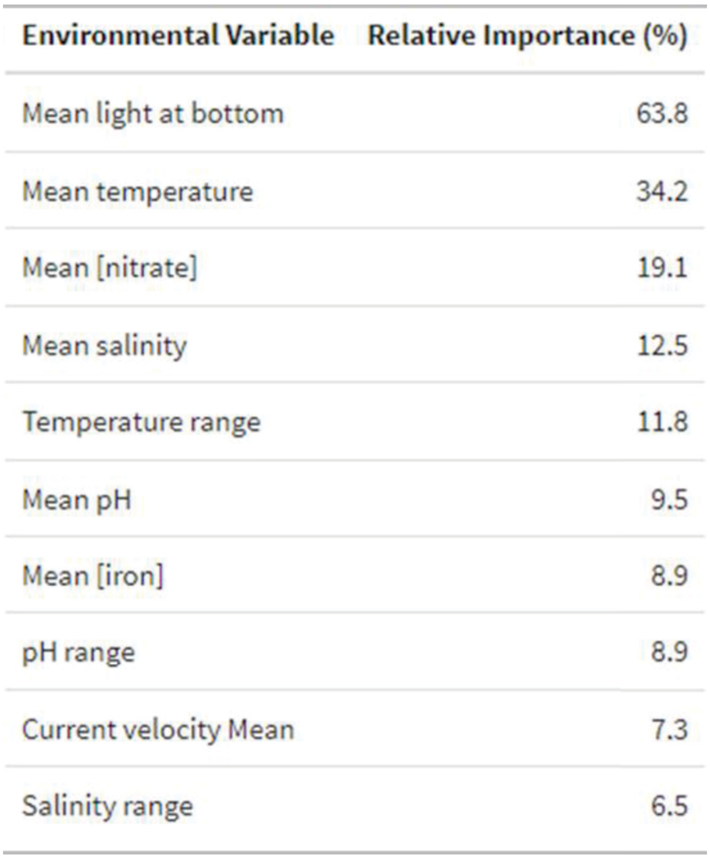
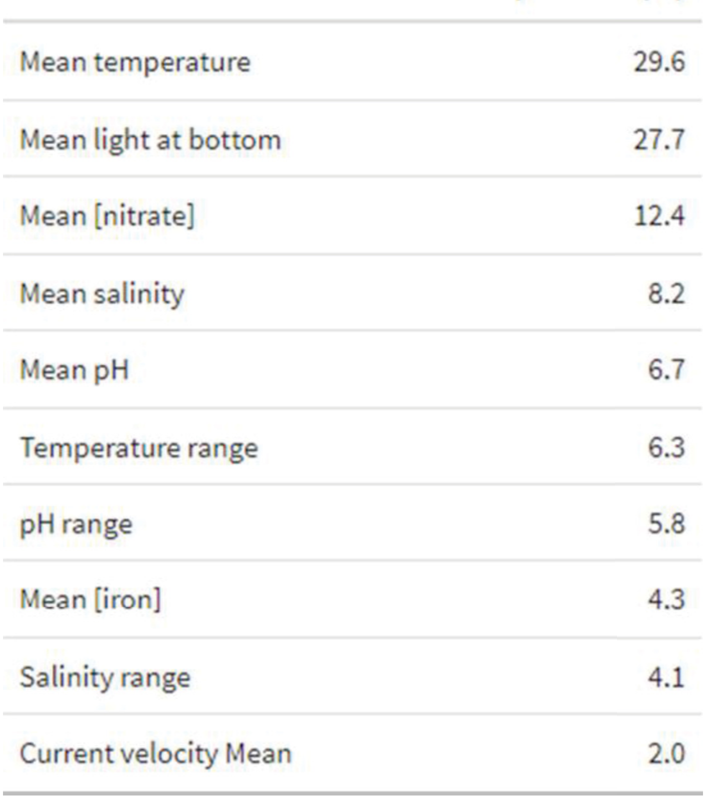
SUPPLEMENTARY MATERIAL

Table S1. Relative variable importance based on Pearson correlation metric combined (averaged) for all models.



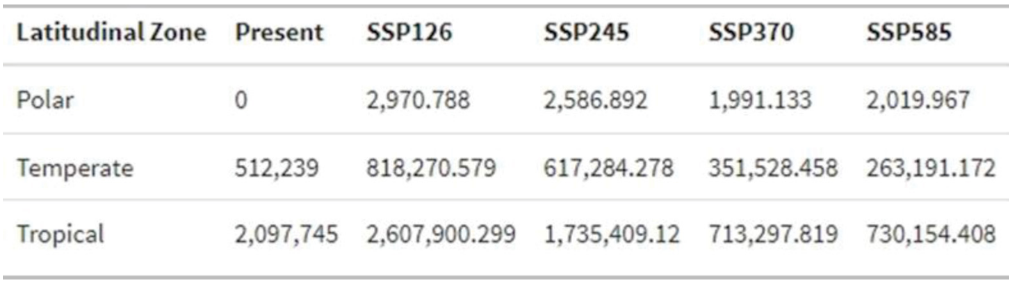
Environmental Variable	Relative Importance (%)
Mean light at bottom	63.8
Mean temperature	34.2
Mean [nitrate]	19.1
Mean salinity	12.5
Temperature range	11.8
Mean pH	9.5
Mean [iron]	8.9
pH range	8.9
Current velocity Mean	7.3
Salinity range	6.5

Table S2. Relative variable importance based on the AUC metric combined (averaged) for all models.

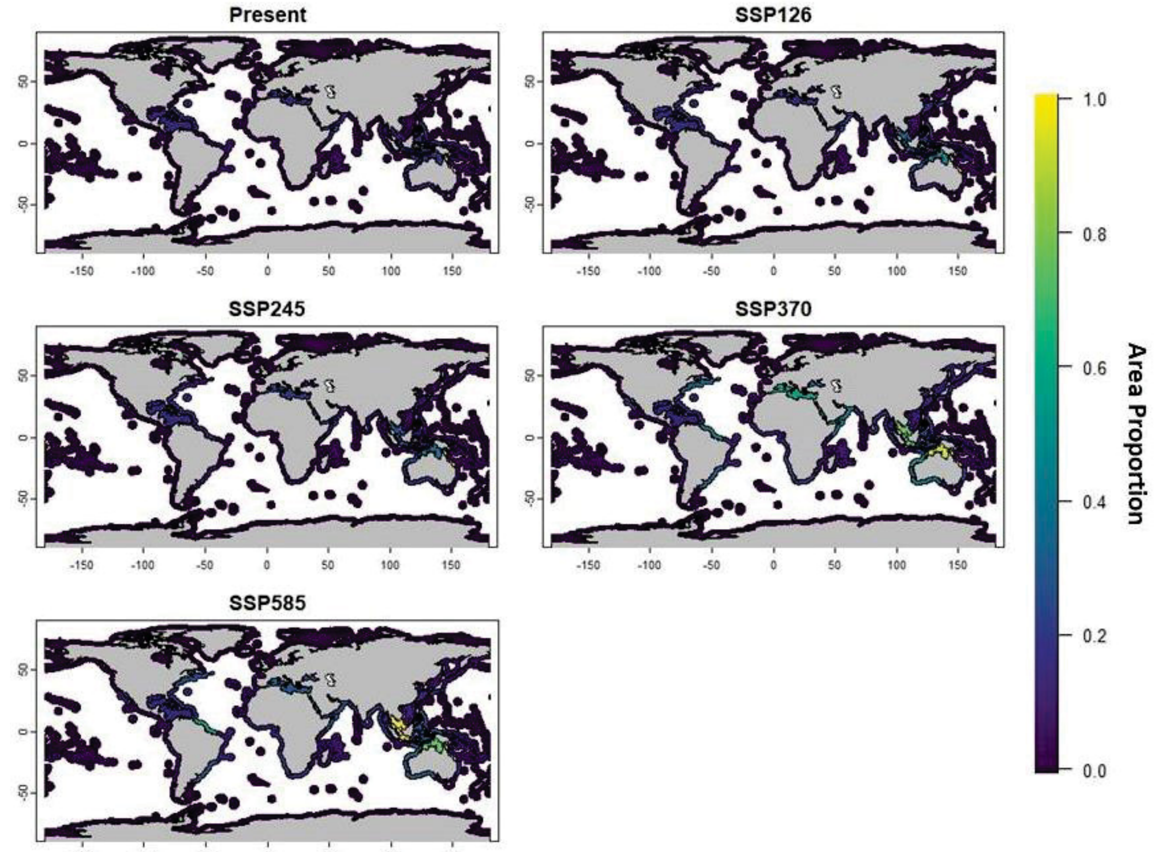


Environmental Variable	Relative Importance (%)
Mean temperature	29.6
Mean light at bottom	27.7
Mean [nitrate]	12.4
Mean salinity	8.2
Mean pH	6.7
Temperature range	6.3
pH range	5.8
Mean [iron]	4.3
Salinity range	4.1
Current velocity Mean	2.0

Table S3. Total area (km^2) with potential presence of *O. cf. ovata* across latitudinal zones and different climate scenarios.



Latitudinal Zone	Present	SSP126	SSP245	SSP370	SSP585
Polar	0	2,970.788	2,586.892	1,991.133	2,019.967
Temperate	512,239	818,270.579	617,284.278	351,528.458	263,191.172
Tropical	2,097,745	2,607,900.299	1,735,409.12	713,297.819	730,154.408



Present

SSP126

SSP245

SSP370

SSP585

Figure S1. Area proportion (normalized for each scenario) of marine provinces with potential presence of *O. cf. ovata* Presence.

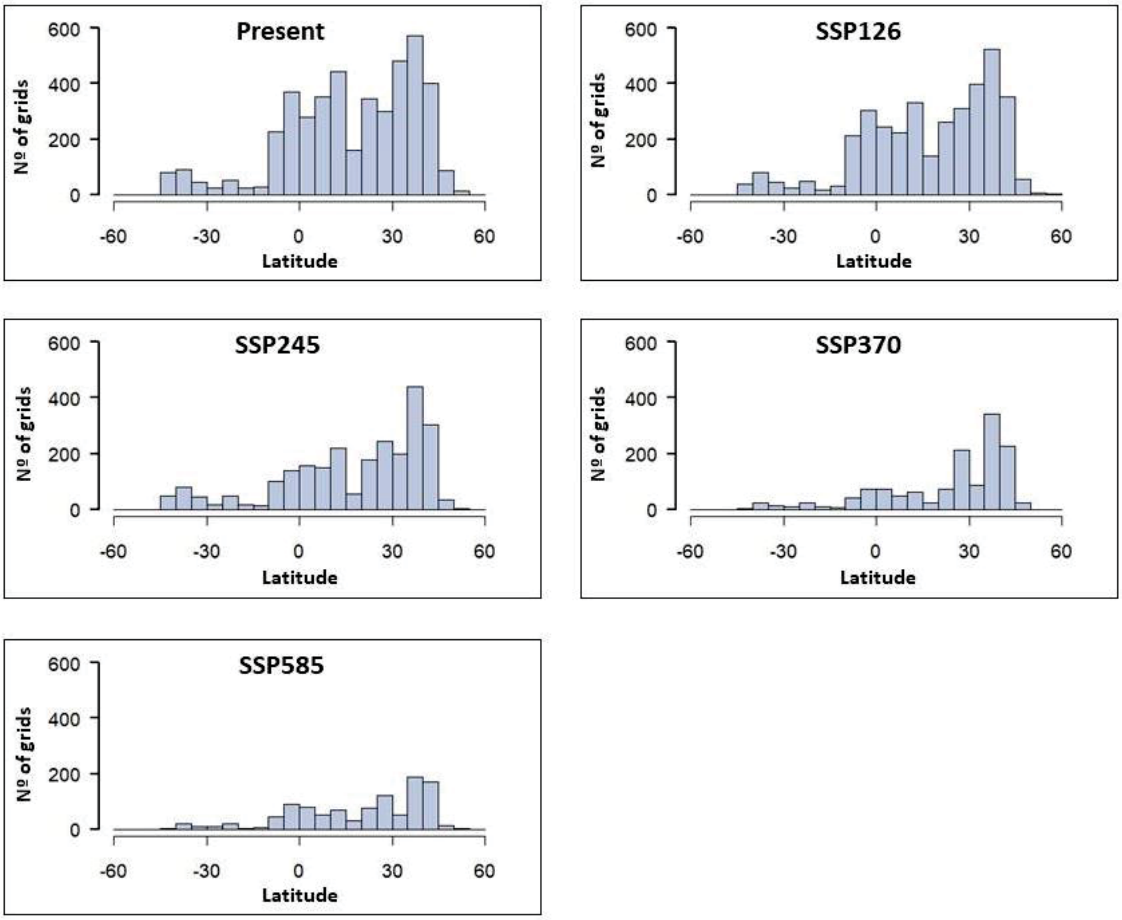


Figure S2. Latitudinal distribution of 100 km² grids containing aquaculture farms subjected to the presence of *O.* cf. *ovata*

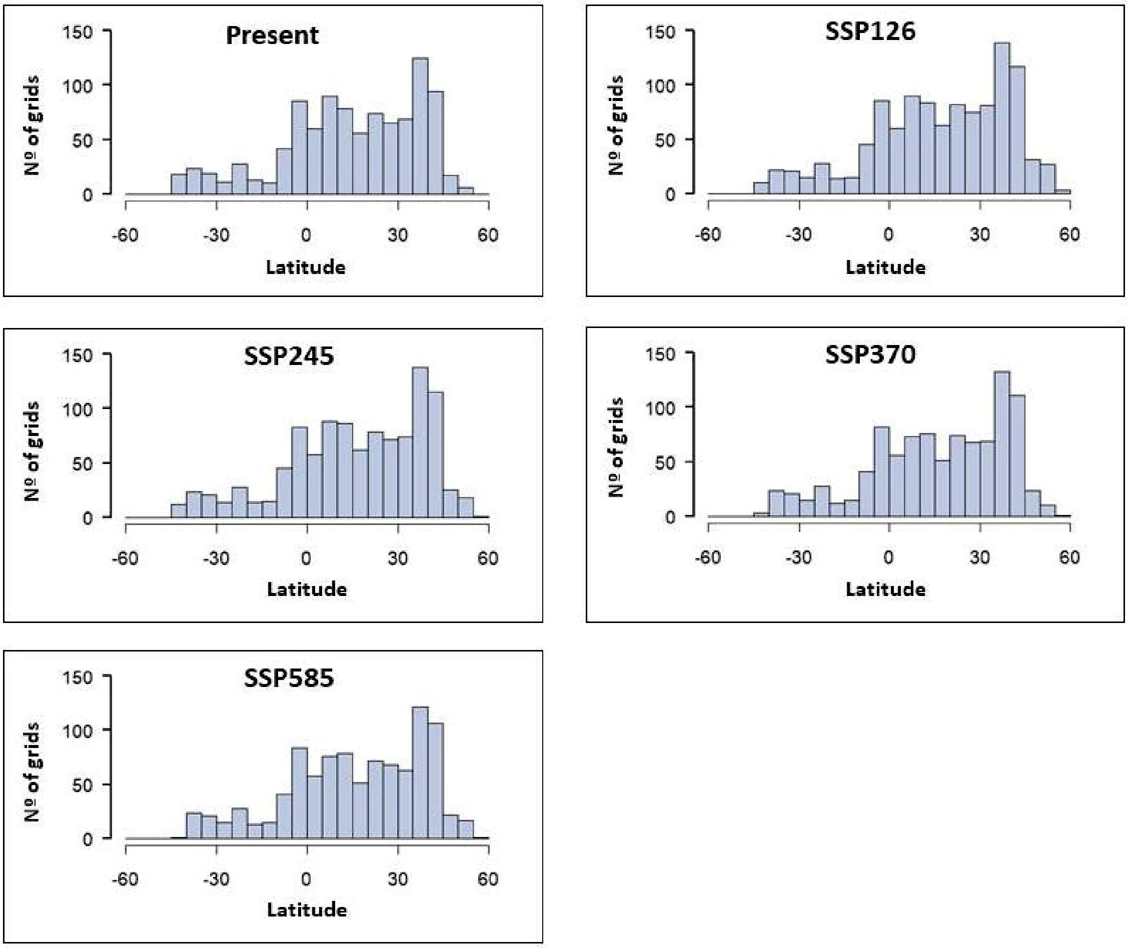
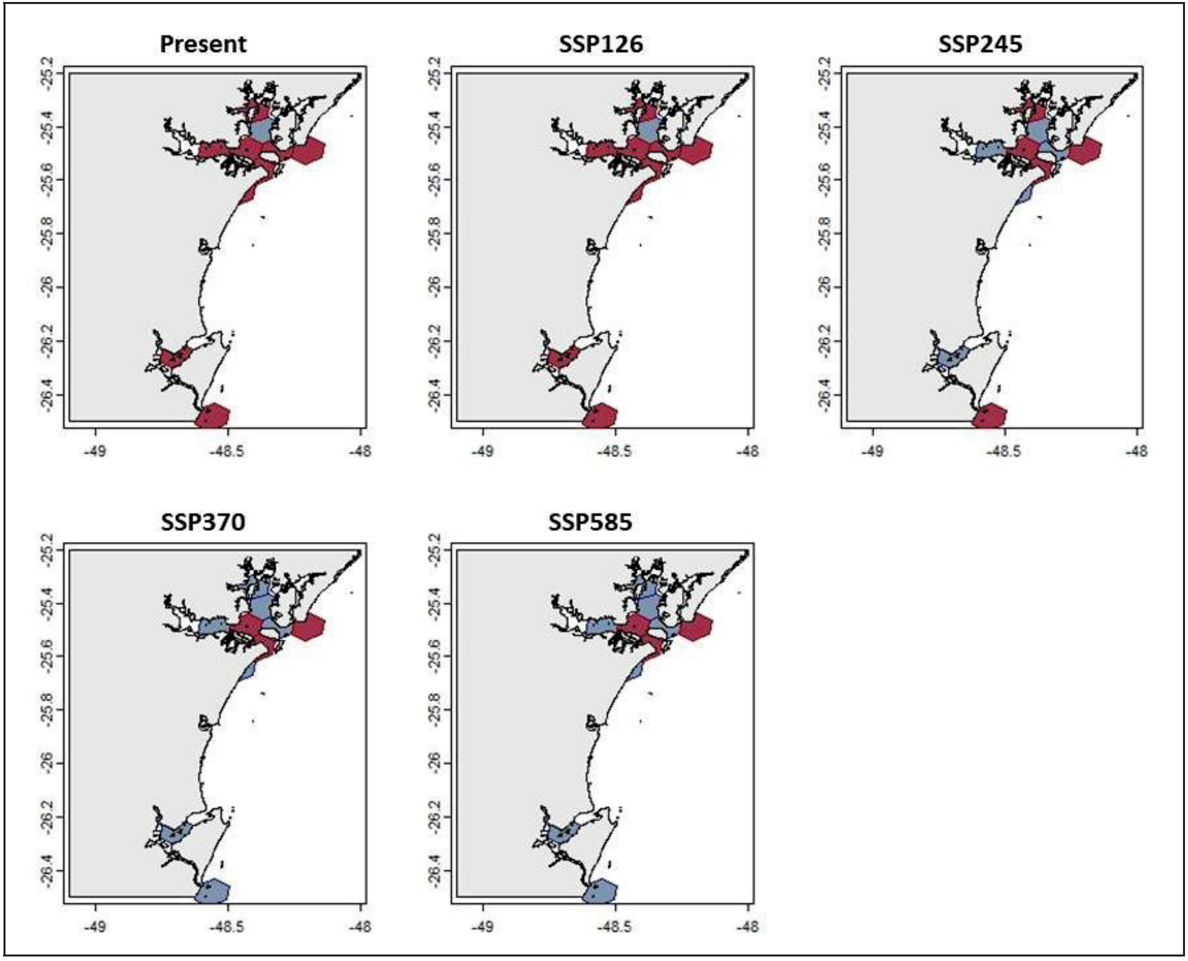


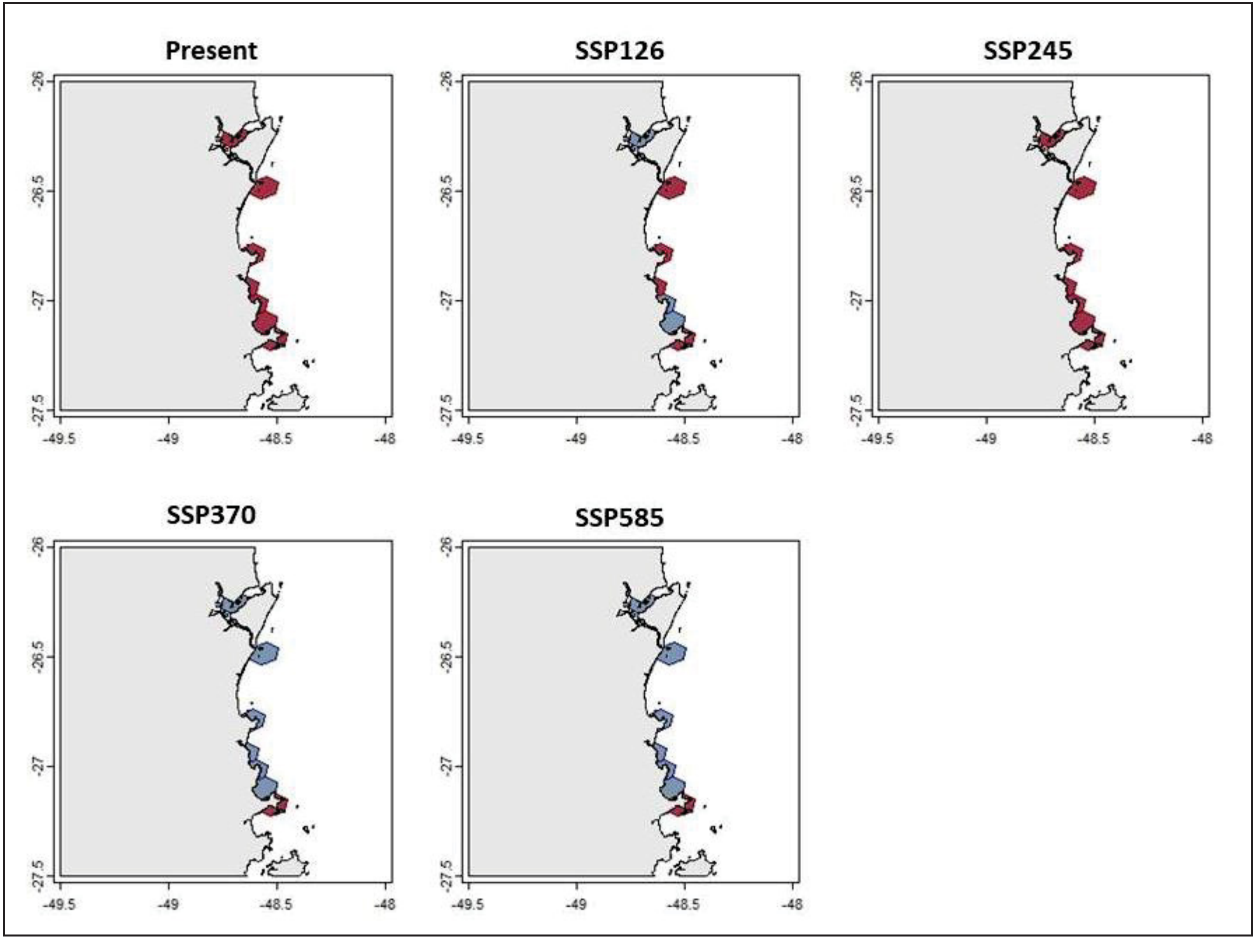
Figure S3. Latitudinal distribution of 10,000 km² grids with mariculture areas and potential presence of *O.* cf. *ovata*.

Figure S4. Maps of marine aquaculture areas (100 km² hexagons) with potential presence (red hexagons) of *O.* cf. *ovata* in some of the major global producing regions: A-D: Brazil – Paraná (A), Northern Santa Catarina (B) Southern Santa Catarina (C), São Paulo (D); E-G: New Zealand – Marlborough Sounds (E), Tasman Bay (F), Hauraki Gulf (G); H-J: Spain – Galicia, Rías Baixas (H), Galicia, Rías Altas (I), Catalonia, Ebro Delta (J); K-N: Portugal – Algarve (K), Ria de Aveiro (L), Estuary of the Sado River (M), Setúbal (N); 0-R: France – Brittany (O), Normandy (P), Pays de la Loire (Q), Provence-Alpes-Côte d'Azur (R) ; S-T : Canada – Northern British Columbia (S), Southern British Columbia (T) ; U-W : Japan – Seto Inland Sea (U), Lake Saroma (V), Funka Bay (W) ; X-Z : China – Yangtze River Delta (X), Pearl River Delta (Y), Shandong (Z). Continent = gray area.

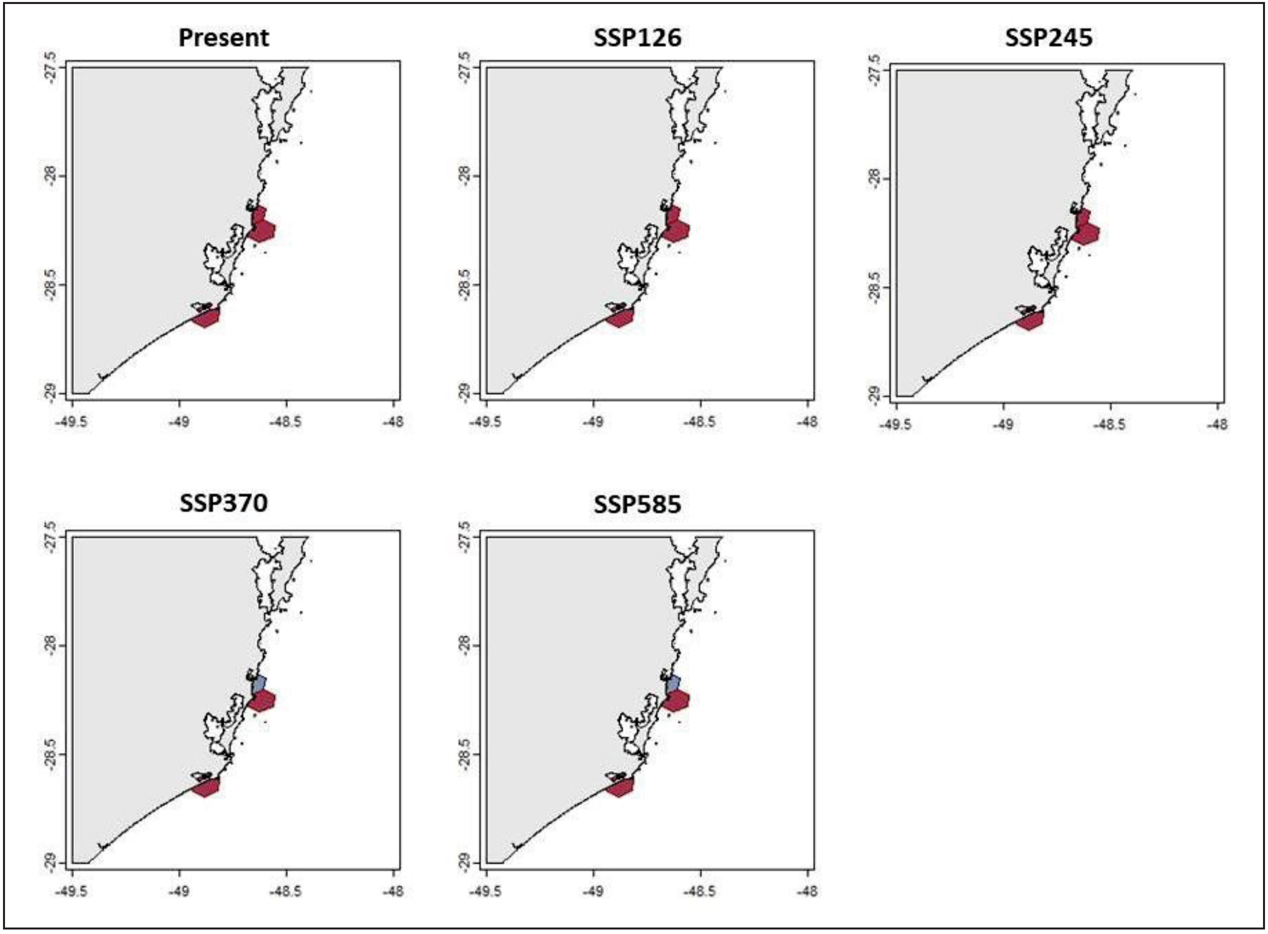
A. Paraná State, Brazil.



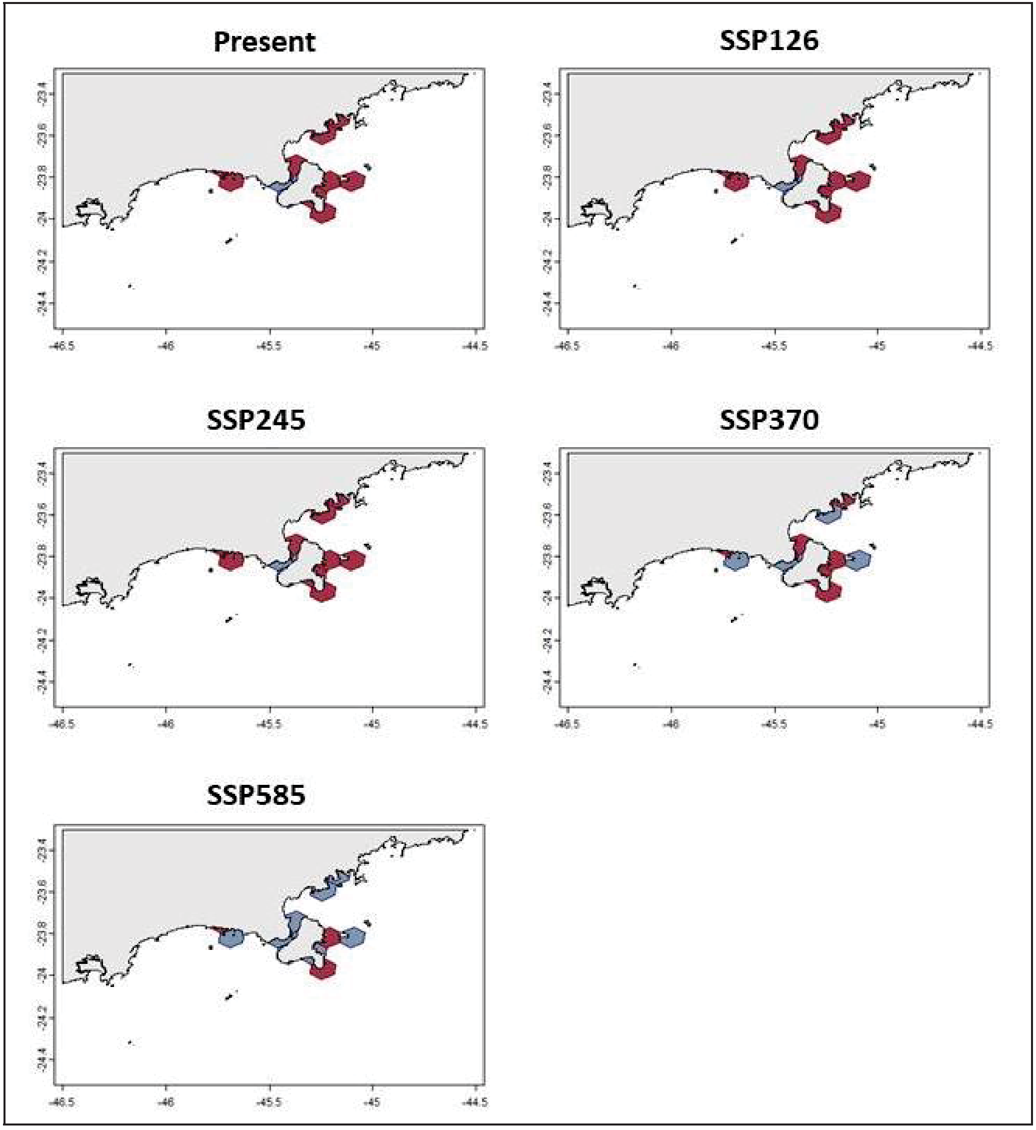
B. Northern Santa Catarina State, Brazil.



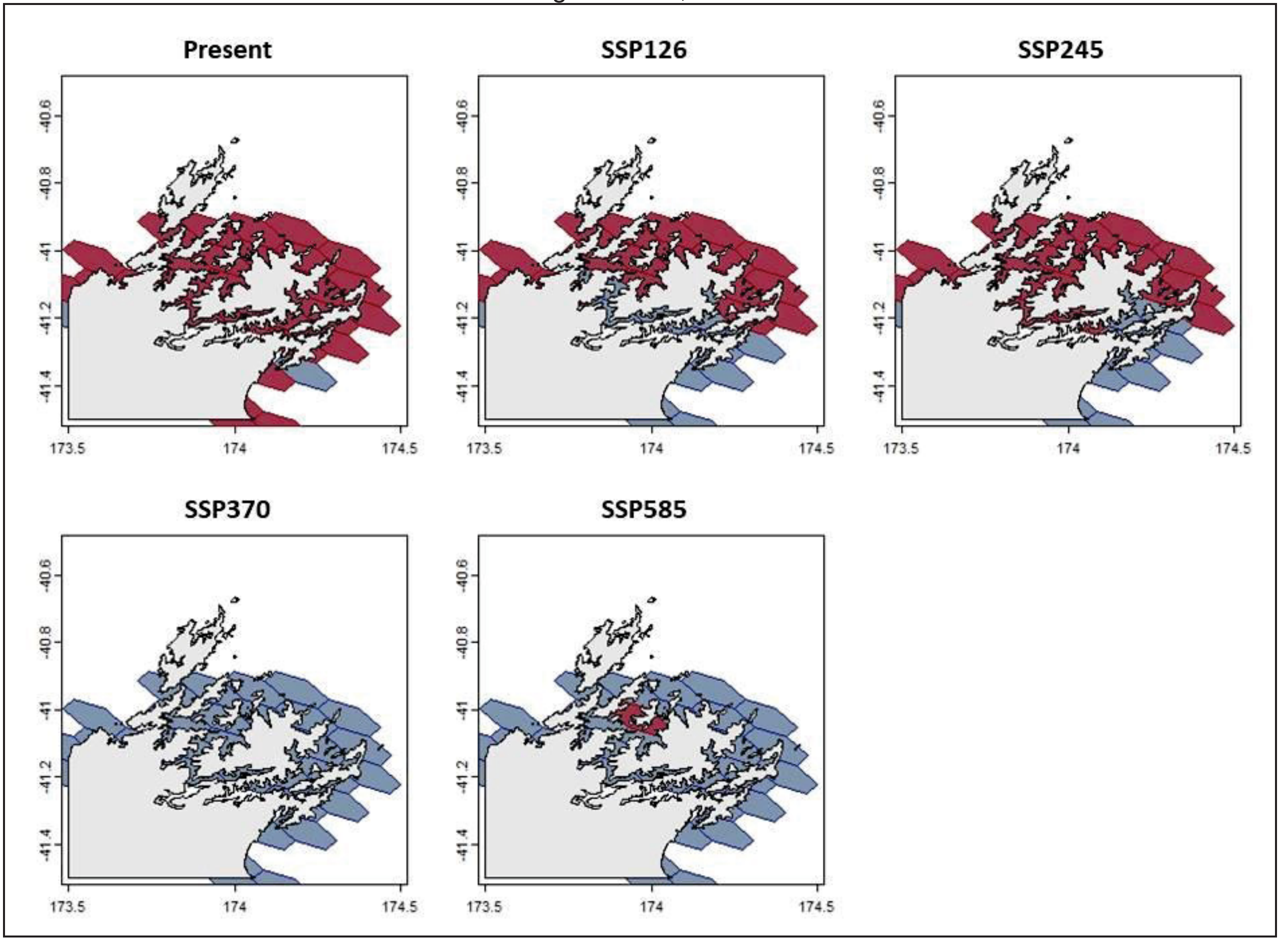
C. Southern Santa Catarina State, Brazil.



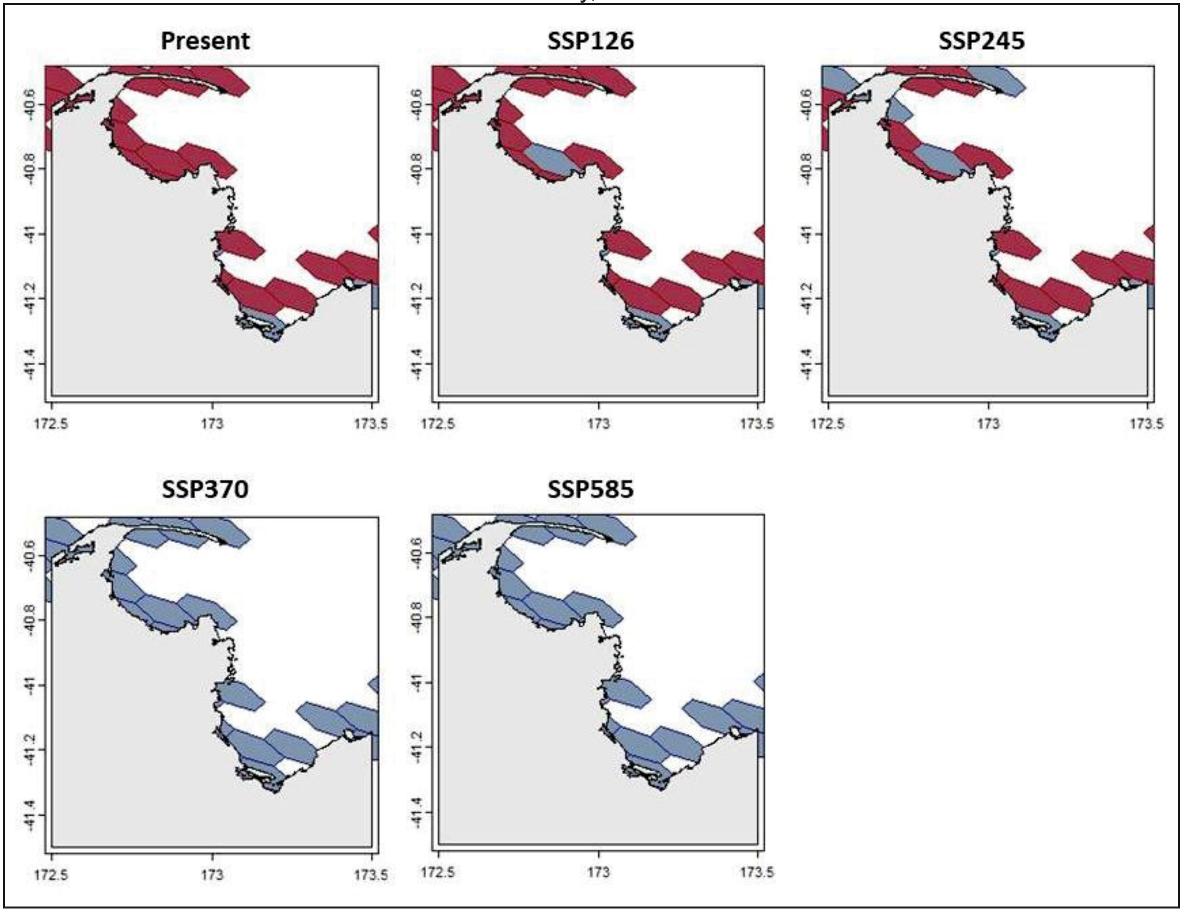
D. São Paulo State, Brazil.



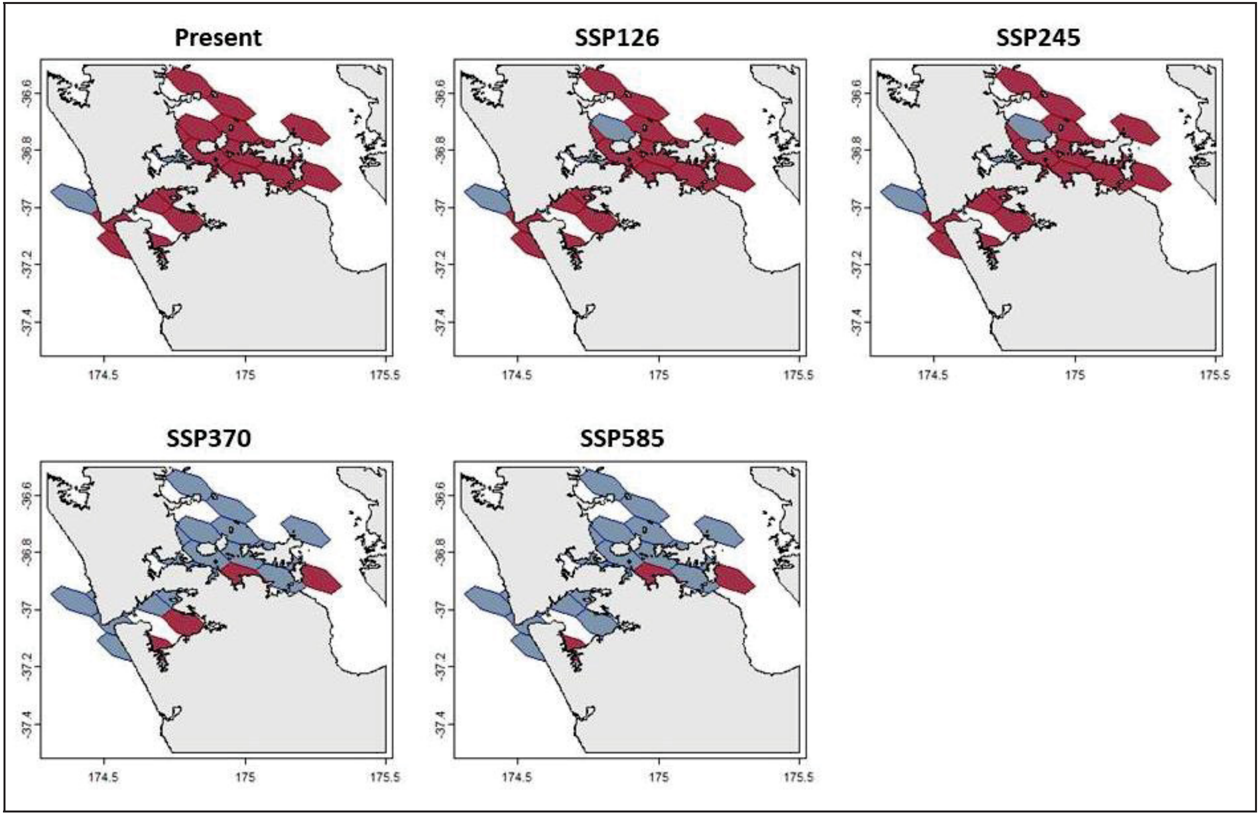
E. Marlborough Sounds, New Zealand.



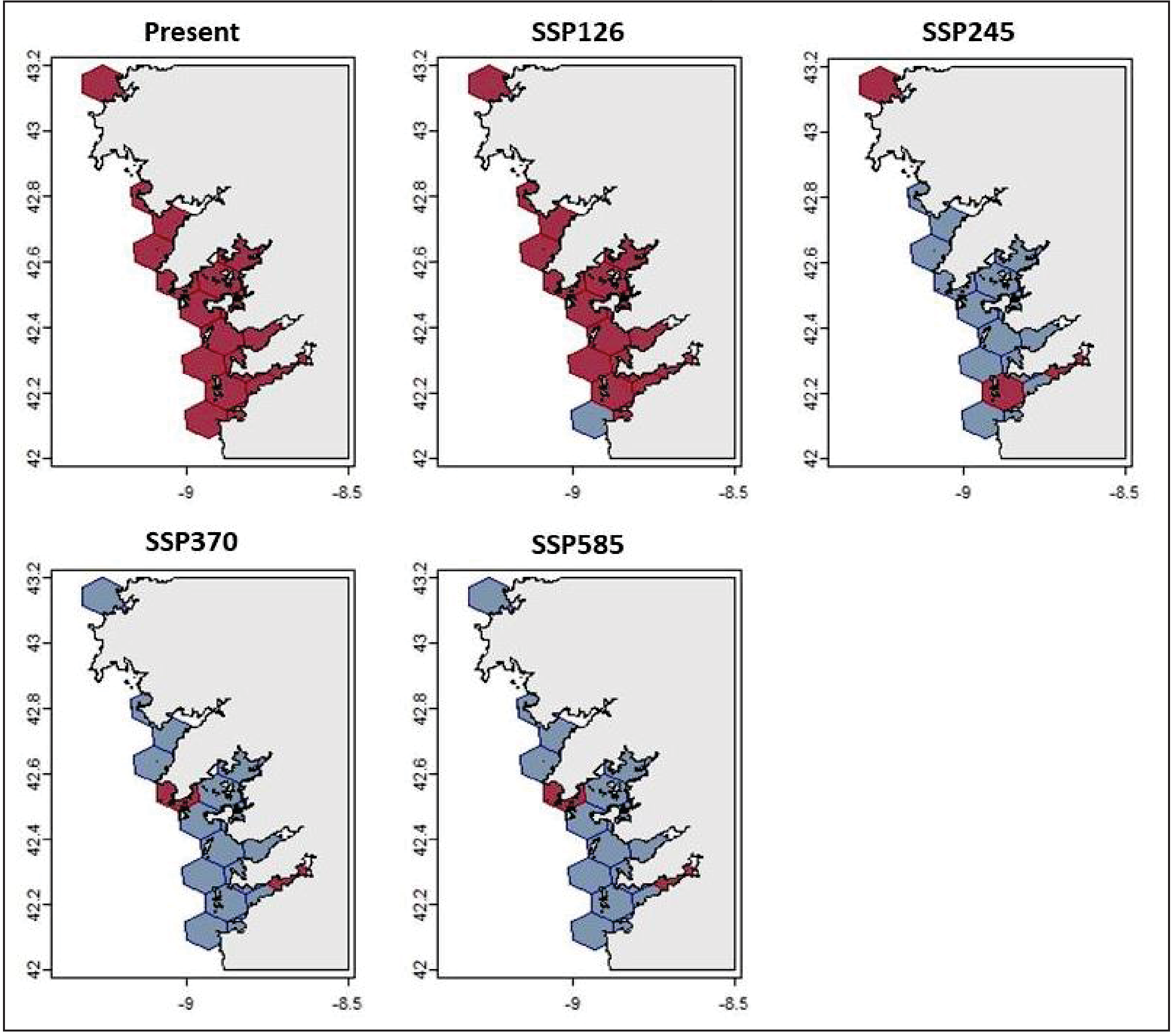
F. Tasman Bay, New Zealand.



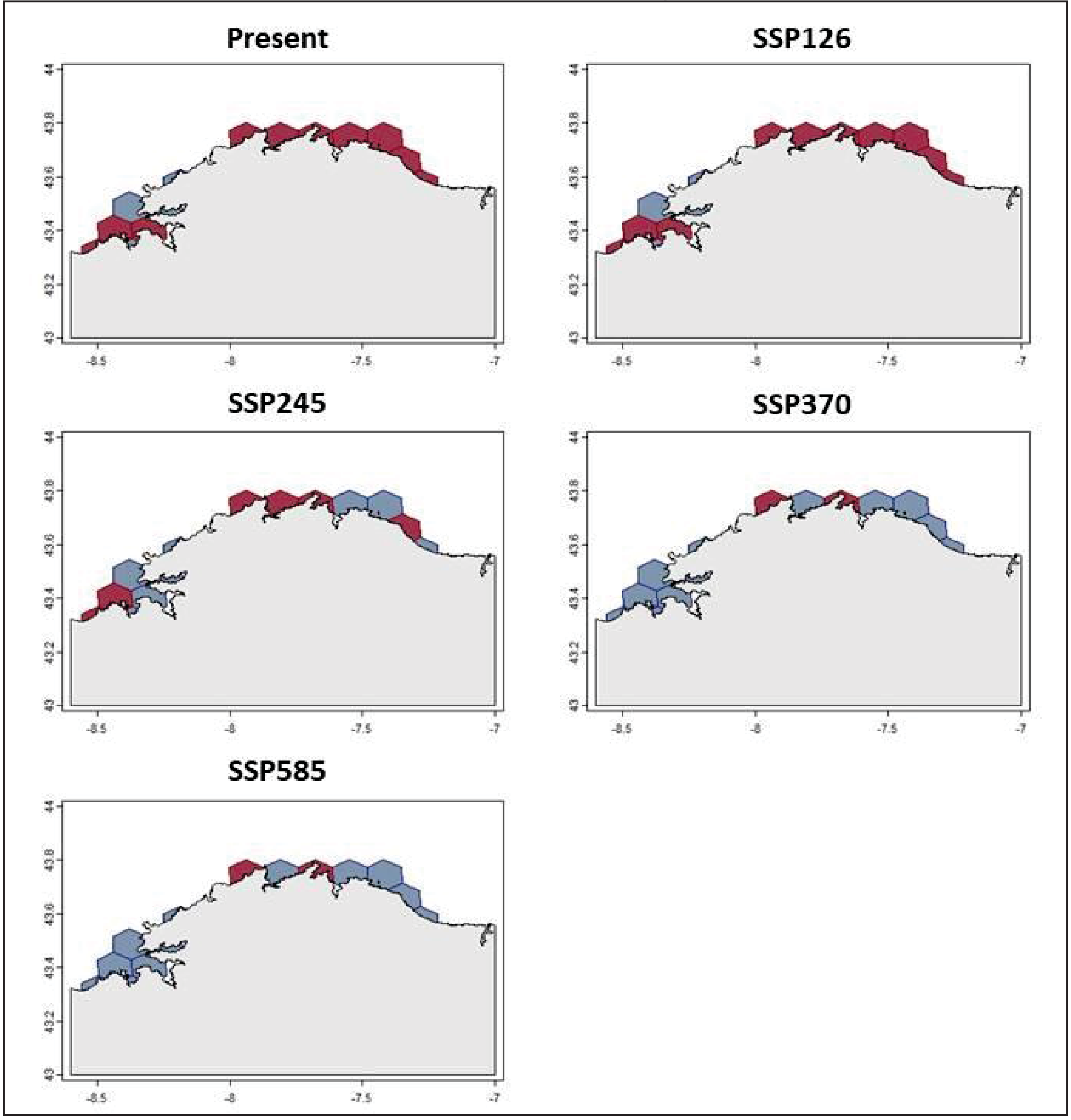
G. Hauraki Gulf, New Zealand.



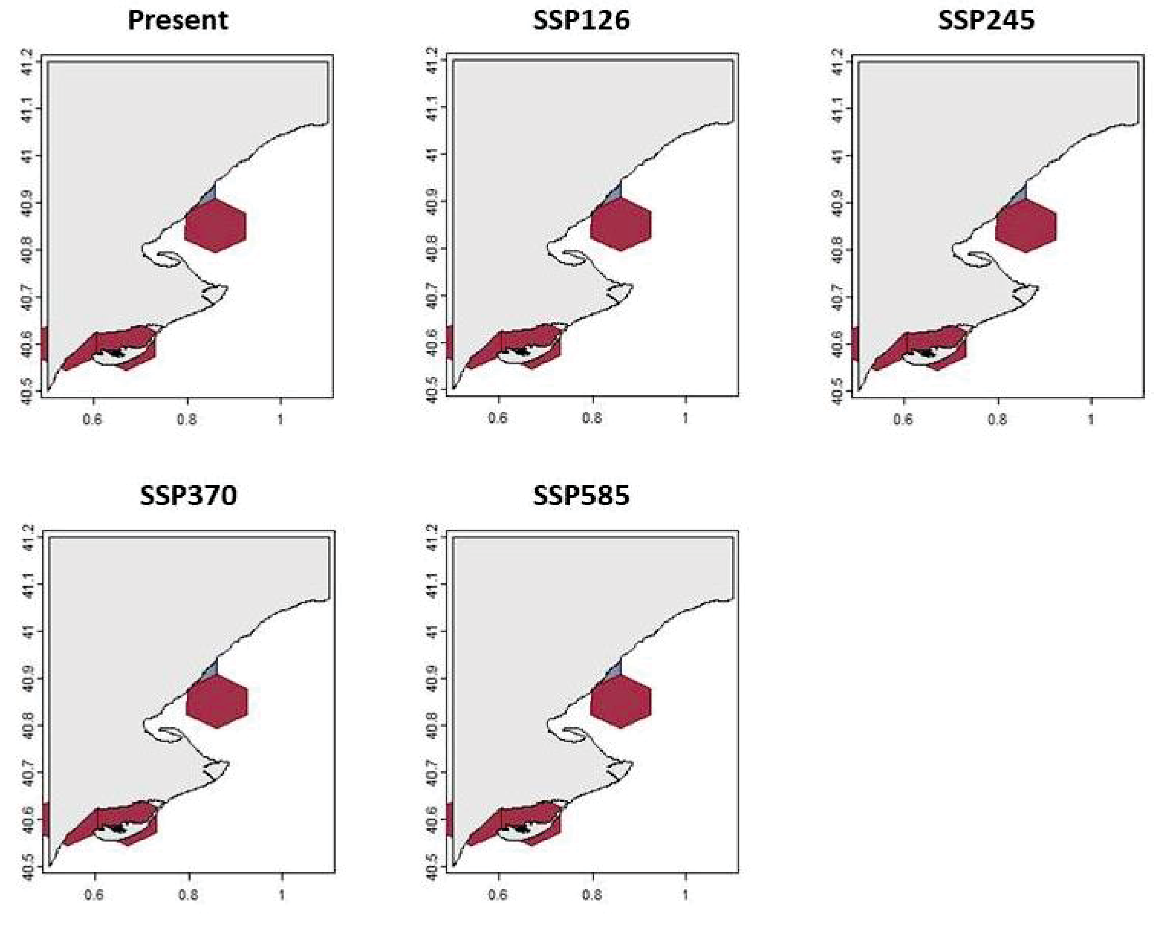
H. Rías Baixas, Galicia, Spain.



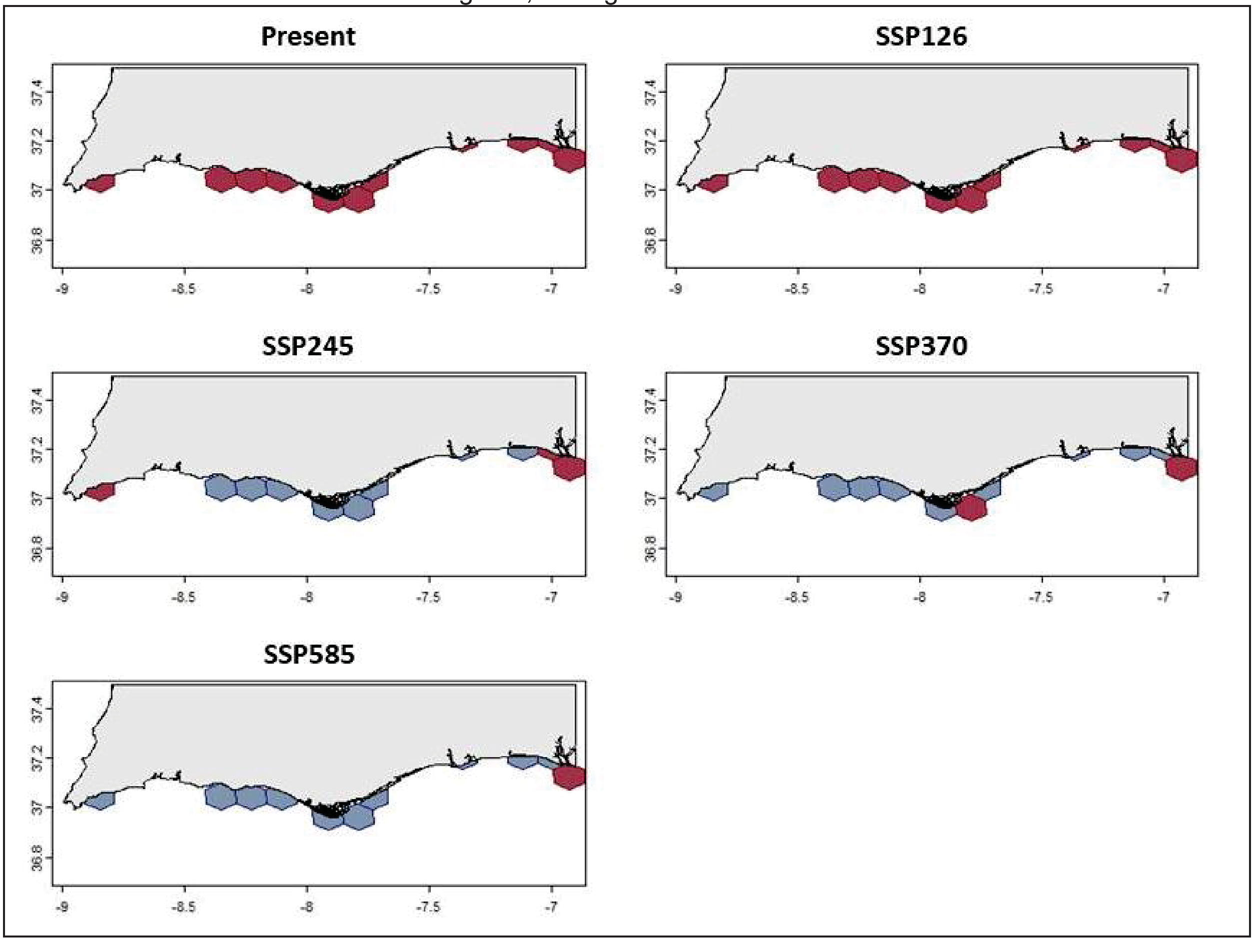
I. Rías Altas, Galicia, Spain.



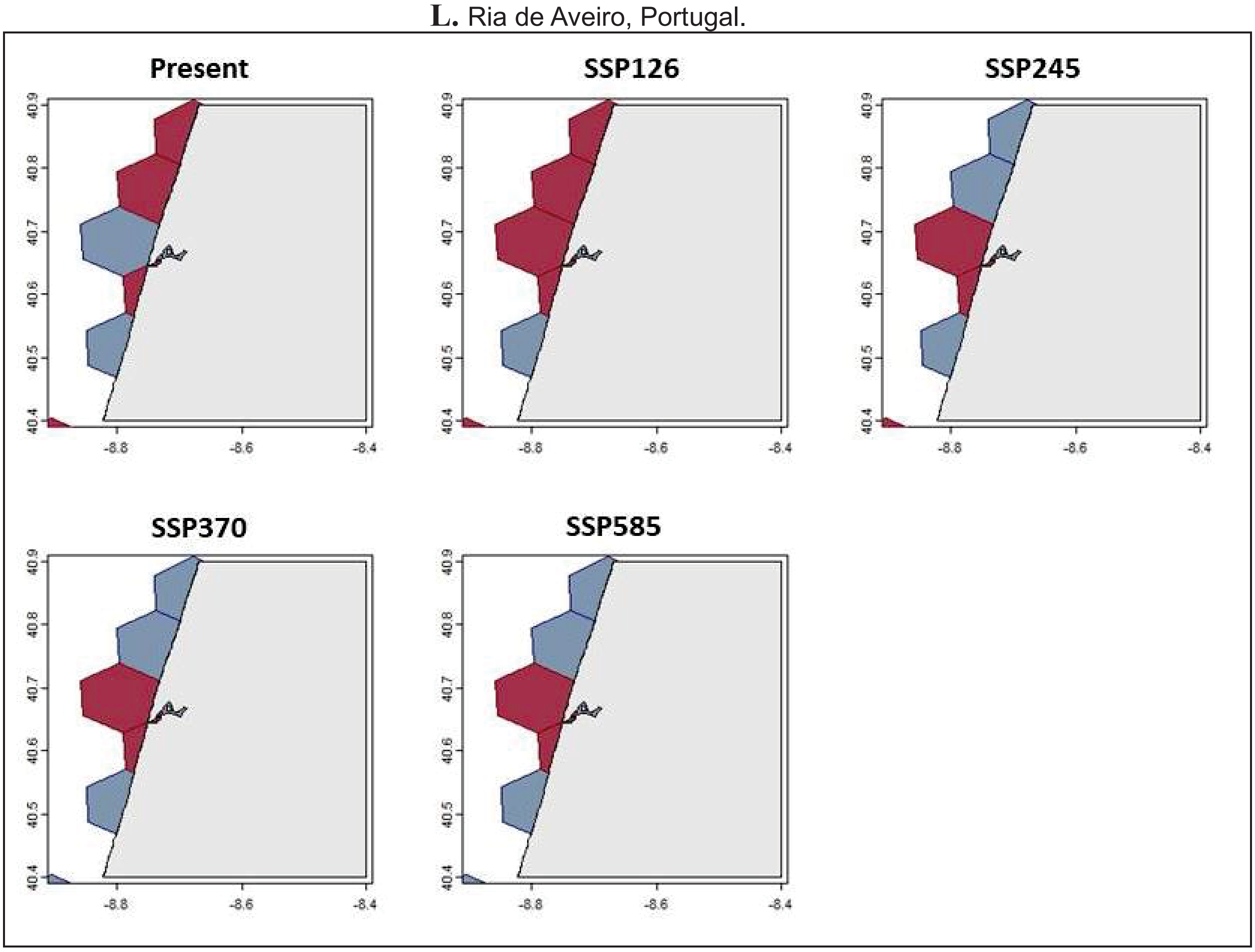
J. Ebro Delta, Catalonia, Spain.



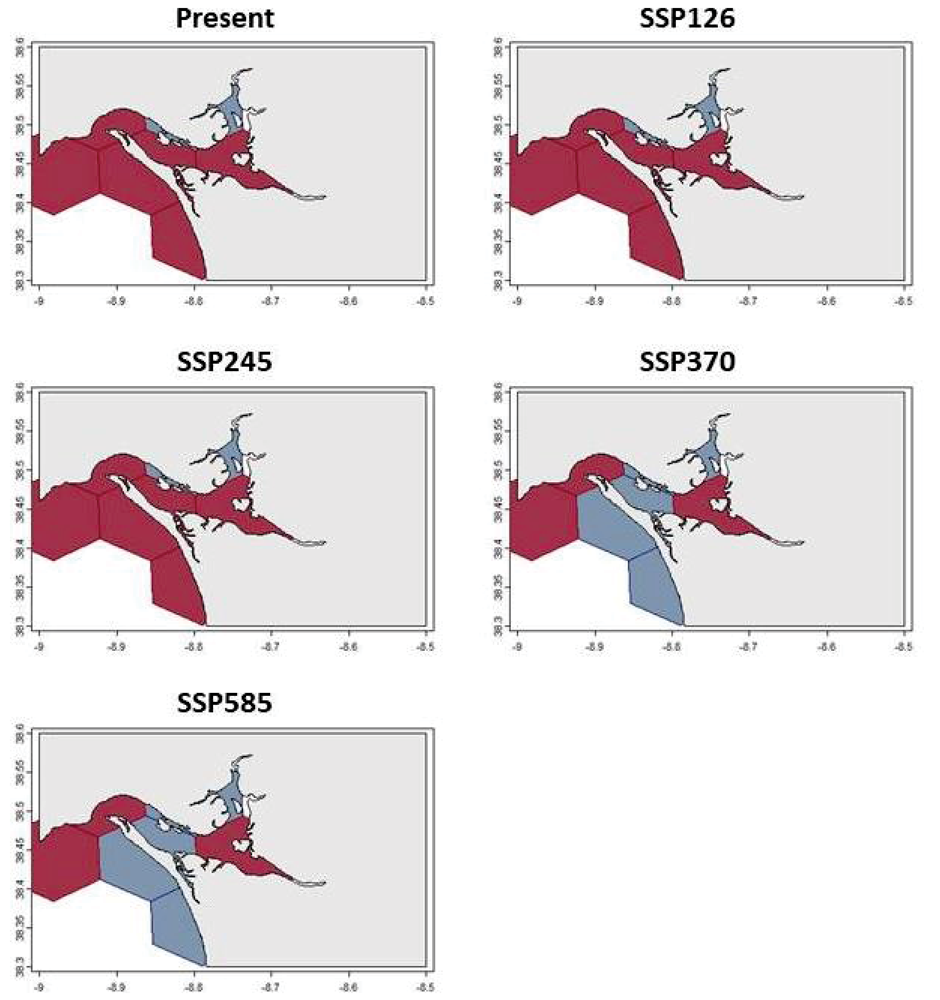
K. Algarve, Portugal.



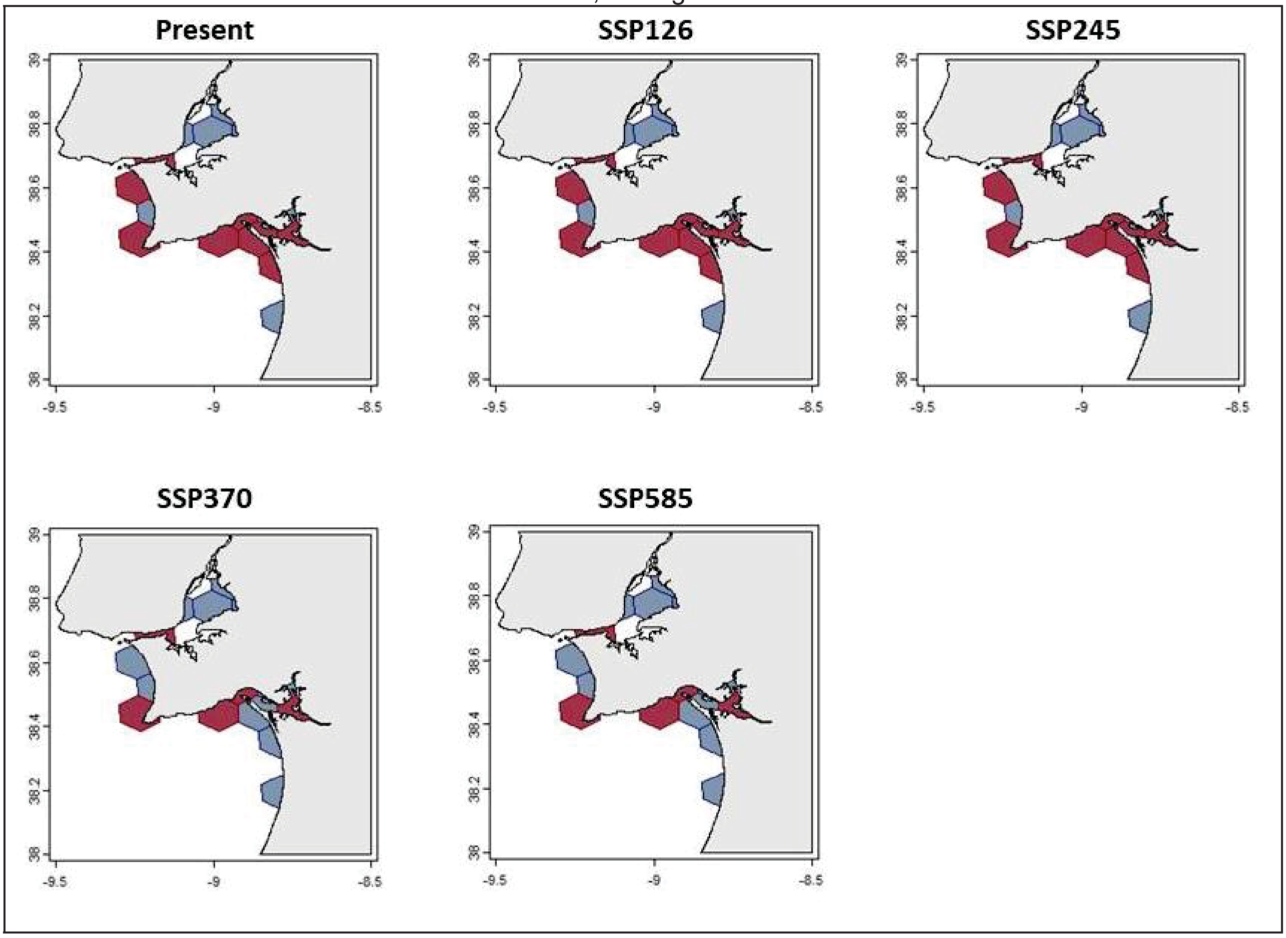
L. Ria de Aveiro, Portugal.



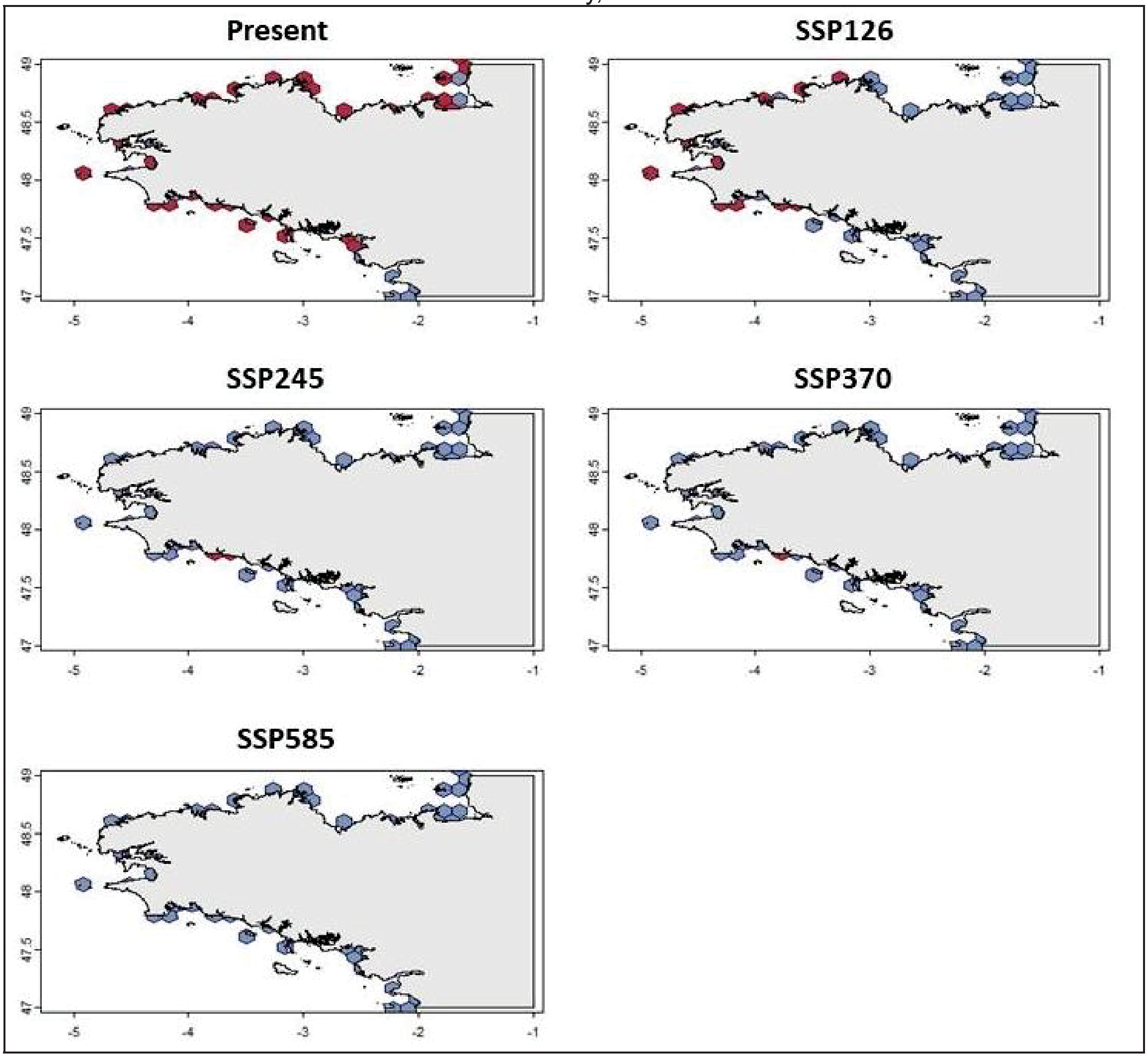
M. Estuary of the Sado River, Portugal.



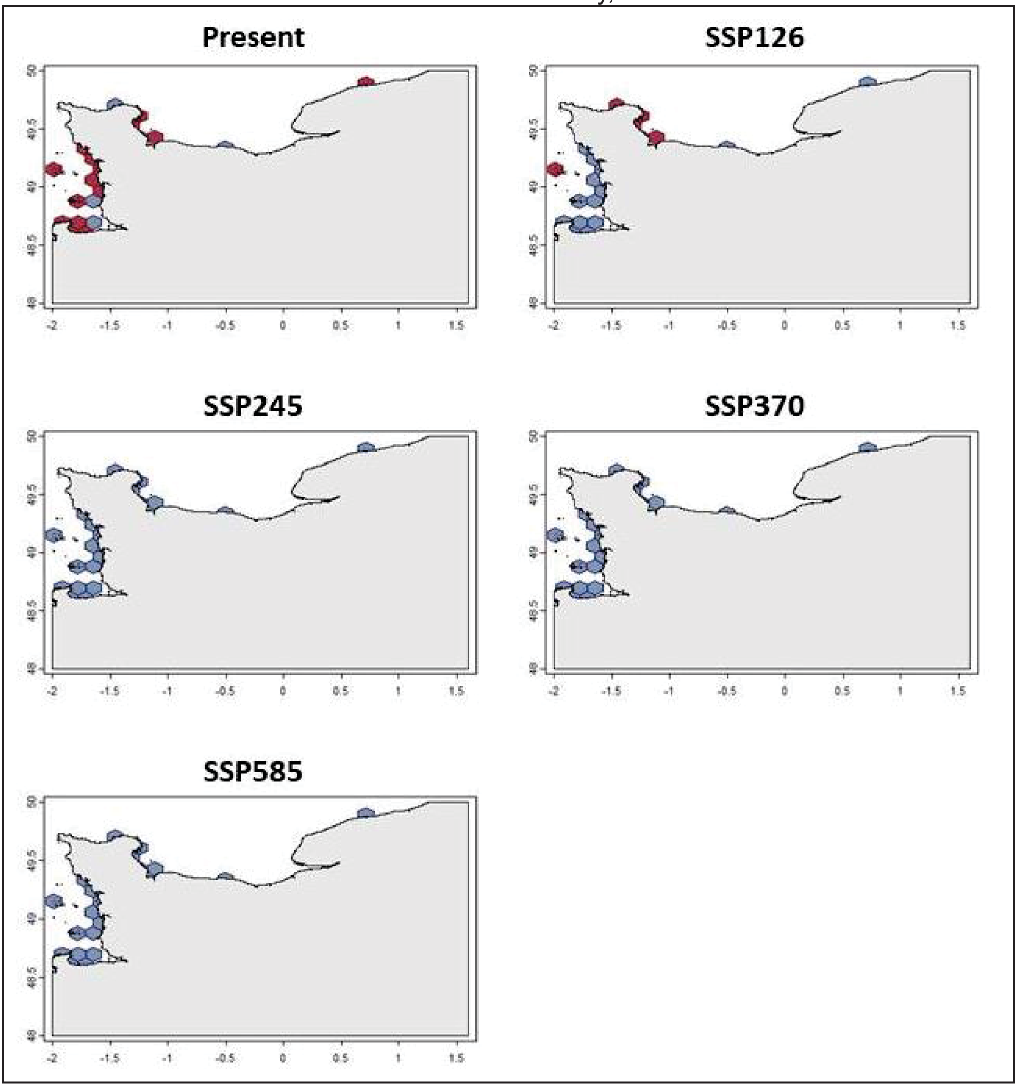
N. Setúbal, Portugal.



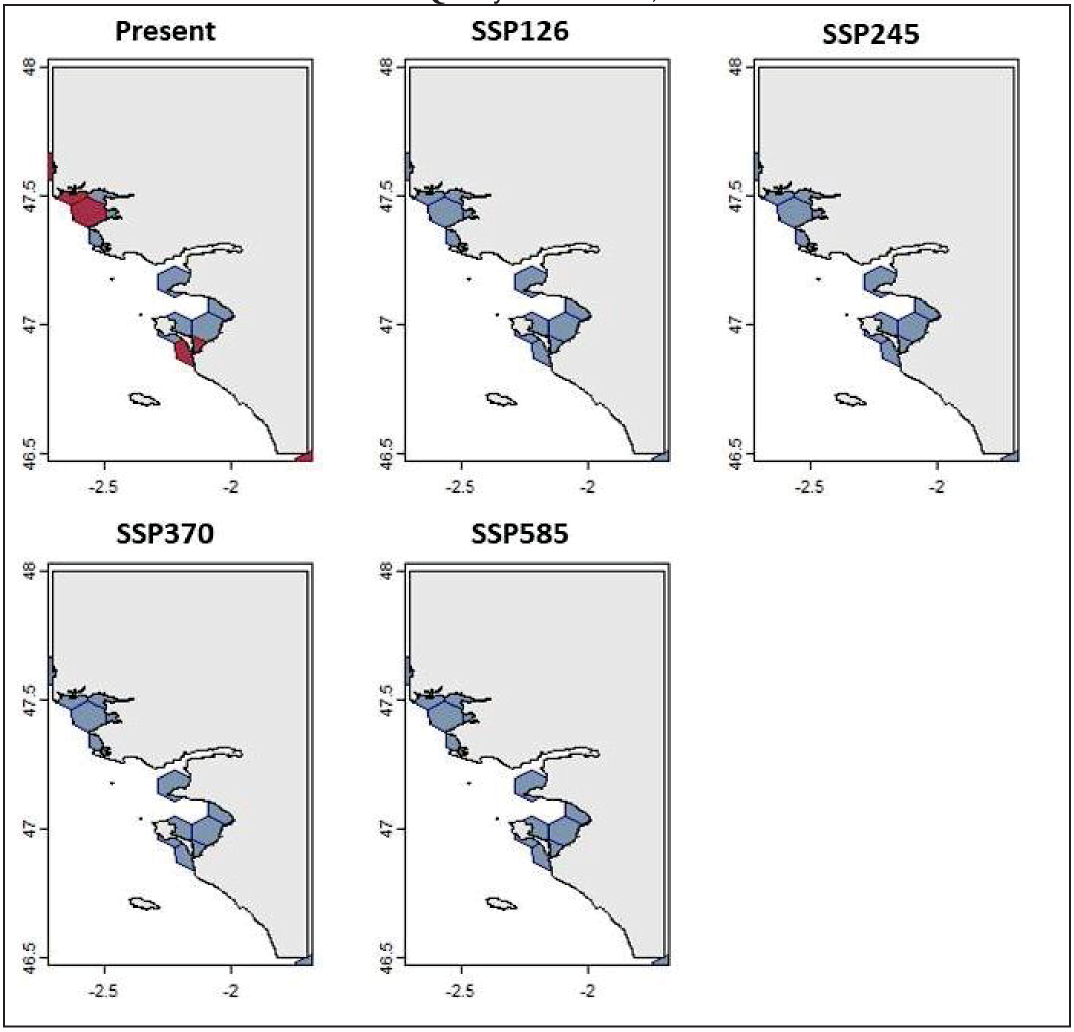
O. Brittany, France.



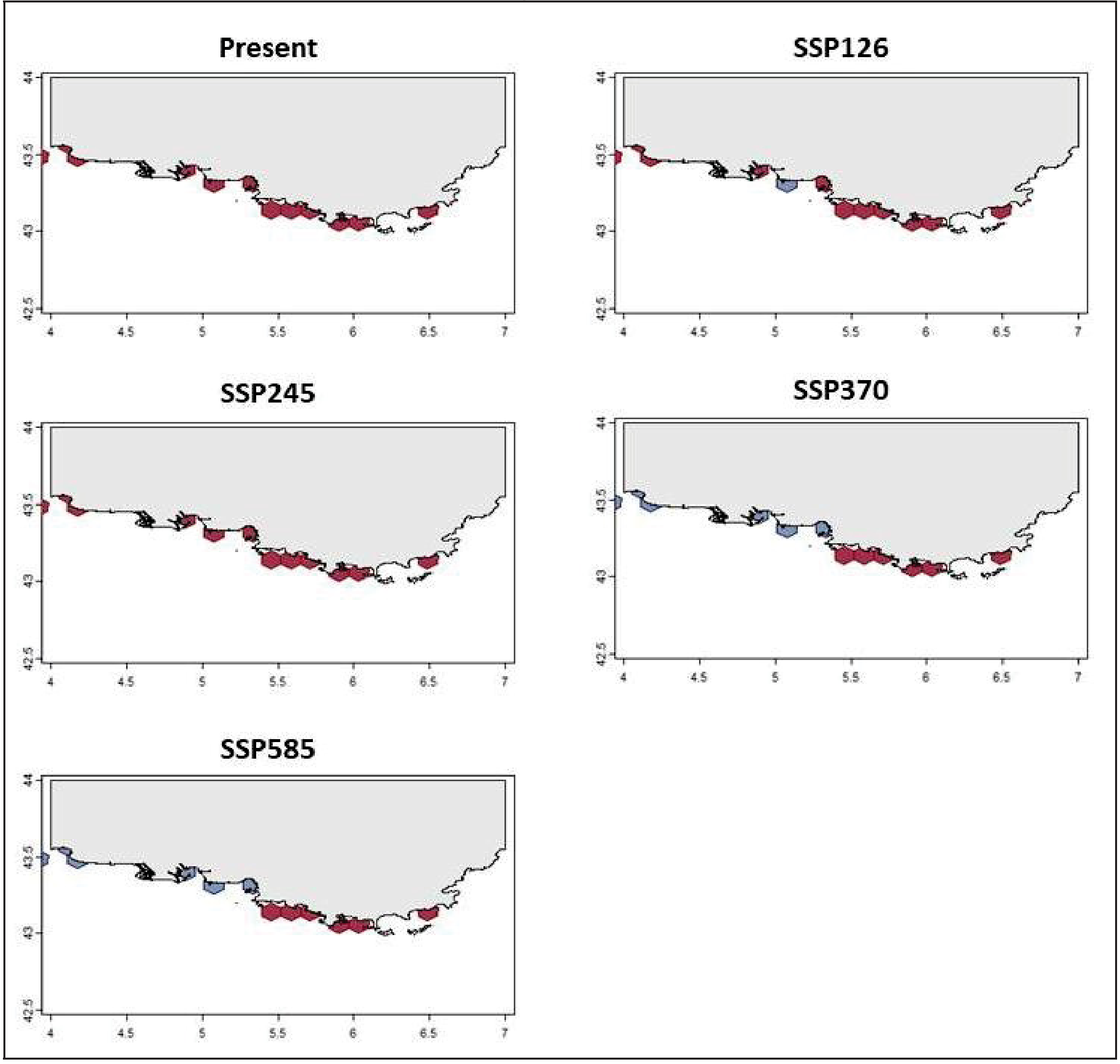
P. Normandy, France.



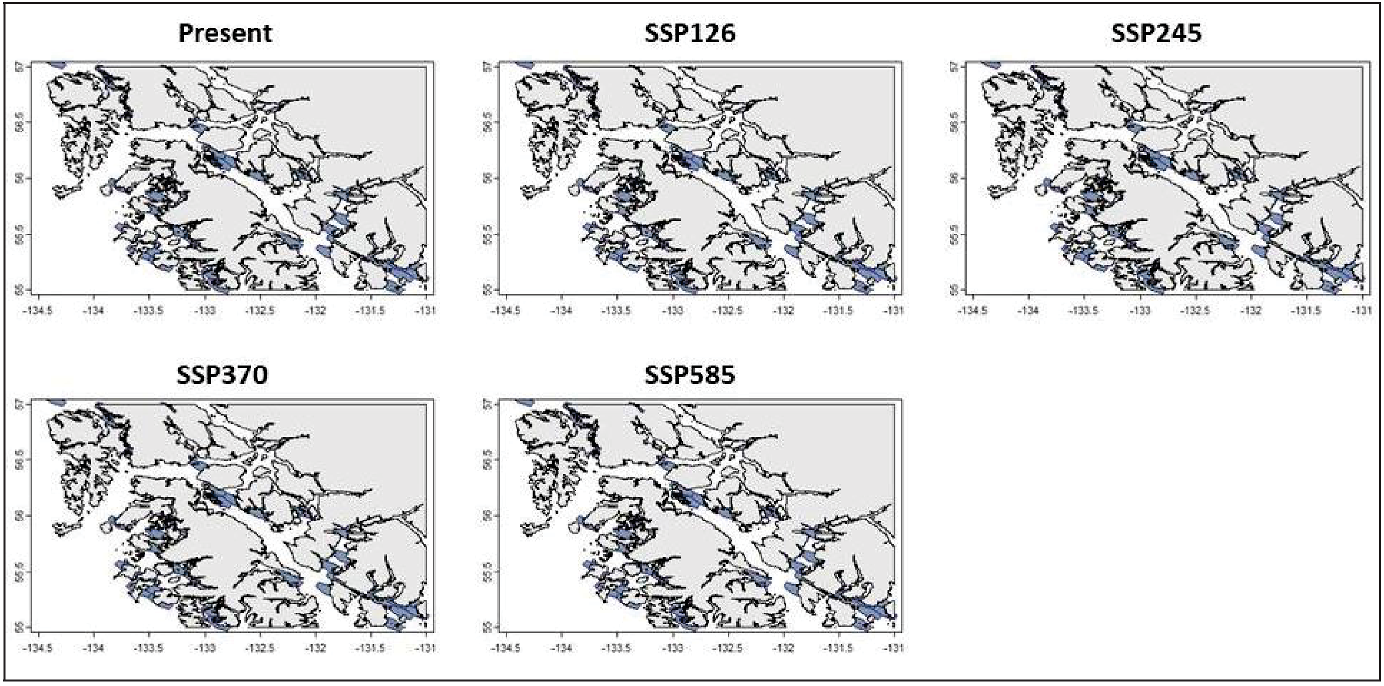
Q. Pays de la Loire, France.



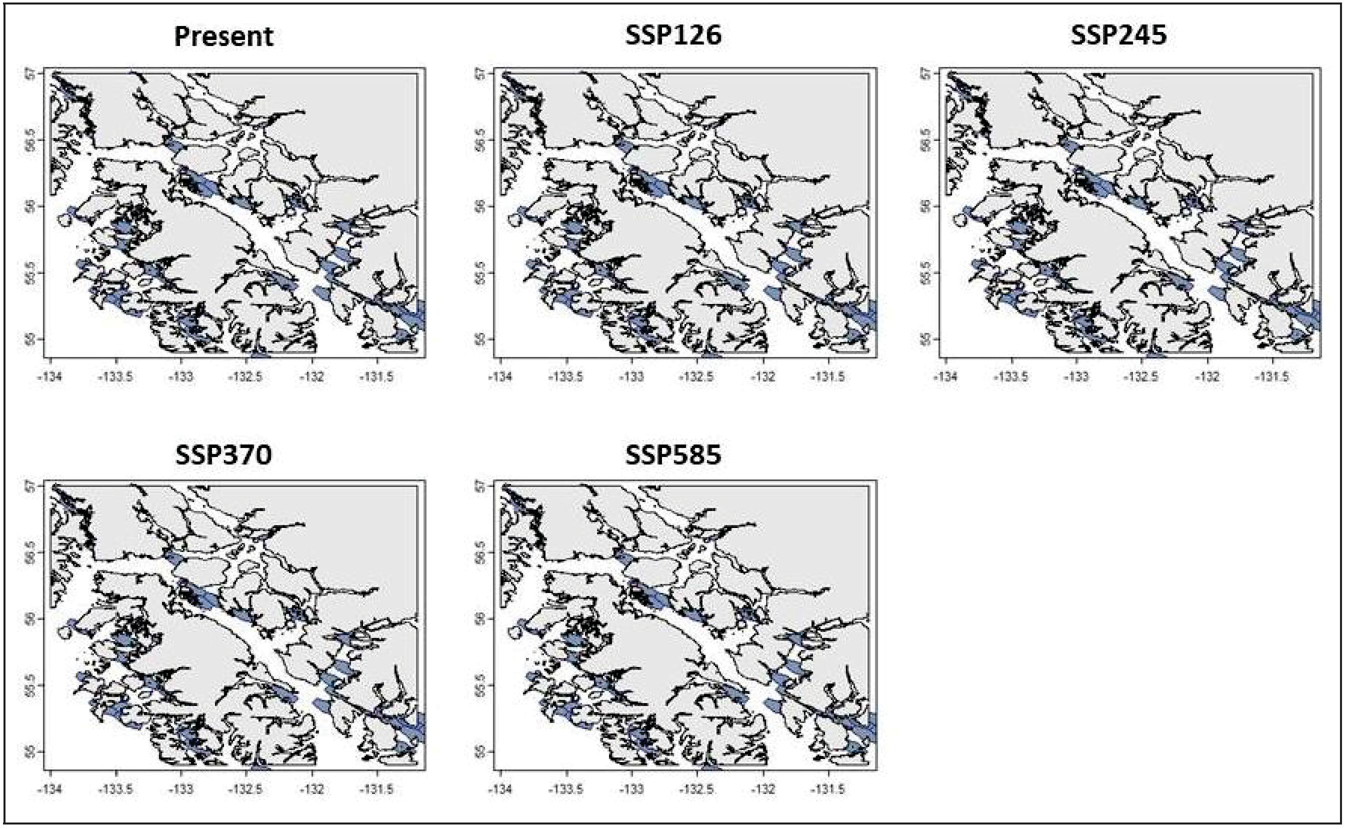
R. Provence-Alpes-Côte d'Azur, France.



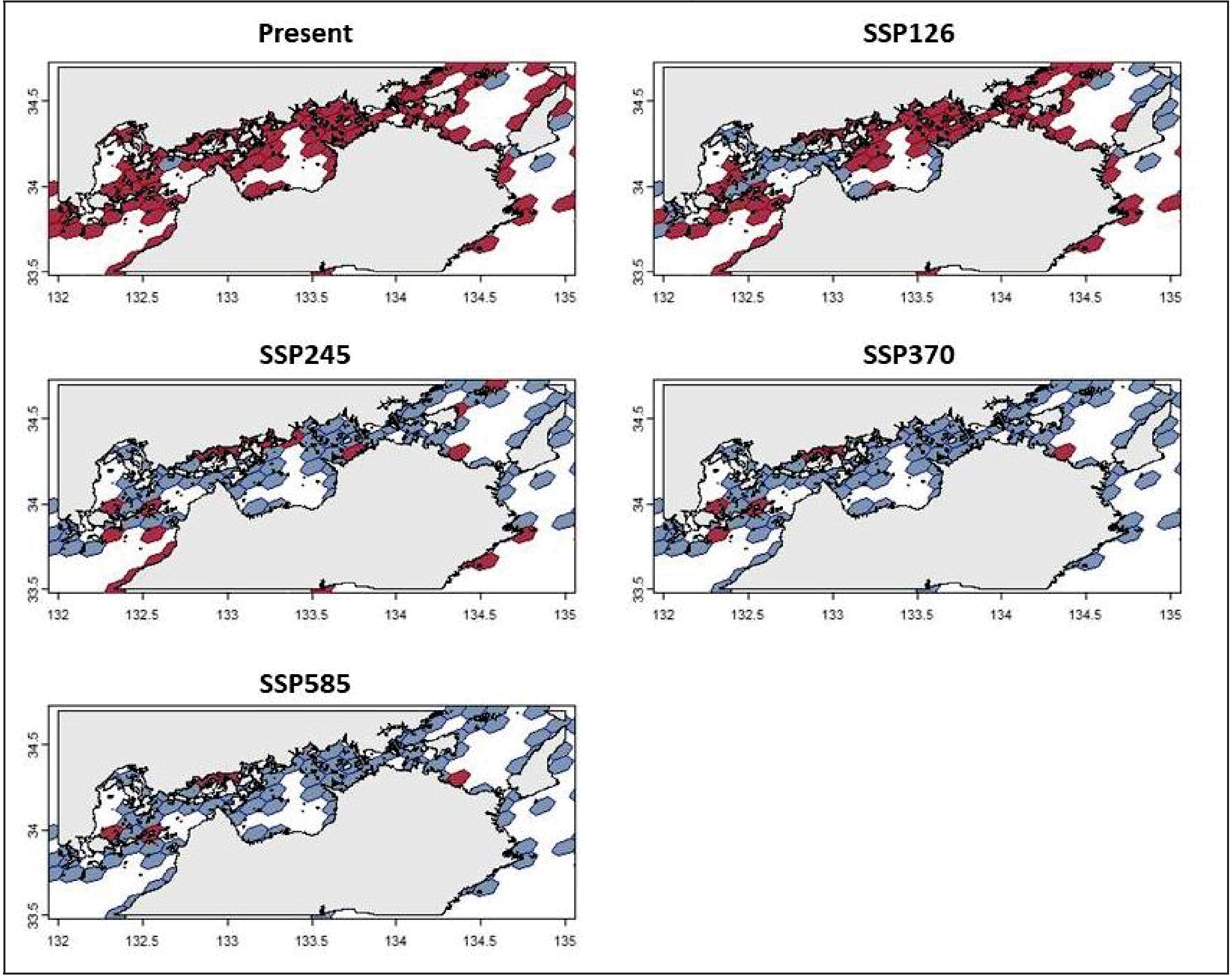
S. Northern British Columbia, Canada.



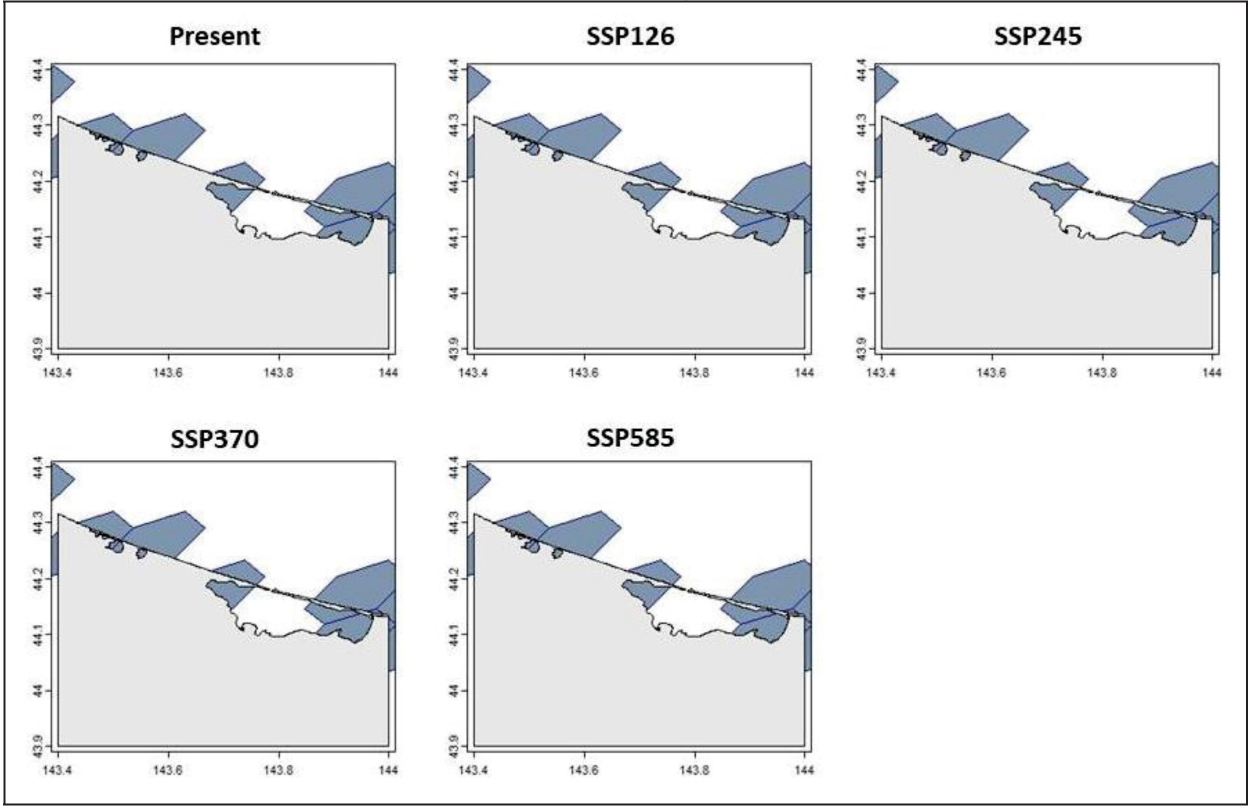
T. Southern British Columbia, Canada.



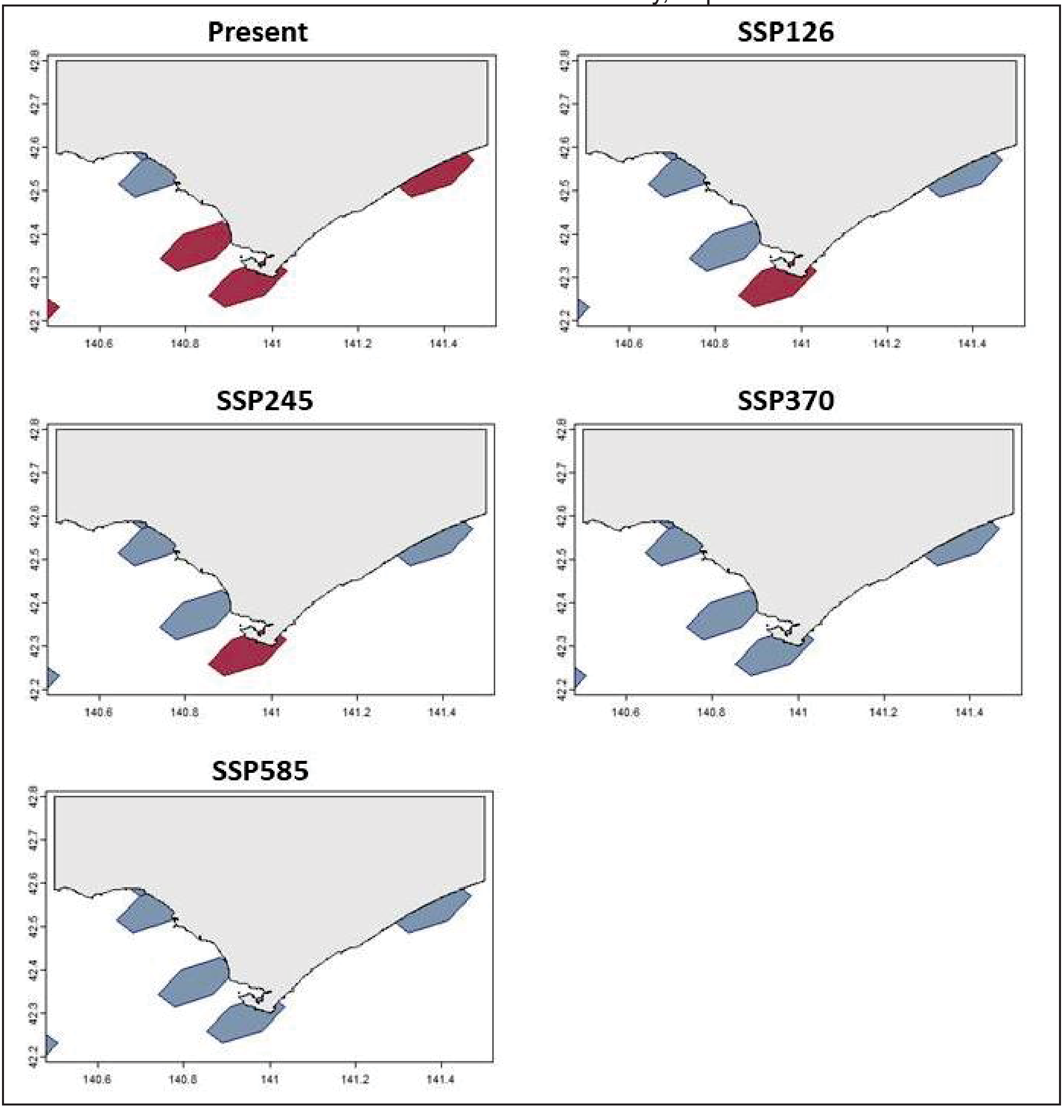
U. Seto Inland Sea, Japan.



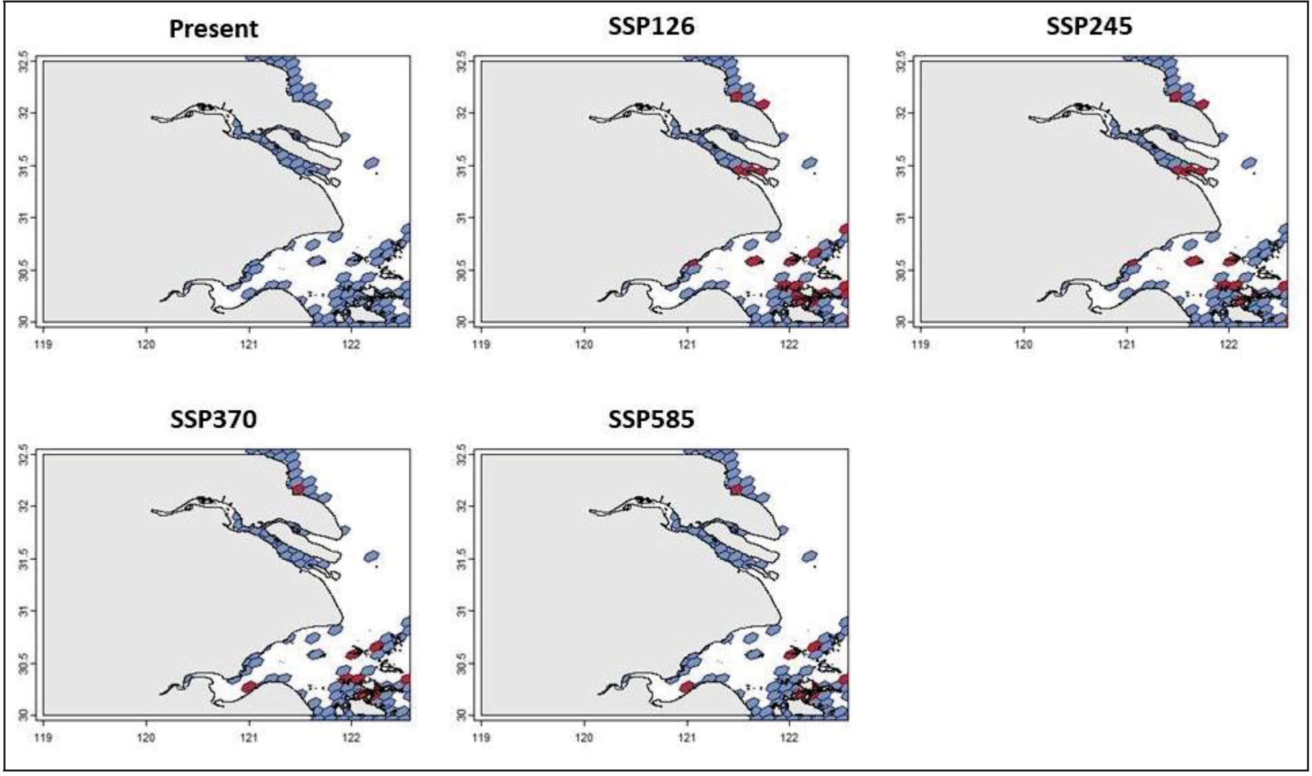
V. Lake Saroma, Japan.



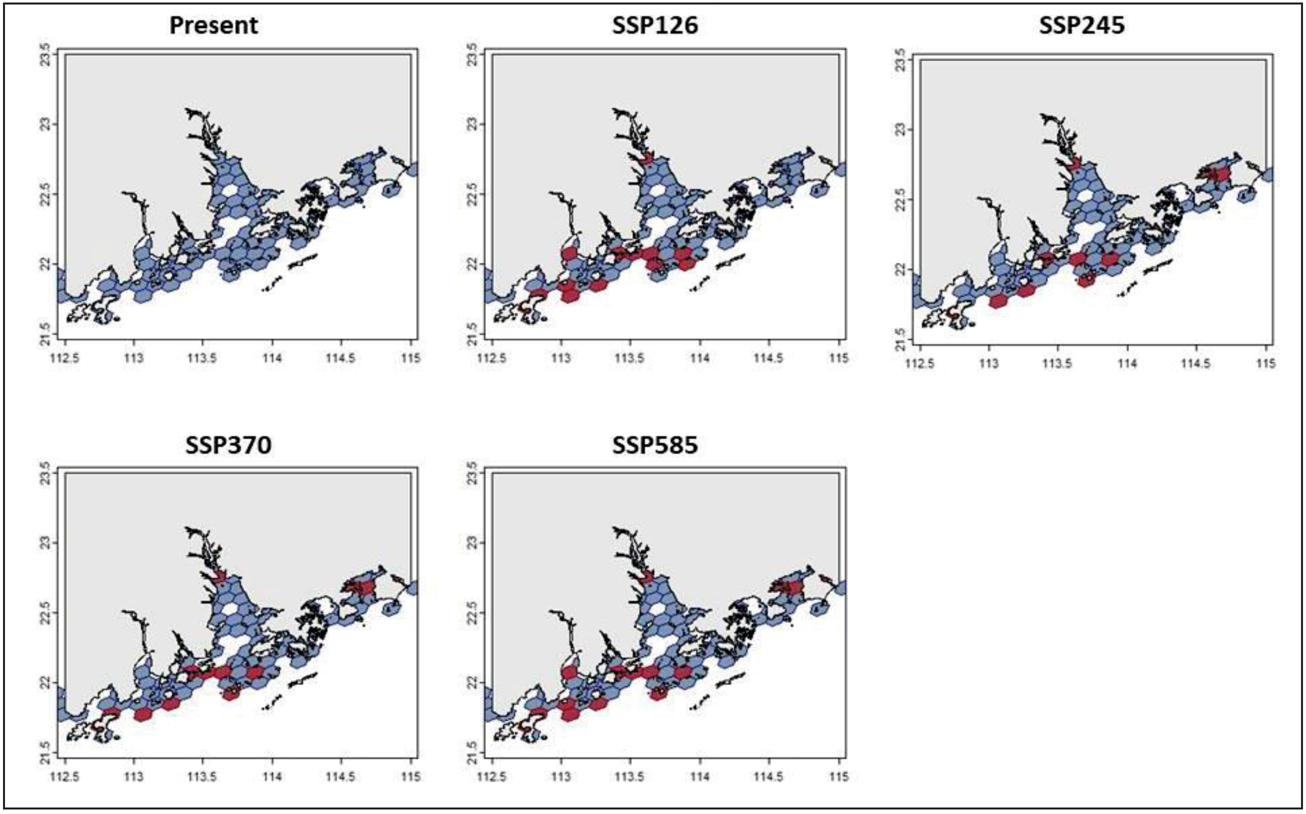
W. Funka Bay, Japan.



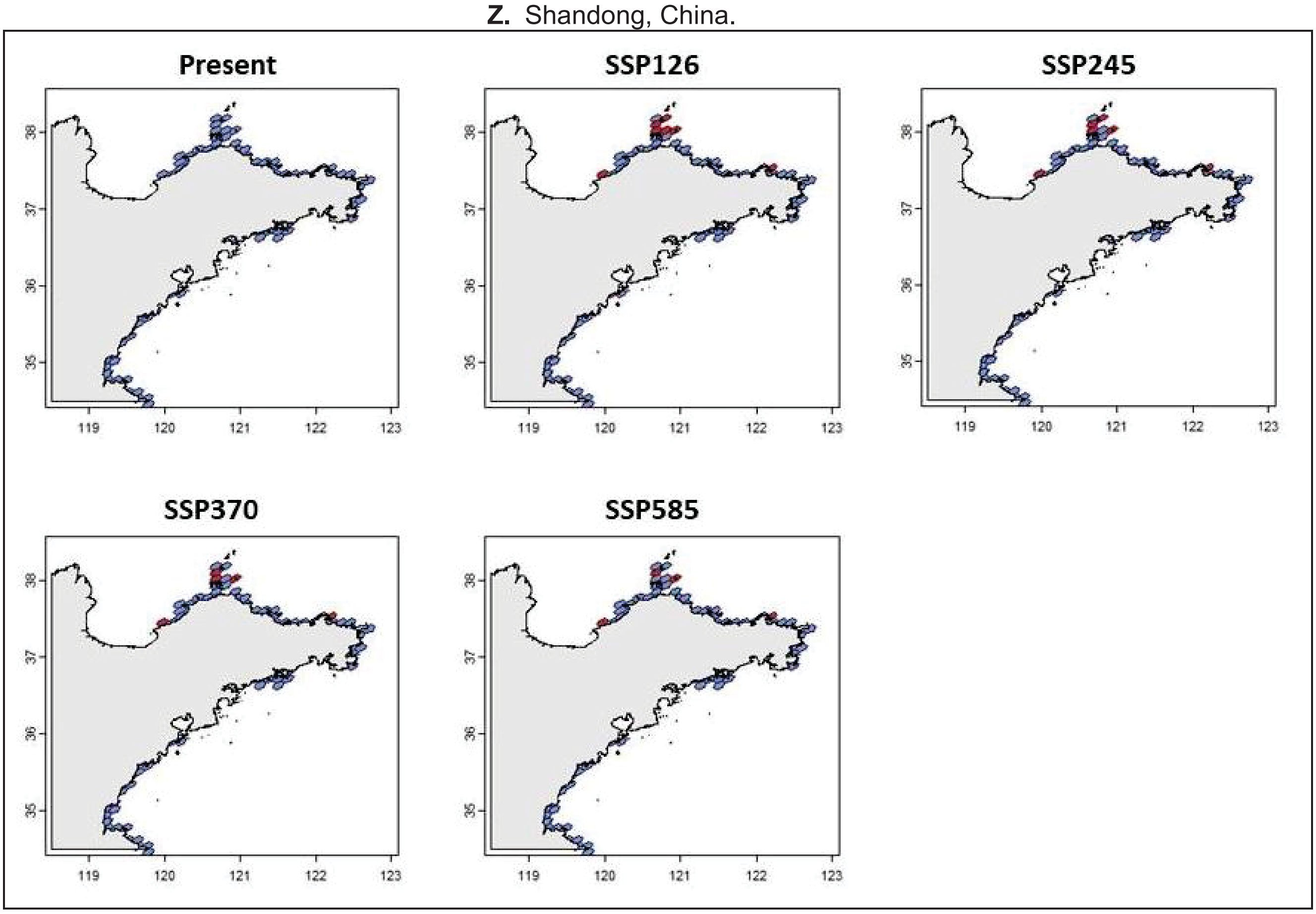
X. Yangtze River Delta, China.



Y. Pearl River Delta, China.



Z. Shandong, China.



4 CONSIDERAÇÕES FINAIS

A microalga toxigênica *O.* cf. *ovata* pode ser compreendida como uma ameaça emergente global, haja vista novos locais que, nos últimos anos, passaram a sofrer com florações desta espécie, associadas a quadros graves de saúde em seres humanos e mortalidade massiva de animais marinhos. Efeitos negativos, inclusive, já foram reportados para vários animais cultiváveis pela aquicultura marinha, como equinodermos, crustáceos, vieiras, mexilhões e ostras. Trata-se de um dinoflagelado bêntico cujas florações nocivas, inicialmente, eram reportadas em climas tropicais e subtropicais, porém, que recentemente vêm sendo reportadas em maiores latitudes. Este trabalho, portanto, contribui substancialmente ao fazer projeções que demonstram que a distribuição geográfica da espécie deve continuar se expandindo para novos locais. O trabalho aponta uma tendência global de expansão da distribuição da espécie em um cenário mais brando de aquecimento, porém, a partir de maiores níveis de emissões de gases de efeito estufa, o clima do planeta deve culminar em condições oceanográficas menos adequadas para a espécie, o que deverá causar alívio em vários locais. Contudo, certas regiões devem permanecer ou passar a estar sob considerável risco. Em todo caso, há uma tendência de expansão da espécie para regiões e locais inéditos diante de todos os cenários climáticos analisados, i.e., do mais brando ao mais severo.

Este estudo traz uma contribuição especial ao setor aquícola marinho, fundamental para a segurança alimentar e a economia oceânica. A tendência global é de diminuição do risco associado à presença de *O.* cf. *ovata* para as áreas aquícolas conforme o clima do planeta aquece. Entretanto, ressalta-se que, em nível regional e local, há locais com produção aquícola que deverão continuar sob risco significativo associado à ocorrência de *O.* cf. *ovata*. Alguns lugares com importante produção aquícola poderão também ser afetados pela expansão desta microalga, passando a experimentar um risco adicional inédito. O estudo chama a atenção, portanto, para a necessidade de que determinadas regiões continuem ou iniciem o monitoramento desta microalga marinha e suas ficotoxinas, consideradas uma ameaça emergente, de modo a prevenir os possíveis danos à saúde humana, ao ecossistema aquático e ao setor aquícola. De modo mais amplo, riscos associados à ocorrência de microalgas formadoras de florações nocivas, a exemplo da espécie-alvo deste estudo, devem ser incorporados ao planejamento espacial marinho das áreas para as quais se projetam tendência de risco perante possíveis cenários de mudanças climáticas.

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