

**UNIVERSIDADE FEDERAL DO RIO GRANDE - FURG
PÓS-GRADUAÇÃO EM OCEANOGRAFIA BIOLÓGICA**

**POTENCIAIS *HOTSPOTS* DE MEGAFauna
MARINHA NO SUL DO BRASIL**

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Ao meu grande amor, minha mãe.

“...I, I wish you could swim
Like the dolphins, like dolphins can swim
Though nothing, nothing will keep us together
We can beat them, forever and ever
Oh, we can be heroes, just for one day...”

David Bowie

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RESUMO

Hotspots biológicos no ambiente marinho são locais de agregação de indivíduos de diferentes espécies em regiões com alta atividade biológica, sendo resultado de uma série de fatores oceanográficos. A identificação dessas áreas de concentração está relacionada com o entendimento da distribuição e do uso do habitat de algumas espécies de vertebrados marinhos, e também dos distintos processos bióticos e abióticos que ocorrem no oceano. O presente trabalho teve o principal objetivo de identificar áreas de maiores probabilidades de ocorrência de diferentes grupos de grandes vertebrados marinhos – incluindo peixes, tartarugas, aves e mamíferos – que habitam as regiões neríticas e oceânicas do sul do Brasil. Para tal identificação foram considerados somente dados de presença desses grupos de megafauna em relação a variáveis ambientais através da modelagem de entropia máxima com uso do *software* Maxent e a sobreposição foi calculada através do *software* ENMtools. Os resultados demonstram que *hotspots* de megafauna marinha no sul do Brasil estão presentes, em sua maioria, nas regiões de quebra de plataforma e de talude continental, entre as isóbatas de 150 e 1000 m. Os maiores valores de similaridade de nicho da megafauna foram obtidos em sobreposições de famílias de mesmo grupo. Exceção para esse padrão são os tubarões da família Carcharhinidae, que demonstraram alta similaridade de nicho com tartarugas (Cheloniidae e Dermochelyidae), assim como os golfinhos (Delphinidae), que apresentaram maior similaridade de nicho com atuns (Scombridae). A abordagem de entropia máxima deste estudo possibilitou a identificação de áreas de maior probabilidade de ocorrência da megafauna marinha, incluindo famílias com espécies ameaçadas de extinção. Estes *hotspots* de biodiversidade

são habitats relevantes para conservação e dão suporte à importância da região como uma área marinha biologicamente ou ecologicamente significativa (EBSA) no Oceano Atlântico Sul-Occidental.

Palavras-chave: habitats favoráveis, *hotspot*, Maxent, modelagem de entropia máxima, sobreposição de nichos, vertebrados marinhos.

ABSTRACT

Biological hotspots in the marine environment are aggregation sites of different species in regions with high biological activity. The identification of such areas has provided understanding of the distribution and habitat use of some species of marine vertebrates, and also of various biotic and abiotic processes occurring in the ocean. This study aimed to identify suitable areas with higher probability of occurrence for large marine vertebrates - including fishes, sea turtles, seabirds and marine mammals - that inhabit the neritic and oceanic regions of southern Brazil. We modeled presence-only data of marine megafauna groups in relation to environmental variables using the maximum entropy approach under the Maxent software. We investigated niche similarities between megafauna families using ENMTools software. Our results showed that marine megafauna hotspots in southern Brazil are present mostly in the continental shelf-break and slope regions, between the 150 and 1000 m isobaths. Niche similarities of megafauna were higher between families of the same group. Two exceptions were observed, of sharks from Carcharhinidae family with turtles (Cheloniidae and Dermochelyidae), and dolphins (Delphinidae) with tunas (Scombridae). Our modeling approach allowed the identification of areas with higher relative suitability for the marine megafauna, including families with species threatened

of extinction. These biodiversity hotspots are relevant habitats for conservation and provide support for considering the region an EBSA (Ecologically or Biologically Significant Marine Area) in the western South Atlantic Ocean.

Key words: hotspot, marine vertebrates, Maxent, maximum entropy modeling, niche overlap, habitat suitability.

INTRODUÇÃO GERAL

Estudos relacionados à distribuição e o reconhecimento de habitats favoráveis para diferentes espécies têm sido recorrentes na comunidade científica. Compreender o uso do habitat de animais marinhos, predizer sua distribuição e identificar suas áreas de maior concentração têm possibilitado o esclarecimento de questões ecológicas relevantes para a conservação e o manejo das espécies (Guisan & Thuiller, 2005; Reese & Brodeur, 2006; Bailey & Thompson, 2009; Elith & Leathwick, 2009b; Guisan *et al.*, 2013).

A concentração de espécies em algum local ocorre, geralmente, devido à sua importância para realização de diferentes atividades biológicas como alimentação e reprodução, ou até mesmo proteção contra a pressão de predação (Palacios *et al.*, 2006). Essas áreas de concentração podem ser definidas como *hotspots*, porém esse termo possui um amplo uso e pode ter várias definições na literatura. *Hotspots* podem ser interpretados como locais com intensa atividade biológica, alta riqueza de espécies, com importantes ligações entre os níveis tróficos, ou como regiões com concentrações de espécies endêmicas (Myers *et al.*, 2000; Worm *et al.*, 2003; Sydeman *et al.*, 2006). Além desses conceitos, *hotspots* também podem ser entendidos como locais que possuem uma alta concentração de animais marinhos que se agregaram a partir de

características oceanográficas e biológicas favoráveis (Palacios *et al.*, 2006), definição esta que foi utilizada neste estudo. Tais características envolvem fatores ou processos físicos, como temperatura, frentes oceânicas e ressurgência, ou feições geológicas, os quais podem influenciar diretamente na produtividade, abundância e distribuição de organismos (Pollard *et al.*, 2002; Friedlaender *et al.*, 2006; Block *et al.*, 2011).

Estudos de identificação de *hotspots* têm auxiliado no entendimento de questões importantes para a megafauna marinha, como a determinação de *hotspots* de animais marinhos com risco de extinção e de *hotspots* de captura incidental em uma escala global (Davidson *et al.*, 2012; Lewison *et al.*, 2014). O reconhecimento desses locais é de importância para as espécies envolvidas, pois permite a criação de áreas de conservação e de planos de ação e manejo que visam à proteção dessas espécies (Hobday & Pelc, 2014).

Discussões para a criação de áreas marinhas protegidas usam, geralmente, informações científicas como base. Por exemplo, em 2008, a Conferência das Partes para a Convenção sobre Diversidade Biológica (*Conference of Parties to the Convention on Biological Diversity*) adotou critérios científicos para a criação Áreas Marinhas Ecologicamente ou Biologicamente Significativa (EBSAs – Ecologically or Biologically Significant Marine Areas) (Dunn *et al.*, 2014), com o intuito de proteger habitats de mar aberto e profundo. Os critérios para a consideração de SA incluem: raridade ou singularidade da área; importância da área para os estágios de vida das espécies; presença de espécies e/ou de habitats ameaçados, em perigo ou em declínio; fragilidade, vulnerabilidade e velocidade de recuperação da área; a produtividade biológica da região; sua diversidade biológica e a naturalidade da área (Druel, 2012). Em

2012, o Brasil propôs locais que necessitam de atenção para medidas de manejo, no contexto da Convenção sobre Diversidade Biológica. Uma dessas áreas, localizada no sul do Brasil, foi classificada com justificativas médias e altas em critérios científicos utilizados para a implementação de uma EBSA (CBD, 2012). Essa área se estende desde o Cabo Santa Marta Grande, no estado de Santa Catarina, até o Chuí, no extremo sul Rio Grande do Sul. A influência de frentes, correntes e de fatores topográficos, bem como o aporte de água continental, favorecem a alta produtividade e fazem dessa área um local importante para vários níveis tróficos (Castello *et al.*, 1998).

Diferentes famílias de megafauna marinha utilizam essa área como um importante local de forrageamento e/ou reprodução. Entre elas, estão famílias de tartarugas (Dermochelyidae e Cheloniidae), aves marinhas (Procellariidae e Diomedidae), golfinhos (Delphinidae), peixes teleósteos pelágicos (Scombridae), raias (Rajidae e Rhinobatidae) e tubarões (Carcharhinidae, Sphyrnidae, Triakidae, Squalidae e Hexanchidae (e.g. Bugoni *et al.*, 2003; Zerbini *et al.*, 2004; Haimovici *et al.*, 2005; Moreno *et al.*, 2005; Vooren *et al.*, 2005; Neves *et al.*, 2006b; Di Tullio *et al.*, 2016). A megafauna marinha chama atenção para medidas de conservação já que esse grupo sofre muitas pressões antrópicas sobre o seu habitat, principalmente capturas dirigidas e incidentais pela pesca, incluindo ainda as mudanças climáticas (Derraik, 2002; Myers & Worm, 2003; Halpern *et al.*, 2008; Barbraud *et al.*, 2012).

A alta produtividade marinha no sul do Brasil favorece recursos pesqueiros, concentrando esforços de pesca desde as áreas costeiras da plataforma continental até as regiões pelágicas do talude (Haimovici *et al.*, 1998, Secchi *et al.*, 2004; Klippel *et al.*, 2005, Castello *et al.*, 2011). Nessa região, são

comuns interações da megafauna marinha com diferentes tipos de pesca, incluindo redes de emalhe, arrasto e espinhel pelágico (Secchi *et al.*, 1997; Vooren & Klipel, 2005; Dalla Rosa & Secchi, 2007, Bugoni *et al.*, 2008; Carvalho *et al.*, 2011; Fiedler *et al.*, 2012; Passadore *et al.*, 2015).

Nessa região, estudos recentes têm identificado padrões de diversidade e distribuição, assim como a determinação de áreas com maior probabilidade de ocorrência de diferentes grupos de megafauna marinha (Amaral *et al.*, 2015; Carman *et al.* 2016; Di Tullio *et al.*, 2016). Porém, ainda pouco se sabe sobre as áreas comuns à maior probabilidade de ocorrência desses grandes predadores e sobre a possível sobreposição de nichos entre eles. Entre os diferentes conceitos de nicho, tem-se o de um conjunto de dimensões ambientais onde uma espécie pode sobreviver interagindo com efeitos bióticos e abióticos (Hutchinson, 1957; Austin, 2002). O entendimento desse conceito ressalta o quanto faz-se importante o conhecimento de locais com possíveis sobreposições de nichos da megafauna marinha.

Técnicas estatísticas de modelagem de distribuição de espécies, ou modelagem de nicho ecológico, como também é conhecida, têm auxiliado na identificação de *hotspots* de biodiversidade. Esse processo inicia com observações de ocorrências de uma ou mais espécies e de variáveis ambientais que possam influenciar a formação de algum habitat preferencial dessas (Franklin, 2010; Peterson *et al.* 2011). Assim, além do conhecimento de locais críticos, modelos de distribuição de espécies também têm auxiliado muito para esclarecer quais fatores ambientais determinam a extensão espacial de alguns grupos (Ainley *et al.*, 2009; Suryan *et al.*, 2012; Bouchet *et al.*, 2015).

Há uma variedade de métodos estatísticos para desenvolver um modelo de distribuição de espécies (e.g. Guisan & Zimmermann, 2000; Elith *et al.*, 2006; Franklin, 2010). Entre tantos métodos, uma abordagem que vem se destacando é a de entropia máxima, que tem sido efetiva para a modelagem de nicho da megafauna marinha e para a determinação de *hotspots* biológicos (Édren *et al.*, 2010; Ainley *et al.*, 2011; Friedlaender *et al.*, 2011; Afán *et al.*, 2013; Pikesley *et al.*, 2013; McClellan *et al.*, 2014; Mugo *et al.*, 2014; Lucifora *et al.*, 2015).

A abordagem com o método de entropia máxima trata de uma modelagem que identifica áreas favoráveis à maior probabilidade de ocorrência, modelando a distribuição geográfica de espécies com dados apenas de presença, permitindo assim se fazer previsões ou inferências a partir de informações restritas, quando não se tem dados de ausência confiáveis (Phillips *et al.*, 2006; Elith *et al.*, 2011). De forma breve, o *software* nomeado Maxent estima a probabilidade de ocorrência das espécies sobre todos os *pixels*, ou células, da área de estudo, estimando uma distribuição que tem maior entropia (mais uniforme ou mais imprevisível) e levando em consideração as restrições impostas pela informação incompleta da distribuição verdadeira e minimizando suposições equivocadas (Phillips *et al.*, 2006; Elith *et al.*, 2011). Dessa forma, é um método muito útil quando se tem dados provenientes de fontes diversas (caso do presente trabalho) e que dificultam a padronização do esforço amostral, podendo produzir bons resultados mesmo com um número limitado de presenças (Phillips *et al.*, 2006, Merow *et al.*, 2013).

A relevância deste estudo está suportada na importância da identificação de *hotspots*, considerados aqui como as áreas de maior probabilidade de ocorrência das famílias da megafauna de interesse. Conhecer quais as áreas em

que a megafauna marinha tende a se agregar fornece informações para a proteção dessas espécies e do seu habitat. Considerando as diferentes feições oceanográficas presentes na área de estudo e heterogeneidade espacial da produtividade primária, a hipótese é de que complexidades batimétricas (quebra de plataforma/talude) e proximidade às frentes oceânicas favorecem a concentração de táxons da megafauna marinha.

OBJETIVO GERAL

Identificar áreas de maior probabilidade de ocorrência de grandes vertebrados marinhos no sul do Brasil.

OBJETIVOS ESPECÍFICOS

1. Determinar as áreas de maior probabilidade de ocorrências das famílias de peixes, tartarugas, mamíferos e aves nas regiões nerítica e oceânica do sul do Brasil;
2. Investigar a sobreposição de nichos entre as famílias dos diferentes grupos de vertebrados marinhos;

MATERIAL E MÉTODOS

A região de estudo está inserida em um polígono que cobre uma área com limites da linha de costa entre o sul da Ilha de Florianópolis, próximo ao Cabo Santa Marta (~28°S) e Chuí (~34°S), até a região oceânica de talude continental e além da isóbata de 1500 m. A produtividade dessa região é explicada por uma

série de fatores oceanográficos ocorrendo simultaneamente e com padrão sazonal, tornando essa região importante para indústria pesqueira (Haimovici *et al.*, 1998). Nessa área, a plataforma e o talude continental são influenciados pela Corrente do Brasil, águas subantárticas trazidas pela Corrente das Malvinas e as descargas de águas continentais que formam a Frente Subtropical de Plataforma (Moller *et al.*, 2008; Piola *et al.*, 2008). A Frente Subtropical de Plataforma é uma frente termo-halina de superfície que se estende desde a proximidade da isóbata de 50m em 32°S até a quebra de plataforma próxima a 36°S, com forte influência de ventos e das águas continentais oriundas do Rio da Prata e da Lagoa dos Patos (Piola *et al.*, 2000; Acha *et al.*, 2004). Além dessas influências, ressurgências na região de quebra de plataforma alteram a concentração de nutrientes, clorofila-a assim como nas densidades de zooplâncton, auxiliando para o aumento da produtividade (Braga *et al.*, 2008; Muelbert *et al.*, 2008).

A megafauna marinha de interesse desse estudo foi representada por diferentes famílias de vertebrados marinhos, incluindo peixes, tartarugas, aves e mamíferos marinhos. Todos os dados de presença são provenientes de diferentes bancos de dados em plataformas *online*, como o GBIF (*Global Biodiversity Information Facility* - <http://www.gbif.org>) e o SIMMAM (Sistema de Apoio ao Monitoramento de Mamíferos Marinhos – <http://simmam.acad.univali.br/site/>), de instituições parceiras, nomeadamente Projeto Tamar e Projeto Albatroz e de projetos de pesquisa e pesquisadores vinculados à Universidade Federal do Rio Grande (FURG), incluindo Projeto Talude, Programa Revizee, Projeto ARGOS, Laboratório de Recursos Demersais Pesqueiros e Laboratório de Ecologia e Conservação da Megafauna

Marinha. Desta forma, esses dados de ocorrência também são provenientes de coletas diferenciadas: registros de avistagens (aves e mamíferos) e registros de captura na pesca incidental de emalhe (elasmobrânquios) e de espinhel pelágico (elasmobrânquios, aves, tartarugas e teleósteos).

Modelagem da distribuição da megafauna marinha

Para a identificação de *hotspots* das famílias de megafauna marinha foi utilizada a modelagem baseada em dados somente de presenças dos táxons de interesse em relação a variáveis ambientais da área de estudo. Para esse tipo de modelagem utilizamos o software Maxent v.3.3.3 (disponível em www.cs.princeton.edu/~schapire/maxent), um dos métodos mais populares para modelagem de nicho ecológico (Merow *et al.*, 2013). Dados de ocorrência geralmente possuem forte viés espacial na coleta de dados, principalmente devido ao grande esforço em determinadas áreas consideradas mais acessíveis que outras para amostragem. Esse viés espacial pode resultar em modelos com interpretações equivocadas e, para minimizar esse efeito, a principal alternativa que o Maxent fornece é utilizar o método de gerar dados de “pseudo-ausências” (*background data*) para a modelagem (Phillips *et al.*, 2009). Essas “pseudo-ausências” geradas irão possuir o mesmo viés espacial que os dados de ocorrência utilizados para gerar os modelos (Phillips & Dudík, 2008). Com a técnica de validação cruzada no software, 10 réplicas dos modelos foram geradas para cada uma das famílias da megafauna marinha. A média dessas réplicas foi considerada como modelo final para a identificação dos *hotspots*. O desempenho da predição dos modelos gerados pelo Maxent foi avaliado de acordo com os valores de Área Sob a Curva (AUC - *Area Under the Curve*). Os valores de AUC demonstram então a acurácia do modelo em taxas que podem

variar de 0,5 a 1,0, sendo que quanto mais próximo de 1,0 melhor é o desempenho e a acurácia do modelo (Phillips *et al.*, 2004). Além dos mapas de maior probabilidade de ocorrência e do valor de AUC, o Maxent também tem como resultado um percentual de contribuição das variáveis para o modelo. Esse percentual foi considerado nesse estudo para a identificação de qual variável teve maior contribuição nas maiores probabilidades de ocorrência.

Variáveis ambientais

As variáveis fisiográficas utilizadas para gerar os modelos de distribuição da megafauna foram batimetria, declividade do fundo oceânico e distâncias da costa. A batimetria foi obtida a partir do modelo tridimensional de elevação do ETOPO1 (Amante & Eakins, 2009), que integra dados terrestres e batimetria dos oceanos com aproximadamente 10 m de acurácia vertical, e é disponibilizado pelo National Geophysical Data Center-NOAA. A variável declividade foi gerada a partir dos dados de batimetria em um SIG (Sistema de Informação Geográfica) com o uso da função *Slope*. A variável distância da costa foi gerada a partir da função da distância Euclidiana, também calculada em um ambiente SIG a partir da linha costa. Variáveis climatológicas também foram incluídas nos modelos, incluindo médias anuais de clorofila-a e de temperatura superficial do mar obtidas a partir de imagens do satélite AQUA-Modis disponibilizadas pelo Ocean Color - NASA's Goddard Space Flight Center (<http://oceancolor.gsfc.nasa.gov/cgi/l3>). Todas as variáveis de interesse foram importadas e processadas no software livre QGIS versão 2.12 (QGIS Development Team 2015) para que ficassem no mesmo sistema de coordenadas (Datum WGS 84) e com a mesma resolução (4 km) e extensão espacial. Foi calculada a correlação de Pearson para as variáveis, antes da

construção dos modelos, a fim de eliminar variáveis altamente correlacionadas (Zuur *et al.* 2010). Percebeu-se alta correlação entre as variáveis batimetria e distância da costa ($>0,8$), então a variável distância da costa não foi inserida na modelagem.

Sobreposição de nichos

A sobreposição de nichos entre as diferentes famílias da megafauna marinha foi quantificada através do índice de Schoener's, que compara a similaridade de nichos entre diferentes espécies. Para essa análise, foi utilizado o *software* ENMTools 1.4, que é de fácil associação com dados gerados pelo Maxent (Warren *et al.*, 2008) e que, através das médias de probabilidade de ocorrência das famílias de megafauna, faz a comparação dos nichos aos pares. A medida da sobreposição de nichos de Schoener's (D) fornece uma interpretação ecológica das similaridades de nichos entre as populações, variando de 0 (quando as espécies não têm sobreposição ao todo) a 1 (quando todos grids de células da área são estimados como semelhantes para ambas espécies) (Warren *et al.*, 2010). Neste trabalho, valores de $D \geq 0.65$ foram considerados altos e indicativos de sobreposição de nichos significativa.

SÍNTESE DOS RESULTADOS

As áreas favoráveis às maiores probabilidades de ocorrência da megafauna marinha, os *hotspots*, concentraram-se – em sua maioria – na quebra de plataforma e talude continental. As únicas famílias que demonstraram áreas de alta probabilidade na região costeira, plataforma interna, foram as famílias de raias Rajidae e Rhinobatidae, e as famílias de tubarões Carcharhinidae,

Sphyrnidae e Triakidae. O índice de similaridade para a sobreposição de nichos das famílias foi considerado alto entre as duas famílias de aves, assim como entre duas famílias de tartarugas e as de elasmobrânquios entre si. Os índices de similaridade foram também foram considerados altos para os tubarões Carcharhinidae comparados às tartarugas Cheloniidae e Dermochelyidae; e para as famílias Delphinidae e Scombridae. Quando sobrepostos os mapas de probabilidade de ocorrência da megafauna marinha identificou-se como áreas de maior probabilidade para a ocorrência dessas famílias a região de quebra de plataforma e talude continental.

CONCLUSÕES

- ✓ Conforme o desempenho do modelo, o Maxent foi considerado um método eficiente para a identificação dos potenciais *hotspots*, áreas de maior probabilidade de ocorrência da megafauna marinha;
- ✓ Através do método de entropia máxima identificou-se a região da quebra de plataforma e talude continental como relevante e com condições adequadas para a ocorrência de diferentes famílias de megafauna marinha;
- ✓ Para as raias e os tubarões, ambas as regiões costeira e de quebra de plataforma foram identificadas como potenciais *hotspots*, i.e., aquelas com condições favoráveis às maiores probabilidades de ocorrência;
- ✓ A sobreposição espacial de nichos de megafauna marinha possivelmente está relacionada com o uso comum do habitat nos diferentes estágios de vida da megafauna marinha, assim como por compartilharem recursos alimentares.

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APÊNDICE

Artigo submetido para a revista: "Diversity and Distributions".

Potential marine megafauna hotspots off southern Brazil

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ABSTRACT

Aim: Biological hotspots in the marine environment are aggregation sites of different species in regions with high biological activity. The identification of such areas has provided understanding of the distribution and habitat use of some species of marine vertebrates, and also of various biotic and abiotic processes occurring in the ocean. This study aimed to identify suitable areas with higher probability of occurrence for different groups of large marine vertebrates -

including fishes, sea turtles, seabirds and marine mammals - that inhabit the neritic and oceanic regions of southern Brazil.

Location: Southern Brazil, western South Atlantic Ocean.

Methods: We modeled presence-only data of marine megafauna groups in relation to environmental variables using the maximum entropy approach under the Maxent software. We investigated niche similarities between megafauna families using ENMTools software.

Results: Our results showed that marine megafauna hotspots in southern Brazil are present mostly in the continental shelf-break and slope regions, between the 150 and 1000 m isobaths. Niche similarities of megafauna were higher between families of the same group. Two exceptions were observed, of sharks from Carcharhinidae family with turtles (Cheloniidae and Dermochelyidae), and dolphins (Delphinidae) with tunas (Scombridae).

Main Conclusion: Our modeling approach allowed the identification of areas with higher relative suitability for the marine megafauna, including families with species threatened of extinction. These biodiversity hotspots are relevant habitats for conservation and provide support for considering the region an EBSA (Ecologically or Biologically Significant Marine Area) in the western South Atlantic Ocean.

Key words: habitat suitability, hotspot, marine vertebrates, Maxent, maximum entropy modeling, niche overlap.

Introduction

Investigating the spatial distribution of marine species and identifying suitable habitats for them has become the focus of many studies. In particular, understanding habitat use, predicting distribution and identifying aggregation

sites has provided clarification for relevant issues in the conservation and management of marine species (Guisan & Thuiller, 2005; Reese & Brodeur, 2006; Bailey & Thompson 2009; Elith & Leathwick 2009b; Guisan *et al.*, 2013).

Individuals aggregate in particular areas usually to carry out important biological activities such as feeding and reproduction, or even to protect themselves from predation pressure (Palacios *et al.*, 2006). When involving several species, such aggregations lead to areas known as biological hotspots. Hotspot is a widely used term with varying definitions: areas with high biodiversity, intense biological activity, with important links between trophic levels, or simply regions where endemic species aggregate (Myers *et al.*, 2000; Worm *et al.*, 2003; Sydeman *et al.*, 2006). In our study, we refer to sites that have high concentrations of marine animals due to favorable oceanographic and biological conditions (e.g. Palacios *et al.*, 2006). These conditions result from a series of oceanographic features and processes involving physical factors such as sea temperature, ocean fronts and upwelling, or geological features, which can directly influence productivity, abundance and distribution of organisms (Pollard *et al.*, 2002; Friedlaender *et al.*, 2006; Block *et al.*, 2011). Identifying such suitable habitats, predicting species distributions and determining hotspots are key steps for the development of actions in favor of biodiversity (Édren *et al.*, 2010; Hobday & Pelc, 2014).

Predators such as sharks, rays, large teleosts, seabirds, turtles and marine mammals represent the marine megafauna and have important roles in the marine environment (Bowen, 1997; Heithaus *et al.*, 2008; Coll *et al.*, 2013; Moore *et al.*, 2014). This group suffers many anthropic pressures at their habitat, mostly directed and incidental catches by fisheries, but also habitat loss, pollution and

climate change (Bugoni *et al.*, 2001; Derraik, 2002; Myers & Worm, 2003; Halpern *et al.*, 2008; Barbraud *et al.*, 2012).

In southern Brazil, the neritic and oceanic portion (outer shelf and continental slope) extending from Cape Santa Marta Grande, in the state of Santa Catarina, to the city of Chuí, in Rio Grande do Sul, is a high productivity area, and a critical habitat for many species (Odebrecht & Garcia, 1998; Castello *et al.*, 1998; Lopes *et al.*, 2006; Duarte *et al.*, 2014). Different taxa of marine megafauna use this area as foraging grounds or for reproduction (Vooren, 1998; Bugoni *et al.*, 2003; Haimovici *et al.*, 2005; Moreno *et al.*, 2005; Vooren *et al.*, 2005; Zerbini *et al.*, 2004; Neves *et al.*, 2006b; Di Tullio *et al.*, 2016). As a consequence, interactions with fisheries, including gill nets, trawl and pelagic longline are common in the region (Secchi *et al.*, 1997, 2004; Vooren & Klipel, 2005; Dalla Rosa & Secchi, 2007; Bugoni *et al.*, 2008; Carvalho *et al.*, 2011; Fiedler *et al.*, 2012; Passadore *et al.*, 2015). The common use of this habitat allows us to deduce that this region is favorable to aggregations of marine animals and, consequently, a potential biological hotspot. Inclusive, decision makers have considered establishing this area as an Ecologically or Biologically Significant Marine Area (EBSA) (Druel, 2012). Recent studies have addressed the diversity and spatial distribution of some species of dolphins, pinnipeds, turtles and seabirds in the region, eventually determining areas of highest probability of occurrence (Amaral *et al.*, 2015; Carman *et al.*, 2016; Di Tullio *et al.*, 2016). However, little is known about marine megafauna hotspots or whether there is niche overlap between these large predators.

Species distribution modeling techniques, including ecological niche modeling, have aided in identifying biodiversity hotspots. This process begins

with observations of occurrences of one or more species and environmental variables that may influence the formation of preferred or suitable habitats (Franklin, 2010; Peterson *et al.*, 2011). Besides the knowledge of critical areas, species distribution models have also helped clarifying which environmental factors determine the spatial extent of some groups (Ainley *et al.*, 2009; Suryan *et al.*, 2012; Bouchet *et al.*, 2015). Among many species distribution modeling methods (e. g. Guisan & Zimmermann, 2000; Elith *et al.*, 2006; Franklin, 2010), the maximum entropy approach has been effective for marine megafauna niche modeling and the determination of biological hotspots (Ainley *et al.*, 2011; Friedlaender *et al.*, 2011; Nachtsheim *et al.*, 2016). This approach using Maxent sets out to model the geographical distribution of species with presence-only data in relation to environmental variables, allowing us to make predictions or inferences from restricted information, when there is no reliable absence data (Phillips *et al.*, 2006; Elith *et al.*, 2011).

Our main objective was to investigate the occurrence of biological hotspots and overlapping marine megafauna niches off southern Brazil. Due to oceanographic features of the area and its high productivity, we hypothesize that regions with greater bathymetric complexities (shelf break/slope), and next to recurring oceanic fronts, have conditions that favor the simultaneous occurrence of a large number of families of marine megafauna.

Methods

Study Area

The study area covers an area limited by the southern line of the island of Florianópolis (~ 28°S) to Chuí (~ 34°S) extending to the oceanic region of outer

shelf and continental slope (Fig. 1A). The productivity of this region is explained by a number of oceanographic factors occurring simultaneously and with seasonal pattern, making this an important region for the fishing industry (Haimovici *et al.*, 1997). In this area, the continental shelf and slope are influenced by the Brazil Current, subantarctic waters brought about by the Malvinas Current and continental water discharges that form the Subtropical Shelf Front (Möller *et al.*, 2008; Piola *et al.*, 2008). This thermohaline surface front extends from near the 50m isobath at 32°S to the shelf break at 36°S, with strong influence of winds and the continental waters coming from the La Plata River and the Patos Lagoon (Piola *et al.*, 2000; Acha *et al.*, 2004). In addition, shelf break upwelling phenomena influence nutrient and chlorophyll-a concentration as well as zooplankton densities, increasing local productivity (Braga *et al.*, 2008; Muelbert *et al.*, 2008).

The marine megafauna in this study were represented by different families of marine vertebrates, including fish, sea turtles, seabirds and marine mammals. The georeferenced presence records used to identify potential hotspots originate from different databases (Table 1), including sighting data (seabirds and cetaceans) and directed or incidental catches in trawl and gillnets (elasmobranchs) or pelagic longline (elasmobranchs, teleosts, seabirds and sea turtles).

Modeling the distribution of marine megafauna

To identify hotspots of marine megafauna families, we modeled presence-only data in relation to environmental variables using the maximum entropy approach under Maxent software v.3.3.3 (available at www.cs.princeton.edu/~schapire/maxent) (Merow *et al.*, 2013). Occurrence data

generally have strong spatial bias in data collection, primarily due to greater effort in certain areas considered more accessible than others for sampling. This bias can result in misinterpreted models, so to minimize this effect Maxent generates background data (Phillips *et al.*, 2009) or pseudo-absences, which have the same sample bias as the occurrence data used to generate the models (Phillips & Dudík, 2008). For model building, different configurations were tested; however, standard Maxent parameters were used as they generated the best predictions (Phillips *et al.*, 2006; Merow *et al.*, 2013). With the cross-validation technique, 10 replicates of the models were generated for each of the marine megafauna families, and the average of these replicas was considered the final model. The predictive performance of models was evaluated according to the AUC (Area Under the Curve), a metric produced by the ROC curve (Receiver Operator Characteristic) which shows a graphic relationship of the values of true positives against the values of false positives. Thus, the AUC is used to identify the probability that a cell containing a presence has a greater predictive value of a cell that does not contain any presence, which are chosen at random (Elith *et al.*, 2006). The AUC values then demonstrate the accuracy of the model at rates that vary from 0.5 to 1.0; the closer to 1.0, the better the performance and accuracy of the model (Phillips *et al.*, 2006). In addition, Maxent provided the percentage contribution of the variables to the models, which was used to identify which variables contributed more to the estimated probabilities.

Environmental data

The physiographic variables used in the megafauna distribution models were bathymetry, seafloor slope and distance to shore. Bathymetry was obtained from the ETOPO1 three-dimensional elevation model (Amante & Eakins, 2009),

with 1 minute horizontal resolution and 10 m of vertical accuracy (available from the National Geophysical Data Center, NOAA). Slope was generated from the bathymetry data in a GIS (Geographic Information System) using the Slope function, and distance from the coastline was generated from the Euclidean Distance function. Annual means of chlorophyll-a and sea surface temperature climatologies obtained from images of AQUA-Modis satellite (available at Ocean Color - NASA's Goddard Space Flight Center) were also included in the models. All variables were imported and processed by the free QGIS version 2.12 software (QGIS Development Team, 2015) so that they were in the same coordinate system and with the same resolution (4km) and spatial extent. After processed, all variables were converted to ASC format files (format required for the modeling process).

Strongly correlated variables can influence species distribution modeling and provide misinterpretations regarding their importance (Zuur *et al.*, 2010), so Pearson correlations between variables were calculated prior to modeling. A high correlation between bathymetry and distance from the coast (> 0.8) was observed, thus the latter was excluded from the modeling process.

Graphical representation of models

The files with occurrence probability values generated by the models were imported into QGIS for representation on maps. The overall hotspot map of marine megafauna was generated from the probability maps of each family by taking the mean value of the relative probabilities per pixel from all maps overlapped.

Niche Overlap

Niche overlap among families of marine megafauna was quantified by the Schoener's index of similarity (Schoener, 1968) using the software ENMTools 1.4 (Warren *et al.*, 2008). This method compares niches in pairs from the mean occurrence probabilities of megafauna families. Schoener's niche overlap index (D) provides an ecological interpretation of niche similarities between populations, ranging from 0 (when the species have no overlap at all) to 1 (when all grid cells are estimated as similar for both species) (Warren *et al.*, 2010). In our study, values of $D \geq 0.65$ were considered high and indicative of significant niche overlap.

Results

Marine megafauna hotspots

A total of 2,934 georeferenced occurrences of 14 families of the megafauna were obtained (Fig. 1B-G). These included two families of seabirds: Diomedidae (N = 752) and Procellariidae (N = 877); two of marine mammals: Delphinidae (N = 316) and Phyllopterygiidae (N = 180); two of sea turtles: Cheloniidae (N = 161) and Dermochelyidae (N = 48); five of sharks: Triakidae (N = 96), Hexanchidae (N = 40), Squalidae (N = 66), Sphyrnidae (N = 71) and Carcharhinidae (N = 66); two of rays: Rajidae (N = 191) and Rhinobatidae (N = 51); and one teleost family: Scombridae (N = 19).

The probability maps generated from the Maxent models are shown in Figs. 2-8. The ROC curves demonstrated good performance and accuracy of the models (Table 2), with high AUC values (0.79 – 0.96) and low standard deviation, indicating uniformity of results. In all final models, the four environmental variables tested were selected, but with different contribution percentages (Table

2). In general, bathymetry was the variable with the largest contribution to the models, followed by the slope (Table 2). However, the suitable areas with high probabilities of occurrence varied according to the different families (Figs. 2-8).

Seabirds: For both families, the variables that contributed the most to the selected models were bathymetry and sea surface temperature (Table 2). The areas of high and medium probability of occurrence were similar, over the continental slope (Fig. 2). The highest probabilities of presence occurred beyond the 150 m and mostly around 1000 m isobath. North of 30°S latitude, high probabilities extended to areas deeper than 1000 m. The Procellariidae family also had an area with a high probability of occurrence beyond the 3000-m depth, near longitude 44°W (Fig. 2).

Sea turtles: The variables with the highest contribution to the sea turtle models were bathymetry and slope. Both families showed relatively similar areas with high probability of occurrence (Table 21 and Fig. 3). High and medium probabilities were estimated between the continental shelf break (about 200m) and around the 1000 m isobath. However, high probability areas for Dermochelyidae concentrated between latitude 30° and 32°S, while for Cheloniidae they extended further south, between 30° and 34°S.

Marine Mammals: Bathymetry was the variable with the greatest contribution to the models for both cetacean families (Table 2). However, different areas of high probability of occurrence were predicted for them (Fig. 4). For the Delphinidae, the variables slope and temperature also contributed with similar percentages to the model (Table 2). The area of high probability of occurrence was continuous and was located north of the 32°S latitude, between the 150 and 1000 m isobaths (Fig. 4). For the Physeteridae, slope and chlorophyll-a also contributed to the

model, and the areas of high probability of occurrence were predicted over the 1000 m isobath or deeper (Table 2 and Fig. 4). For this family, three distinct areas of high and medium probability of occurrence stood out, which are: 1) close to 34°S; 2) between 30 and 32°S; and 3) near the Santa Marta Cape (~ 29°S).

Sharks: Bathymetry, followed by slope, was the variable with the highest contribution to models for Carcharhinidae, Hexanchidae and Squalidae (Table 2). The area with the highest probability of occurrence of Carcharhinidae was estimated near the coast, while areas with medium probability were located between the shelf break and the continental slope (Fig. 5). The Hexanchidae family, when compared to other families of sharks, presented a narrower area of high probability of occurrence, located between the shelf break and continental slope (Fig. 5). Areas of high and medium probabilities of Squalidae were similar to the Hexanchidae, but also included shallower waters of the continental shelf south of 33°S (Fig. 5). Chlorophyll-a and bathymetry contributed the most to the Sphyrnidae model (Table 2). High occurrence probabilities for this family were predicted in coastal areas, especially south of 30°S, whereas areas of medium probability also extended to deeper areas of the continental shelf and continental slope (Fig. 5). For the Triakidae model, chlorophyll-a contributed the most, followed by slope and bathymetry (Table 2). Areas of high probability of occurrence for this family were located on the shelf break and continental slope south of 30°S, and at the coastal zone near latitude 34°S. Some discontinuous areas of medium probability were also predicted along the coastal zone (Fig. 5).

Rays: The variables with the highest contribution were different for the two families of rays resulting also in different areas of high probability of occurrence. For the Rajidae, bathymetry was the most influential variable in the model (Table

2), which showed two areas of high probability associated with the shelf break and the coastal zone north of 32°S (Fig. 6). Bathymetry and chlorophyll-a contributed the most to the Rhinobatidae model. The high probability of occurrence for this family was limited to the area south of the study area (~ 34°S), on the inner shelf and coastal areas (Fig. 6). Areas of medium probability were distributed to the south of 30°S.

Tunas: Bathymetry and chlorophyll-a contributed the most to the Scombridae model. The highest probabilities of occurrence were predicted around the 1000 m isobath south of 30°S. In addition, a medium probability area near the same depth was predicted at 29°S (Fig. 7).

Overall megafauna hotspot map: the area with high probability of occurrence for megafauna groups followed the bathymetric gradient of the region, including areas near the shelf break (~ 200 m deep) and deeper waters of the continental slope. Medium probability areas were also found near the coast (Fig. 8).

Niche Overlap

Shoener's niche overlap index (D) ranged from 0.05 to 0.92 (Table 3). The highest D values were obtained between families of the same taxon: seabirds (D = 0.92) and sea turtles (D = 0.82). However, niche overlap was considered low (D = 0.49) between the two cetacean families. Between the shark families, with the exception of low overlap between Carcharhinidae and Hexanchidae (D = 0.33), the index values ranged between 0.60 and 0.74. The two ray families Rajidae and Rhinobatidae showed relatively high overlap (D = 0.68). High niche overlap was also observed between Rajidae and the shark families Triakidae (D = 0.79), Sphyrnidae (D = 0.66) and Squalidae (0.74). In addition, high niche

overlap values were found between Carcharhinidae and the sea turtles Cheloniidae ($D = 0.70$) and Dermochelyidae ($D = 0.65$), and between Delphinidae and Scombridae ($D = 0.66$).

Discussion

Our study showed areas of high probability of occurrence and niche overlap for 14 families of marine megafauna that inhabit waters of subtropical western South Atlantic, off southern Brazil. Understanding the mechanisms that lead to the formation of a hotspot is a key step for identifying areas of ecological importance (Hazen et al.2013). Key habitats for marine megafauna can be identified from locations with high probabilities of occurrence (Édren et al.2010; Moura et al.2012). Analyses that take into account higher taxonomic levels help understanding how a community uses a certain habitat, unlike species-specific analyses which identify ecological responses relevant to only one species of interest (McClellan et al.2014; Myers, 2000). The identification of important habitats for marine megafauna can be used to prioritize areas that fit the criteria for the creation of areas of biological or ecological relevance (Ecologically or Biologically Significant Areas - EBSAs), enabling the conservation and management of biodiversity and its habitat (Dunn et al.2014).

Different habitat modeling tools have been used to identify biodiversity hotspots. In this work, we used the maximum entropy method implemented with the Maxent software, which relates presence data of the families with environmental variables (Phillips *et al.*, 2006). The AUC values, which evaluate the model's performance, ranged from 0.79 to 0.96 and were considered excellent. Other studies that have also used the maximum entropy approach to model marine megafauna found similar AUC values to ours. Marine megafauna

distribution models in the English Channel and the North Sea region, with taxa similar to our study, resulted in AUC values ranging from 0.69 to 0.92 (McClellan *et al.*, 2014). On the other hand, distribution models including one species of albatross, three of sea turtles and two of pinnipeds in the region of the La Plata River region, Uruguay, resulted in AUC values from 0.86 to 0.93 (Carman *et al.*, 2016).

Areas of high probability of occurrence of marine megafauna were found on both the continental shelf and slope, depending on the family. Yet, in general, such areas were concentrated mainly on the shelf break and continental slope, probably due to the high productivity and food availability for the megafauna. This region is influenced by oligotrophic waters brought about by the Brazil current during most of the year (Niencheski & Filmann, 1998), and by subantarctic waters rich in nutrients brought by the Falklands current, which advance over the continental shelf mainly during the winter period (Piola, 2005). Continental water discharges from the Patos Lagoon and the La Plata River also influence the productivity of coastal and continental shelf waters (Seeliger & Odebrecht, 1998; Acha, 2004). Therefore, the south continental shelf and slope are influenced by the action of different water masses of the Brazil Current, the Falklands current and continental waters forming the Subtropical Shelf Front, which is controlled by seasonal wind patterns (Möller *et al.*, 2008, Piola *et al.*, 2008). The shelf break also experiences a seasonal pattern of upwelling occurrences of Subtropical Water origin and, depending on their intensity, these events lead to nutrient enrichment and increased productivity (Brandini, 1990; Castello *et al.*, 1998). All these processes occurring together with seasonal variations are responsible for high biological productivity from the coastal zone to the continental slope

(Castello *et al.*, 1998; Duarte *et al.*, 2014), and likely provide suitable habitats for the megafauna investigated in our study.

When we analyzed the maps of occurrence of the megafauna families individually, we observed that the higher probabilities were generally aggregated at two main areas: one neritic (in the coastal zone and inner shelf) and the other more oceanic (shelf break and slope). The distributions of the families were influenced in different ways by the variables in the models, though bathymetry contributed the most to most taxa. Bathymetry was also the variable that most contributed to models of marine megafauna in the La Plata River region (Carman *et al.*, 2016), as well as in the distribution modeling of Delphinidae (Varassim, 2014) and of three *Stenella* species (Amaral *et al.*, 2015) on the Brazilian coast. More so, bathymetry was one of the variables that best explained the foraging movements of two seabird species of the Procellariidae family in the Mediterranean Sea (Afán *et al.*, 2013). Distributions of marine turtles in the Tropical Pacific Ocean and sharks in the Gulf of Mexico were best explained by distance from the coast and chlorophyll-a, respectively (McKinney *et al.*, 2012; Peavey, 2010). Such differences in the contributions of environmental variables among the taxa were also observed in this study as follows.

The distribution of hotspots for the two families of seabirds (Diomedidae and Procellariidae) was also influenced by sea surface temperature, in addition to bathymetry. For these seabirds, the areas of high probability of occurrence increased to the north, at latitudes lower than 30°S. This area is located close to the Santa Marta Cape, known for the upwelling events of Central Atlantic water, rich in nutrients that are resuspended increasing local productivity (Castello & Möller, 1977; Matsuura, 1986). In this region at the northern part of the study

area, there is greater influence of the Brazil Current, which has higher surface temperatures that may contribute to the observed pattern. In addition, the shelf break and slope region is an important foraging and feeding ground for about 20 species from these two families that disperse from the colonies during the austral winter and are more abundant during this period in which they find the energy resources that sustain their migratory cycles (Vooren, 1998; Neves *et al.*, 2006b; Olmos *et al.*, 2006; Colabuono & Vooren, 2007).

The area of highest probability of occurrence of the Delphinidae family was enclosed in the waters near the shelf break and slope, especially north of 32°S. In addition to depth and slope, temperature was also a variable that contributed significantly to the explanatory power of models. The Delphinidae family includes around 36 species, with a wide variety of foraging strategies and prey including fish, cephalopods and other marine mammals (Lopes *et al.*, 2012; Santos & Haimovici, 2002). There is also a wide spatial distribution in this family, with species that inhabit warmer or tropical waters, such as *Stenella frontalis*, *S. attenuata*, *S. longirostris* (Moreno *et al.*, 2005) and *Steno bredanensis* (Lodi & Hetzel, 1998), or a much wider spectrum including cold waters such as *Orcinus orca* (Ford, 2009). The most abundant species in the Delphinidae database were *S. frontalis* and *Delphinus delphis*, however *S. frontalis* has an occurrence pattern further north of the Rio Grande do Sul State (Moreno *et al.*, 2005; Tavares, 2010; Di Tullio *et al.*, 2016). Therefore, the influence of temperature on the Delphinidae model may be partly explained by the higher densities of *S. frontalis* in coexistence with *D. delphis*, in the northern part of the study area (Di Tullio *et al.*, 2016), where temperature is slightly higher from influence of the Brazil Current.

The Physeteridae family, monospecific and represented by the sperm whale (*Physeter macrocephalus*), is one of the cetacean families with higher occurrences in waters over the continental slope of southern Brazil (Di Tullio *et al.*, 2016). This species preys on a variety of items, but mainly on prey associated with great depths such as squids of the *Illex* genus from the shelf break and slope region (Clarke *et al.*, 1980; Whitehead, 2003). In addition to bathymetry and slope, chlorophyll-a concentration showed a significant contribution to the selected model. Productivity is an important factor in observed diversity patterns of cetacean that inhabit deep waters such as *P. macrocephalus* (Jaquet & Whitehead, 1996). The increased productivity of the shelf break and slope also seems to influence the seasonal presence of sperm whale prey at the southernmost part of the study area (Santos & Haimovici, 2000; Haimovici *et al.*, 2014).

Sea turtles also showed major influences from bathymetry and slope for the areas of high and medium probability of occurrence. Species representative of the Cheloniidae family, *Caretta caretta* and *Chelonia mydas*, feed primarily on the coastal zone of the study area, targeting on shellfish, fish, crustaceans and green algae (Bugoni *et al.*, 2003; Santos *et al.*, 2011). The Dermochelyidae family, represented by *Dermochelys coriacea*, is known to inhabit oceanic waters where the species prey on gelatinous zooplankton such as celenterates (Almeida *et al.*, 2011; Saba, 2013). Our results show that these families occur in areas of shelf break and continental slope. The area of high probability of occurrence for *D. coriacea* is similar to that found by Carman *et al.* (2016). For *C. caretta*, the most abundant species in the occurrence data for Cheloniidae, the results did not follow the pattern observed by Carman *et al.* (2016), of higher probability of

occurrence in the coastal region. This difference, however, is likely because juvenile individuals in that region use the estuarine habitat for feeding (González Carman *et al.*, 2016), whereas *C. caretta* juveniles in our study area seem to prefer the pelagic environment of the shelf break and slope (Giffoni *et al.*, 2008; Pons *et al.*, 2010).

Sharks and rays varied in their patterns of occurrence. They were the only megafauna groups in our study that included families with higher probability of occurrence in the coastal region of the continental shelf. Such pattern is due to the presence of newborn and juvenile sharks and rays (Vooren & Klimpel 2005; Galina, 2006). The families with high and medium probability of occurrence in the coastal zone and inner shelf were Sphyrnidae, Carcharhinidae and Rhinobatidae. This region is characterized by high chlorophyll-a concentrations and high productivity (Acha *et al.*, 2004). These factors coupled with the low depth make this area a key region for the development of these individuals, due to greater food availability and lower predation risk (Simpfendorfer & Heupel, 2012). Thus, species of Carcharhinidae, Sphyrnidae, Rajidae and Rhinobatidae take advantage of using this coastal region as nursery grounds (Vooren & Klimpel, 2005). The results for Carcharhinidae and Sphyrnidae, pointing to the shelf break and beyond, can be explained by the use of this habitat by juveniles/subadults of *Prionace glauca* and adults of *Sphyrna lewini* and *S. zygaena* (Kotas, 2004; Carvalho *et al.*, 2011). *Prionace glauca* shows latitudinal segregation, with adults being distributed at latitudes lower than 30°S and sub-adults and juveniles at latitudes above, with higher abundance on the shelf break off Rio Grande do Sul State and at the Rio Grande Elevation (Montealegre-Quijano & Vooren, 2010; Carvalho *et al.*, 2011). Adults of *S. lewini* and *S. zygaena*, in turn, occupy the end

portion of the shelf and adjacent regions, with intraspecific seasonal variations in abundance (Kotas, 2004). The Rajidae and Rhinobatidae rays also show this pattern of newborns at the coastal region and adults in areas with greater depths (Vooren *et al.*, 2005). In our study, the areas of high probability of occurrence of these two families were different. Rhinobatidae was concentrated mostly in coastal areas, while Rajidae had areas with high probability over the shelf break, indicating that these individuals in our dataset were probably recorded in different periods of their life cycle.

Sharks of the Triakidae family showed aggregations both on the shelf break and in smaller areas of higher probability of occurrence in coastal areas, regions with high concentrations of chlorophyll-a and productivity. In fact, their model had a high contribution of the chlorophyll-a variable. The Squalidae family had an area of high probability of occurrence on the shelf break and a smaller area at the inner shelf. This family occurs in areas 40 to 300 meters deep, ranging between species, and are considered bottom sharks, occurring at the coastal region when juveniles (Calderon, 1994), what explains their presence on the shelf region. The Hexanchidae family (*Hexanchus griseus* and *Heptranchias perlo*) is distributed in areas between 100 and 300 meters deep, except for one species (*Notorynchus cepedianus*) that can occur in shallow waters in winter (Soto, 1999), but that was not present in our dataset.

The diet of elasmobranchs is widely diverse. Rays feed on crustaceans, fish, polychaetes and other benthic invertebrates, whereas sharks, in addition to the above prey, also feed on cephalopods or other smaller sharks (Aguiar & Valentin, 2010). Therefore, the observed variation in areas of occurrence of the families of rays and sharks may be linked not only to the different use of habitat

throughout their life cycle, but also to changes in habitat use related to the distribution of their preferred prey.

Areas of high probability of occurrence for the Scombridae were identified between the shelf break and the continental slope. The tunas included in our study (*Thunnus alalunga*, *T. obesus* and *T. albacares*) inhabit the outer continental shelf, slope and deep water, migrating seasonally during the winter to southern Brazil, where they become an important fishery resource (Castello, 1998; Haimovici *et al.*, 1998). Their prey includes cephalopods, mainly of the genus *Illex*, which are abundant over the shelf break and continental slope (Schwingel & Mazzoleni, 2004; Gasalla *et al.*, 2010; Haimovici *et al.*, 2014). Despite the low sample size of tuna records in our dataset, we believe this was not an issue for detecting areas of high probability of occurrence for this family. Other studies using Maxent for niche modeling with limited number of occurrences showed no problem with sample size for identification of suitable areas (Shcheglovitova & Anderson, 2013; Peter *et al.*, 2016). Furthermore, the Maxent is known for not having major limitations on the required number of occurrences, and is one of methods with better predictive power for different sample sizes such as 10, 30 and 100 records (Pearson *et al.* 2007; Wiza *et al.*, 2008).

Niche overlap between some families in our study was demonstrated by the results of the Schoener's index. The high similarity found between the two sea turtle families may be explained by the occurrence of Cheloniidae juveniles in the same pelagic habitat of Dermochelyidae turtles (Almeida *et al.*, 2011; Santos *et al.*, 2011). The seabirds that also showed considerable amount of similarity are likely using the same areas to feed (Neves *et al.*, 2006b). Rays and

sharks also showed high levels of similarity in our study. Although few studies have compared these two groups in the region, we believe the high similarity is probably caused the wide trophic niche they occupy (Aguilar & Valentin, 2010), often sharing the habitat during their life cycles (Vooren & Klippel, 2005). In other areas along the Brazilian coast, sharks and rays show different patterns in the use of nursery areas, which can be seasonal, but may also coexist depending on resource availability in the area (Yokota & Lessa, 2006).

The high niche overlap between Delphinidae and Scombridae was expected. Studies in the North Atlantic and the Western Pacific show that associations between small tunas and dolphins are common and beneficial for foraging or reducing the risk of predation (Clua & Grosvalet, 2001; Scott *et al.*, 2012; Goyert *et al.*, 2014). This high overlap may be associated with the common prey for both families. *S. frontalis* and *D. delphis*, the two cetacean species with most records in our dataset, prey on cephalopods such as the *Doryteuthis* genus, which is present in the tuna diet (Scwingel & Mazzoleni, 2004; Melo *et al.*, 2010). In addition, our data includes records of larger Delphinidae such as *Orcinus orca* and *Pseudorca crassidens*, which interact with surface longline fisheries in the same region where areas of high probability of occurrence of these families were detected (Secchi & Vaske Jr., 1998; Dalla Rosa & Secchi, 2007; Passadore *et al.*, 2015) and, potentially, may also prey naturally on tunas. The horizontal niche overlap between the different families suggests that these environments have sufficient productivity to support the ecological requirements of these groups.

The marine megafauna hotspots demonstrated in this study from the overlapping map of relative probabilities of occurrence identified the shelf break and continental slope region as an important area for the covered taxa. Our study

area (from Santa Marta Cape, in Brazil, to Chuí, at the border with Uruguay) has been included in the discussions of the Convention on Biological Diversity, aimed at considering it an Ecologically or Biologically Significant Marine Area (EBSA). Among the scientific criteria evaluated by the Convention, the study area has medium and high justifications (low on only one criterion) to make it an EBSA. The favorable arguments include: area of particular importance to the life stages of species, area of importance to threatened, endangered or declining species or habitats, and area with biological productivity (CBD, 2012).

Several species representing the families addressed in our study are threatened by anthropogenic factors present in the region, such as interactions with intense fishing activity (Bugoni *et al.*, 2008; Vooren & Klipel, 2005; Carvalho *et al.*, 2011). According to IUCN (International Union for Conservation of Nature and Natural Resources, 2016) criteria, the albatross *Tallassarque cholorhynchos* is threatened of extinction and the sea turtle *Dermochelys coriacea* is considered critically endangered. In addition to these species, sharks (*Sphyrna* spp., *Prionace glauca*, *Mustelus* sp., *Galeorhinus galeus*) and rays (*Rhinobatos horkelli* and *Sympterygia* spp.) that integrate our dataset are included in lists of endangered species at the national and state levels, occupying the vulnerable and critically endangered categories (Portaria Nº 445 of 17 December 2014, Ministry of the Environment; Decreto nº 51.797 of 8 September 2014, Diário Oficial do Rio Grande do Sul). Among other factors that may affect marine megafauna in the study area, there is also the potential for oil and gas exploration in the region. The Pelotas Basin, which overlaps with part of the megafauna hotspots, has been assigned blocks of interest to the oil and natural gas exploration (MME, 2015). Therefore, the marine megafauna hotspots we

identified by modeling the presence of several species of marine vertebrates reinforces the ecological importance of the region, and should be considered in future actions aimed at the management and conservation of these taxa and their habitat.

The models we fitted with Maxent demonstrated important areas to the marine megafauna, emphasizing the importance of modeling studies using presence-only data when information on sampling effort is either difficult to integrate or absent (Graham *et al.*, 2004). The areas with estimated probabilities of occurrence reflect relative habitat suitability for the presence of marine megafauna conditioned on the environmental variables included in the models (Phillips *et al.*, 2006; Elith *et al.*, 2011), and should not be considered as the actual distribution of these groups at a particular moment, but as potential occurrence areas. One important aspect that requires careful attention when interpreting our results is that the analyses were conducted at the family level, and do not consider species-specific characteristics except for families represented by a single species. The use of data from different sources and collection efforts, including sightings and incidental or direct captures, represents another potential caveat, as some efforts focused on the shelf break and continental slope, and others on the continental shelf. While this broad scope of the data was desirable to best represent the marine megafauna, it might have also introduced some spatial biases. Nevertheless, Maxent is considered robust in this regard (Elith *et al.* 2011; Friedlaender *et al.*, 2011), as specific measures were implemented as part of the modeling process to minimize potential spatial biases, such as generating background data, eliminating duplicate records and using cross-validation techniques. Yet, it is possible that some relevant areas for the marine

megafauna were not identified. For instance, the coastal zone of the study area is an important feeding area for adult sea turtles (Santos *et al.*, 2011), but only medium relative probabilities of occurrence were predicted for the Cheloniidae in this area. Therefore, presence records relating to particular species life stages might have influenced some of our results. Furthermore, some species show clear seasonal distribution patterns in the region, such as sharks of the genus *Sphyrna* (Kotas, 2004). Seasonal variations in occurrence probabilities were not considered in our models due to data limitations. Obtaining additional presence records for some of the megafauna families, especially on the continental shelf, and fitting seasonal models will help improving the identification of marine megafauna hotspots in the subtropical western South Atlantic.

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BIOSKETCH

Suelen Goulart is a biologist; her interests are focused on ecology and conservation of marine megafauna using species distribution models. This work constituted her Master's dissertation under the supervision of L.D.R.

Author contributions: S.G. and L.D.R conceived the idea; J.C.D.T., B.B.G., L.G.C. and L.D.R collected the data; S.G. and L.D.R. conducted the analysis and led the writing, all authors provided comments and revisions to the manuscript.

Table 1. Data types and sources of occurrence records of different groups of marine vertebrates used for modeling the marine megafauna off southern Brazil.

Marine Megafauna	Type of data	Source
Seabirds	Sightings and incidental captures in pelagic longline	Projeto Albatroz
Marine Mammals	Sightings and incidental captures	Projeto Talude and SIMMAM
Sea Turtles	Incidental captures in pelagic longline	Projeto TAMAR
Sharks	Incidental and target captures in pelagic longline and gillnet	Programa Revizee, Laboratório de Recursos Pesqueiros Demersais, GBIF and ECOMEGA
Rays	Incidental captures in bottom longline and gillnet	Programa Revizee, Laboratório de Recursos Pesqueiros Demersais and GBIF
Tunas	Pelagic longline catches	Projeto ARGO and GBIF

Table 2. Area under the curve (AUC) values, standard deviation of AUC (sd) and percentage contribution of variables in the models generated by Maxent for each of the megafauna families. Bat = bathymetry; Decl = slope; Temp = temperature; Clo-a = Chlorophyll-a.

Megafauna	AUC	AUC (sd)	Variable Contribution (%)			
			Bat	Slope	Temp	Chlo_a
Seabirds						
Procellariidae	0.81	0.02	34.8	12.1	48.9	4.1
Diomedeidae	0.82	0.02	36.5	20.7	36.5	6
Sea turtles						
Cheloniidae	0.82	0.04	47.2	40.8	9.5	2.5
Dermochelyidae	0.84	0.08	43.9	44.4	10.3	1.4
Mammals						
Delphinidae	0.90	0.02	43.8	24	23.4	8.8
Physeteridae	0.93	0.02	54.9	24.7	3.4	17.1
Sharks						
Carcharhinidae	0.79	0.07	81.4	9.6	7	1.9
Hexanchidae	0.96	0.01	74.5	16.4	1.6	7.4
Squalidae	0.92	0.06	55.9	30.9	0.9	12.4
Sphyrnidae	0.85	0.05	34.4	5.3	5.7	54.6

Triakidae	0.91	0.03	19.3	20.9	1.8	58.1
Rays						
Rajidae	0.88	0.02	80.5	11.8	3.9	3.7
Rhinobatidae	0.92	0.02	52.2	4.8	2.2	40.8
Tunas						
Scombridae	0.91	0.07	66.6	13.6	0.1	19.8

Table 3: Values of Schoener's index (D) of niche overlap (with varying rates from 0 to 1) of marine megafauna families. Tri =Triakidae; Car=Carcharhinidae; Che=Cheloniidae; Del=Delphinidae; Der=Dermochelyidae; Dio=Diomedidae; Hex=Hexanchidae; Phy=Physeteridae; Pro=Procellariidae; Raj=Rajidae; Rhi=Rhinobatidae; Sco=Scombridae; Sph=Sphyrnidae; Squ=Squalidae. Highlighted Values show high similarities between families of different taxa and between Rajidae and three families of sharks.

FAMÍLIAS	Tria	Car	Che	Del	Der	Dio	Hex	Phy	Pro	Raj	Rhi	Sco	Sph	Squ
Tri	1	0.62	0.42	0.58	0.37	0.17	0.49	0.24	0.17	0.79	0.59	0.56	0.66	0.78
Car		1	0.70	0.62	0.65	0.51	0.33	0.41	0.50	0.58	0.49	0.61	0.74	0.60
Che			1	0.58	0.82	0.63	0.26	0.56	0.60	0.35	0.25	0.57	0.56	0.42
Del				1	0.62	0.39	0.55	0.49	0.37	0.53	0.30	0.66	0.54	0.61
Der					1	0.64	0.32	0.58	0.63	0.31	0.18	0.59	0.49	0.38
Dio						1	0.15	0.45	0.92	0.14	0.07	0.33	0.34	0.20
Hex							1	0.21	0.15	0.46	0.21	0.41	0.28	0.56
Phy								1	0.41	0.16	0.05	0.59	0.37	0.24
Pro									1	0.14	0.07	0.31	0.32	0.19
Raj										1	0.68	0.53	0.66	0.74
Rhi											1	0.36	0.60	0.55
Sco												1	0.59	0.57
Sph													1	0.59
Squ														1

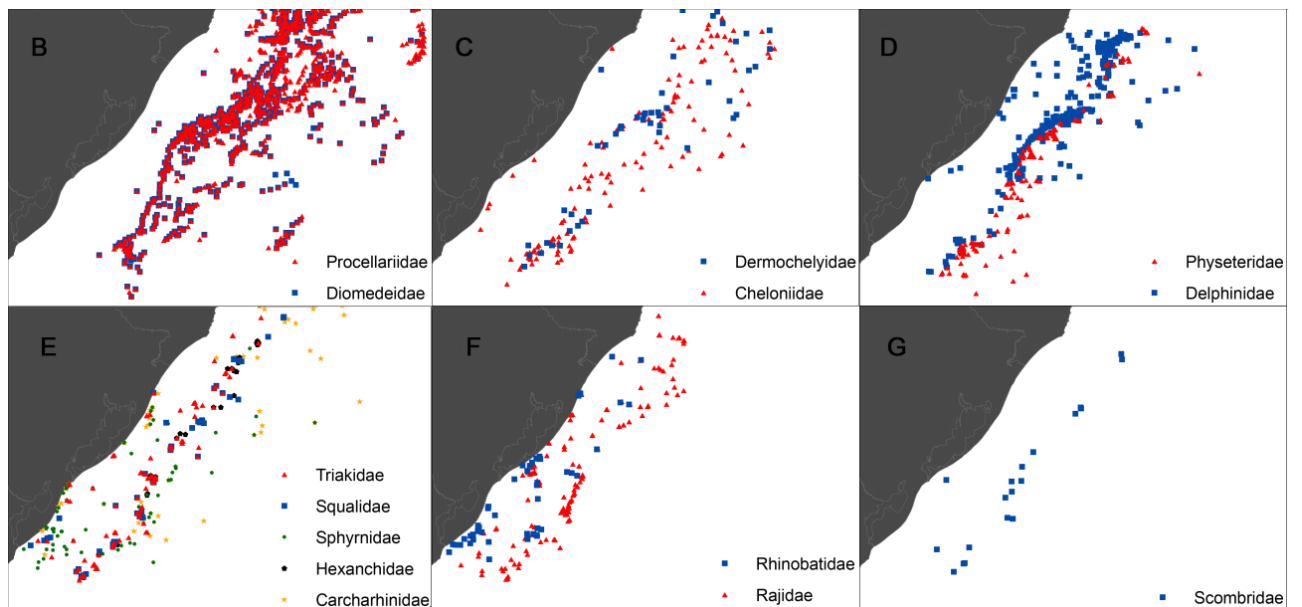
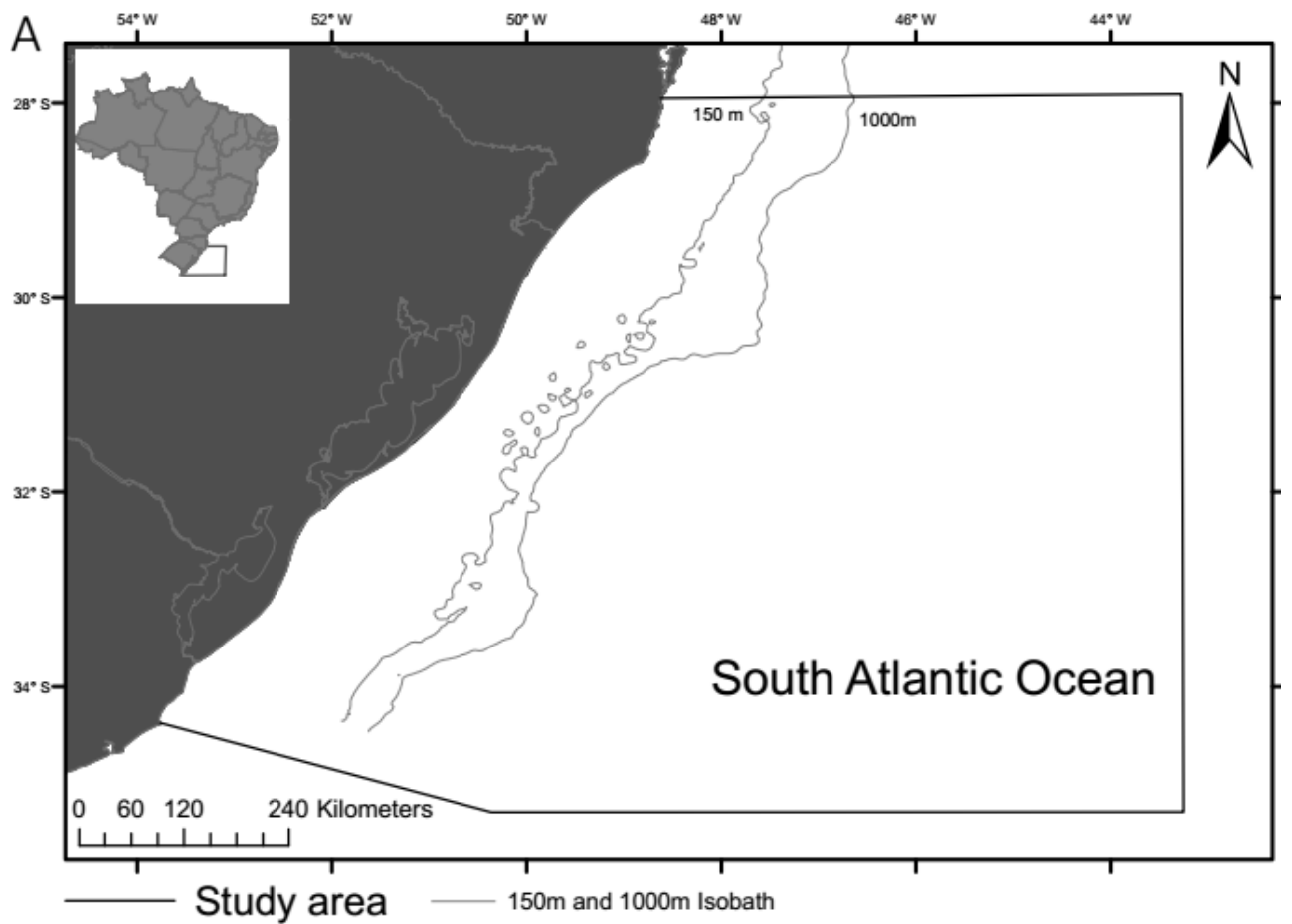


Figure 1: Study area for modeling marine megafauna (A) and presence data of (B) seabirds, (C) sea turtles, (D) marine mammals, (E) Sharks, (F) Rays and (G) Tunas.

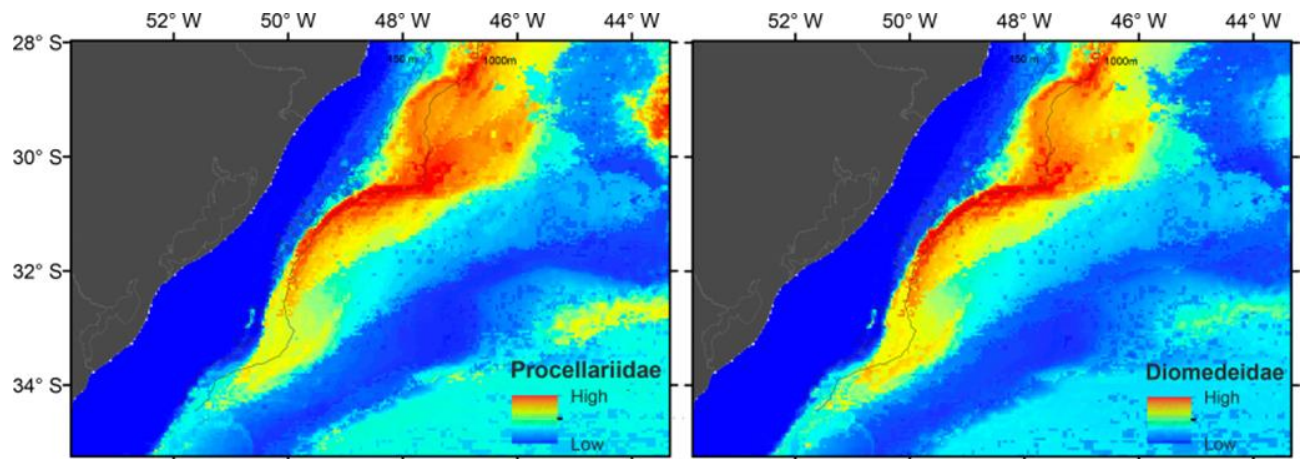


Figure 2: Areas of high probability of occurrence of seabirds of the Procellariidae and Diomedaeidae families off southern Brazil obtained by Maxent.

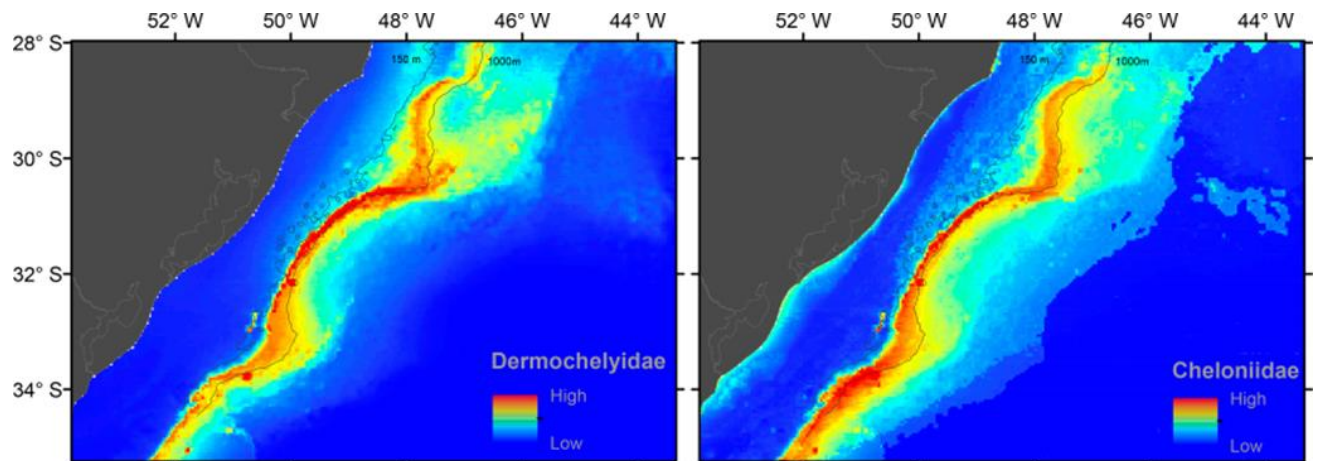


Figure 3: Areas of high probability of occurrence of sea turtles of the Dermochelyidae and Cheloniidae families off southern Brazil obtained by Maxent.

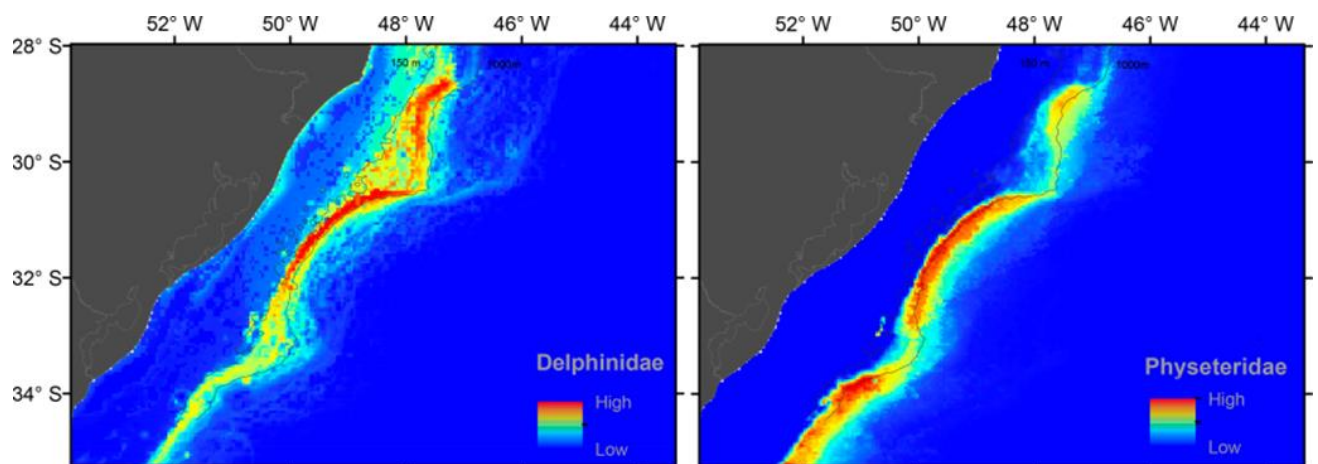


Figure 4: Areas of high probability of occurrence of cetaceans of the Delphinidae and Physeteridae families off southern Brazil obtained by Maxent.

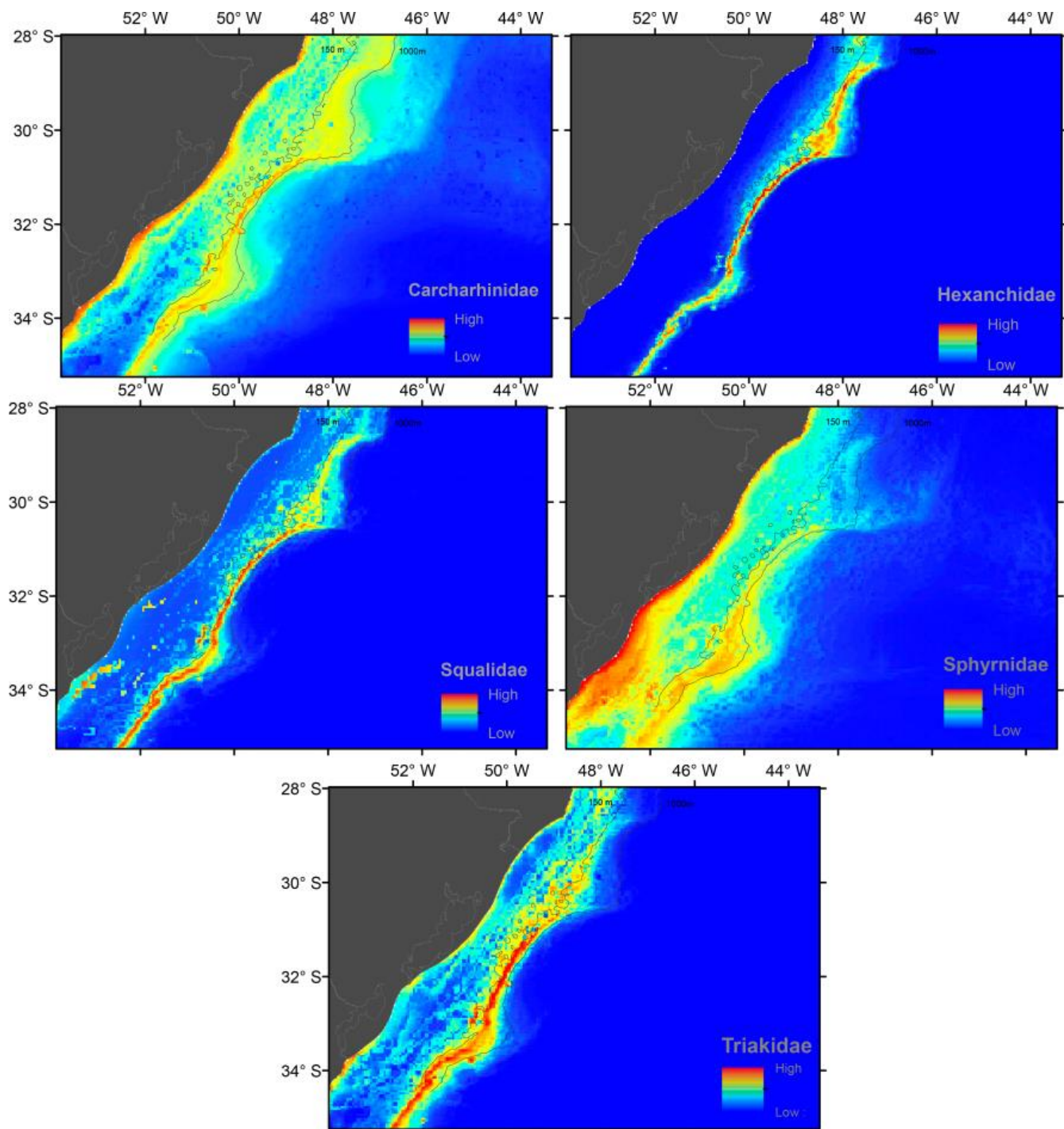


Figure 5: Areas of high probability of occurrence of sharks of the Carcharhidae, Hexanchidae, Squalidae, Sphyrnidae and Triakidae families off southern Brazil obtained by Maxent.

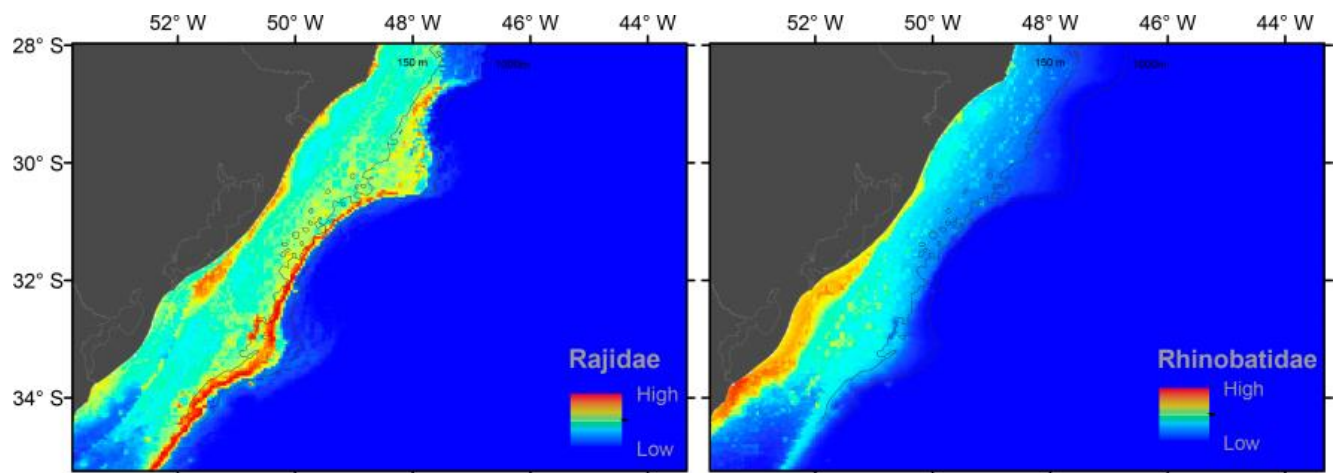


Figure 6: Areas of high probability of occurrence of rays of the Rajidae and Rhinobatidae families off southern Brazil obtained by Maxent.

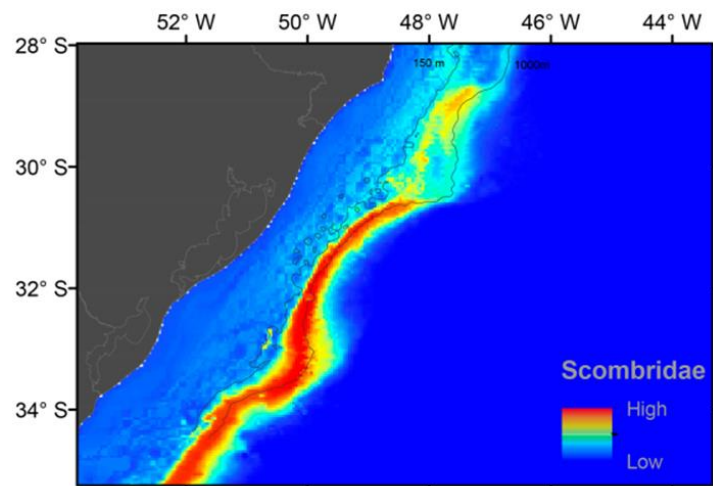


Figure 7: Areas of high probability of occurrence of tunas (Scombridae) off southern Brazil obtained by Maxent.

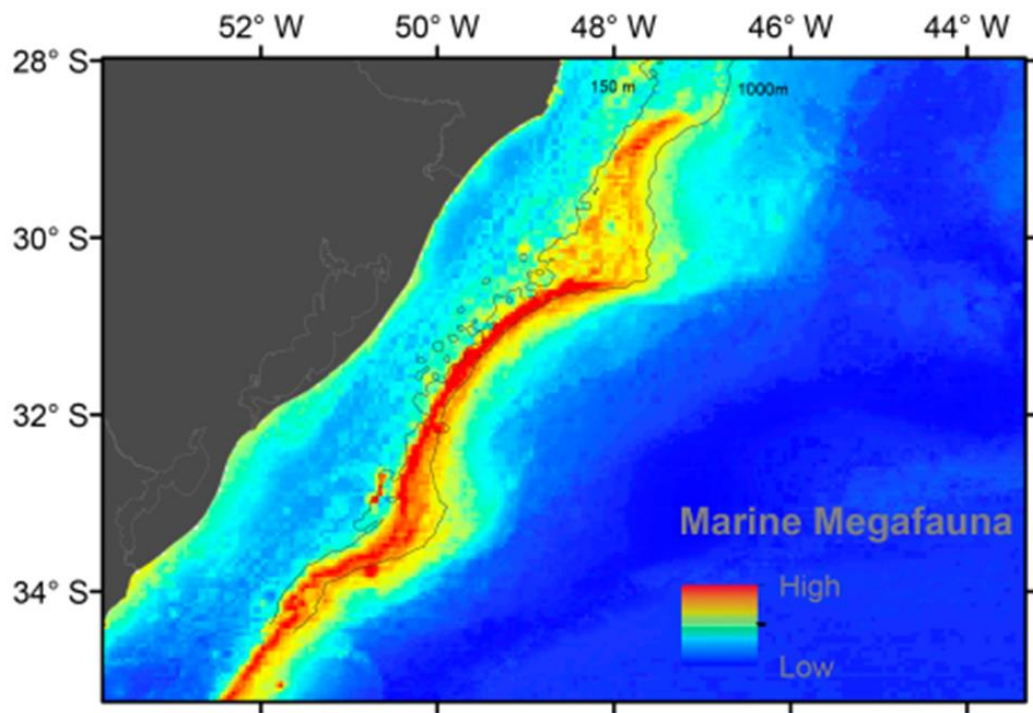


Figure 8: Marine megafauna hotspots off southern Brazil obtained by calculating the mean relative occurrence probabilities per pixel from the probability maps of all families overlapped.