

Luiza Becker Pereira

**ECOLOGIA TRÓFICA DOS ECÓTIPOS COSTEIRO E
OCEÂNICO DE *Tursiops truncatus* NO SUL DO BRASIL**

Dissertação submetida ao Programa de
Pós-Graduação em Ecologia da
Universidade Federal de Santa
Catarina para a obtenção do título de
Mestre em Ecologia.
Orientador: Prof. Dr. Fábio Gonçalves
Daura Jorge
Coorientadora: Prof^a Dr^a Silvínia Botta

Florianópolis
2019

Ficha de identificação da obra elaborada pelo autor,
através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Pereira, Luiza Becker
ECOLOGIA TRÓFICA DOS ECÓTIPOS COSTEIRO E OCEÂNICO
DE *Tursiops truncatus* NO SUL DO BRASIL / Luiza
Becker Pereira ; orientador, Fábio Gonçalves Daura
Jorge, coorientador, Silvina Botta, 2019.
69 p.

Dissertação (mestrado) - Universidade Federal de
Santa Catarina, , Programa de Pós-Graduação em ,
Florianópolis, 2019.

Inclui referências.

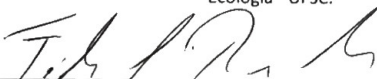
1. . 2. Ecologia trófica. 3. Isótopos estáveis. 4.
Ecótipos. 5. Cetáceos. I. Daura-Jorge, Fábio
Gonçalves. II. Botta, Silvina. III. Universidade
Federal de Santa Catarina. Programa de Pós-Graduação
em . IV. Título.

"Ecologia trófica dos ecótipos costeiro e oceânico de *Tursiops truncatus* no sul do Brasil"

Por

Luiza Becker Pereira

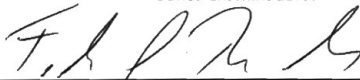
Dissertação julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (013/2019/PPGECO) do Programa de Pós-Graduação em Ecologia - UFSC.



Prof. Dr. Fábio Gonçalves Daura Jorge

Coordenador(a) do Programa de Pós-Graduação em Ecologia

Banca examinadora:



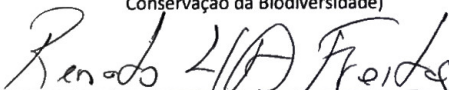
Dr. Fábio Gonçalves Daura-Jorge (Universidade Federal de Santa Catarina)

Orientador(a)

Prof. Dr. Fábio Gonçalves Daura Jorge
Coordenador do PPG em Ecologia
CCB/UFSC Portaria nº 725/2018/GR



Dr. Pedro Fruet - participação por videoconferência (Instituto Chico Mendes de Conservação da Biodiversidade)



Dr. Renato Hajenius Aché de Freitas (Universidade Federal de Santa Catarina)

Florianópolis, 15 de março de 2019.

À minha família, às minhas raízes.

AGRADECIMENTOS

À CAPES pela bolsa durante estes dois anos de mestrado.

À Pós-Eco pela oportunidade, cuidado e também por, juntamente com a Pró-Reitoria de Pós-Graduação, conceder auxílios em eventos importantes tanto para o desenvolvimento deste trabalho quanto para a minha formação. Estes auxílios, mesmo que pequenos, foram fundamentais.

À Cetacean Society International e à Society for Marine Mammalogy pelos fundos que garantiram o pagamento do envio e das análises de isótopos estáveis de todas as amostras coletadas neste projeto.

Ao comitê organizador da 11th International Conference on the Applications of Stable Isotope Techniques to Ecological Studies (IsoEcol 2018) por conceder a beca de inscrição no evento.

E aos membros da banca, por lerem o trabalho e contribuírem com suas reflexões.

É um pouco difícil pensar em escrever os agradecimentos deste processo de dois anos que foi o nascimento e desmame da dissertação sem lembrar das inúmeras e incríveis pessoas que estiveram comigo ou simplesmente cruzaram de forma marcante o meu caminho, fosse na rotina de trabalho ou no simples caminhar da minha vida durante este período.

Primeiramente gostaria de agradecer aos meus orientadores, Fábio e Silvina, que acreditaram no projeto e souberam respeitar meu tempo e meu processo. Agradeço por todos os aprendizados que tive com cada um. Ao Paulo, que apesar de não ser no papel, continua de alguma (ou muitas) forma(s) sendo um orientador pra mim. Sem vocês o caminhar nesta trilha cheia de pedregulhos, como tem se mostrado a academia para mim, seria um tanto mais doloroso. Neste sentido, agradeço igualmente à todos os colegas e (felizmente) também amigos dos laboratórios (LAMAq e ECOMEGA) e da Pós-Ecologia/UFSC, que me ajudaram a perceber que os momentos difíceis eram apenas momentos.

À Karla Scherer por toda a ajuda e apoio ao longo das coletas. E aos demais funcionários da UFSC, em especial do LAMEB e da secretaria integrada de pós-graduação, por toda a atenção e por auxiliarem em processos burocráticos de forma prática e eficiente.

Ao curso de campo Ecologia do Pantanal (ECOPAN 2017), professores, funcionários e colegas. Pela oportunidade de aprender tanto e em tantos aspectos.

À Gabriela Oms e à Julia Pierry pelo nosso caminhar, a amizade de vocês me ajuda a lidar com a vida de forma mais madura, sou muito grata pelo nosso encontro. Ao João do Valle Pereira, pelas ajudas na reta final e pela parceria.

À Liane Dias, agradeço por todas as trocas. Minha trajetória nesses dois anos de mestrado, que na realidade sinto como se tivesse começado alguns meses antes, foi muito mais engrandecedora por isso.

À Clarissa Teixeira, pelo prazer de poder trabalhar com uma pessoa tão incrível e que entendia tudo o que eu estava passando. Que essa parceria persista!

Agradeço também às amigas da vida, pessoas que me acompanham desde minha infância e que me ajudam a me enxergar com mais clareza quando tudo parece desfocado demais. Em especial ao Daniel Dias, obrigada por me ouvir tantas vezes e obrigada por compartilhar de tantas divagações sobre a vida, sobre a ciência e sobre nós mesmos.

Com especial importância, agradeço à minha família. Por me apoiar e me incentivar de tantas formas. Por ser do jeitinho que é e que me fez/ajudou a ser do jeitinho que sou. Em particular à minha mãe, Elizabeth, ao meu pai, Clovis, e à minha irmã, Diana, que me ajudam todos os dias a perceber que toda dificuldade no caminho não passa de uma oportunidade de aprendizado e crescimento.

E, por fim, agradeço também à todos que, ao longo do processo, de alguma forma se interessaram e quiseram saber do meu trabalho. Percebo que traduzir este tipo de conhecimento para diferentes pessoas e realidades é um dos maiores desafios da ciência e é o que mais me motiva a continuar aprendendo.

“Eu sou feito de restos de estrelas
Como o corvo, o carvalho e o carvão
As sementes nasceram das cinzas
De uma delas depois da explosão
Sou o índio da estrela veloz e brilhante
Que é forte como o jabuti
O de antes de agora em diante
E o distante galáxias daqui”

(Lenine)

RESUMO

A compreensão do nicho ecológico é fundamental para entender a distribuição das espécies, mas sua aplicação para espécies muito móveis, como de cetáceos, é complexa. Isótopos estáveis de carbono e nitrogênio tem sido utilizados para estimar o nicho isotópico, proxy do nicho ecológico. No Atlântico Sul Ocidental (ASO), dois ecótipos do golfinho-nariz-de-garrafa, costeiro e oceânico, co-ocorrem em uma área estreita da costa. Até o momento, nenhum estudo buscou investigar os aspectos ecológicos que permitiriam esta aparente sobreposição de nicho, que pressupõe competição por recursos. Aqui, analisamos as composições isotópicas de carbono e nitrogênio ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) das camadas de crescimento de dentina nos dentes de indivíduos dos dois ecótipos ($N_{\text{costeiro}} = 15$ e $N_{\text{oceânico}} = 13$) para investigar as dimensões trófica, espacial e temporal do nicho isotópico de ambos. Mais especificamente, investigamos: (1) diferenças no valores de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ entre os ecótipos; (2) mudanças ontogenéticas no uso de recursos em cada ecótipo; e (3) o grau de especialização individual de cada ecótipo. Para cada ecótipo: calculamos a área padrão de elipse corrigida para pequenas amostras (AEc) e o grau de sobreposição das mesmas; ajustamos modelos aditivos generalizados mistos aos dados de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ para verificar mudanças ontogenéticas no uso de recursos; e, consideramos a razão entre a variância dentro de cada indivíduo pela variância dentro da população/ecótipo como um índice de especialização individual para cada um. Apenas os valores de $\delta^{13}\text{C}$ diferiram entre os ecótipos ($\delta^{13}\text{C}_{\text{costeiro}} = -12,7\text{‰}$ e $\delta^{13}\text{C}_{\text{oceânico}} = -14,3\text{‰}$; $t = 4,87$; $df = 26$; $p\text{-value} < 0,0001$) e uma pequena sobreposição das AEc foi verificada. O desmame ocorre entre 2-3 anos de idade para ambos. E especialização individual foi observado em ambos ecótipos. Nossos resultados sugerem um grau partição de nicho espacial entre os dois grupos, mas reforça a hipótese de distribuição parapátrica com uma “zona de contato” entre os dois ecótipos. A dieta do ecótipo costeiro é fortemente associada a habitats costeiros e estuarinos e do ecótipo oceânico a habitats pelágicos.

Palavras-chave: Especialização individual. Nicho isotópico. Ontogenia.

ABSTRACT

The comprehension of the ecological niche is key to understand the distribution of species. For highly mobile species such as cetaceans applying this concept by conventional methods is challenging. Carbon and nitrogen stable isotopes have been used to estimate the isotopic niche, a proxy for the ecological niche. In the western South Atlantic Ocean (wSAO), coastal and offshore ecotypes of the bottlenose dolphin co-occur in a narrow coastal strip area. However, no study has investigated the ecological aspects allowing this overlapped distribution, which foresees some kind of resource competition. Here, we analysed carbon and nitrogen isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of dentin growth layer groups in each individual tooth ($N_{\text{coastal}} = 15$ and $N_{\text{offshore}} = 13$) to investigate the trophic, spatial and temporal dimensions of the isotopic niche of both ecotypes. Specifically, we aimed to evaluate: (1) variations in mean isotopic values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between ecotypes; (2) ontogenetic shifts on resources use within ecotypes; and (3) the degree of individual specialization of each ecotype. We calculated the Standard Ellipse Areas corrected for small sample sizes (SEAc) for each ecotype and measured the degree of overlap between them, we also adjusted Generalized Additive Mixed Models to age-specific data of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to verify ontogenetic variations in resources use. To estimate the degree of individual specialization we used the ratio of mean within individual variation by that of the population. Mean isotopic values differed significantly only for carbon values ($\delta^{13}\text{C}_{\text{coastal}} = -12.7\text{‰}$ and $\delta^{13}\text{C}_{\text{offshore}} = -14.3\text{‰}$; $t = 4.87$, $df = 26$, $p\text{-value} < 0.0001$) and a small overlap between both ecotypes SEAc was observed. Weaning occur around 2-3 years old for both ecotypes. And individual specialization was evident in both ecotypes. Our results suggest a degree of habitat partitioning, but reinforce the hypothesis of a parapatric distribution with a “contact zone” of both ecotypes. The coastal ecotype’s diet is strongly associated with coastal and estuarine habitats whereas the offshore ecotype explores mostly pelagic prey.

Keywords: Individual specialization. Isotopic niche. Ontogeny.

LISTA DE FIGURAS

Figure 1 Study area and stranding points of the 28 specimens (15 coastal and 13 offshore) analysed for this study. Some stranding points are overlapped. Skull morphology was used to distinguish ecotypes; orange circles represent stranding of coastal bottlenose dolphins (*T. t. gephyreus*) and green lozenges represent stranding of the offshore bottlenose dolphins (*T. t. truncatus*). The Brazilian states of São Paulo (SP), Paraná (PR), Santa Catarina (SC) and Rio Grande do Sul (RS) are shown at the lower map to the left. The upper map at the left side represents South America. _____ 37

Figure 2 Violin-plot with distribution of (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ values for costal [c] and offshore [o] ecotypes of bottlenose dolphin. Points represent mean values with standard deviation. Difference between mean values was only significant for $\delta^{13}\text{C}$ values ($p < 0.0001$) _____ 41

Figure 3 Predicted $\delta^{13}\text{C}$ (above) and $\delta^{15}\text{N}$ (below) values in tooth GLGs of the coastal and offshore bottlenose dolphin's ecotypes based on a fitted generalized additive mixed model. Graphs a) and c) represent the coastal ecotype (orange line) and graphs b) and d) represent the offshore ecotype (green line). Coloured lines are the predicted curve, while grey limits represent the approximated 95% point-wise confidence intervals. The approximate significance of smooth terms for coastal ecotype was $F = 7.076$, offshore ecotype was $F = 1.487$. _____ 43

Figure 4 Isotopic Standard Ellipses adjusted for small sample sizes (SEAc) representing the isotopic niche for coastal and offshore ecotypes of bottlenose dolphins, generated with individual's mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values excluding GLGs 1 and 2, considering all individuals sampled (a), separated by sex (b) and separated by age class (c). In (b), female's ellipses (solid lines) are defined by circles and male's ellipses (dashed lines) are defined by triangles; In (c), calves ellipses (solid lines) are defined by circles and young/adults ellipses (dashed lines) are defined by triangles. _____ 45

Figure 5 Individual bottlenose dolphin's $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) values as young/adult plotted against its isotope values as a calf. Calf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are represented by the isotopic values of the 3rd GLG, while young/adult values are represented by the mean isotopic values of GLGs >3 (4th GLG upwards). Ecotypes are differentiated by colour, orange for coastal (left) and green for offshore (right). The r^2 , the F-statistics and p-values are shown on top of each graph. _____ 47

Figure 6 Individual carbon (a) and nitrogen (b) isotopic ontogenetic profiles from coastal (n = 15) and offshore (n = 13) bottlenose dolphins (each line represents all samples for an individual). And within individual component (WIC) (c) and the degree of individual specialization (WIC/TNW) (d), calculated for carbon and nitrogen isotope compositions in both bottlenose dolphin's ecotypes. WIC/TNW ration range from 0 when all individuals are specialists to 1 when all are generalist. Squares represent mean \pm SD. Pairwise comparisons of WIC and WIC/TNW were conducted separately for $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values by a bootstrap with 1000 replicates; no significant difference was observed between ecotypes. _____ 48

SUMÁRIO

1	INTRODUÇÃO GERAL	15
1.1	REFERÊNCIAS	22
2	ARTIGO: “FROM POPULATION TO INDIVIDUALS, A TOOTH TALE: ECOLOGICAL DIFFERENCES BETWEEN COASTAL AND OFFSHORE ECOTYPES OF THE BOTTLENOSE DOLPHIN”	31
2.1	INTRODUCTION	32
2.2	MATERIAL AND METHODS	36
2.2.1	<i>Sample collection and preparation</i>	36
2.2.2	<i>Age estimation</i>	38
2.2.3	<i>Stable Isotope Analysis (SIA)</i>	38
2.2.4	<i>Data Analysis</i>	39
2.3	RESULTS	40
2.3.1	<i>Variation of $\delta^{13}C$ and $\delta^{15}N$</i>	40
2.3.2	<i>Ontogenetic variation in isotopic composition</i>	41
2.3.3	<i>Isotopic niche variation</i>	43
2.3.4	<i>Temporal consistency and individual specialization</i>	46
2.4	DISCUSSION	49
2.5	REFERENCES	53
3	CONSIDERAÇÕES FINAIS	65
	APÊNDICE A	67

1 INTRODUÇÃO GERAL

Um ponto central em ecologia e fundamental para a conservação das espécies e dos ecossistemas é a compreensão da distribuição das mesmas e dos fatores que influenciam esta distribuição (Begon 2007). No início do século XX J. Grinnel, ao tentar explicar a distribuição de uma espécie de ave, atribuiu o conceito de nicho ao conjunto de necessidades dessa espécie no ambiente, associando a estas necessidades tanto fatores abióticos como temperatura e umidade, quanto bióticos como a cobertura vegetal dos locais de ocorrência da espécie (Grinnel 1917). Um outro conceito de nicho ecológico, atribuído a C. S. Elton, passou a considerar que a existência de uma espécie em uma dada área depende da sua relação com a comunidade e ecossistema local, sendo assim, o nicho ecológico de uma espécie é determinado em geral pelas interações desta com as demais (Elton 1927).

Ao longo dos anos, inúmeros foram os trabalhos que tentaram definir e discorrer sobre o conceito de nicho ecológico, muitas vezes mesclando os conceitos de nicho Grinnelliano e Eltoniano, igualando o primeiro à noção de nicho potencial ou fundamental – correspondendo aos locais de potencial ocorrência da espécie, em função de nesses se verificar condições ambientais favoráveis à mesma; e o segundo à ideia de nicho realizado – relativo a áreas de real ocorrência das espécies, dadas as suas interações com a estrutura da comunidade e com outras espécies locais (Vandermeer 1972). Talvez uns dos trabalhos mais marcantes para a definição de nicho ecológico tenham sido os trabalhos de G. E. Hutchinson que, apesar de muito relacionados às ideias de Grinnel, formalizaram o conceito, sendo este correspondente a um hipervolume n-dimensional, determinado pelas inúmeras variáveis ambientais (bionômicas e scenopoiéticas) relevantes à sobrevivência da espécie. Assim, qualquer ponto encontrado dentro deste hipervolume corresponde a um ambiente propício para a ocorrência da espécie em questão, o que ele definiu como nicho fundamental (Hutchinson 1957). Para a definição de nicho realizado, o autor retomou a ideia de exclusão competitiva de Gause, a qual defende que duas espécies não podem ocupar o mesmo espaço, de modo que os nichos realizados de duas espécies em uma mesma comunidade não deveriam se sobrepor (Hutchinson 1957; Vandermeer 1972).

A partir daí inúmeros trabalhos passaram a ser desenvolvidos na busca de compreender como tantas espécies, inclusive similares, poderiam co-ocorrer, o que difundiu largamente a importância da competição para a estruturação das comunidades (Chase e Leibold

2003). Neste sentido, para coexistirem, duas espécies/populações com necessidades similares irão ou sobrepor seus nichos, no caso de haver abundância de recursos, ou particionar o nicho, de modo que cada uma delas deve explorar recursos distintos, evitando assim que os gastos derivados da co-ocorrência (e.g., competição/predação) impeçam a persistência de suas populações (e.g., Bearzi 2005). No entanto, a aplicabilidade destes conceitos pode ser bastante complexa dado que em teoria uma infinidade de dimensões compõem o nicho ecológico de cada espécie (Chase e Leibold 2003).

Com o avanço das tecnologias e com a integração de novas técnicas aos estudos ecológicos, diferentes formas de se investigar a distribuição das espécies surgiram e tornaram o conceito de nicho ecológico mais palpável. O desenvolvimento dos Sistemas de Informação Geográfica, por exemplo, permitiram grandes avanços. Ao modelar fatores como temperatura, precipitações e relevo em função de pontos de ocorrência das espécies passou a ser possível inferir sobre seus potenciais locais de ocorrência, permitindo assim uma visão mais global de sua distribuição (Soberón 2007). A modelagem de nicho por esta abordagem, no entanto, pouco capta das interações ecológicas, ou as capta de forma bastante indireta, estando muito relacionado aos conceitos de nicho fundamental e potencial, sobretudo, em virtude de que pouco ainda se sabe sobre como as interações realmente influenciam na distribuição de cada espécie (Soberón e Nakamura 2009).

Uma ferramenta que nas últimas décadas tem permitido acessar as interações tróficas e, ao mesmo tempo, algumas características do tipo de ambiente que habita cada espécie (características bionômicas e scenopoiéticas do nicho ecológico, respectivamente) é a análise de isótopos estáveis. Isótopos são átomos de um mesmo elemento químico, que apresentam mesmo número de prótons, porém diferem quanto ao número de nêutrons. A distribuição dos isótopos estáveis leves e pesados pelo planeta se dá de forma desigual, sendo que para muitos elementos, como hidrogênio (H), carbono (C), nitrogênio (N), oxigênio (O) e enxofre (S), a proporção do isótopo leve representa mais de 95% dos átomos destes elementos nos sistemas. Para estudos ecológicos, isto é muito útil, pois permite que isótopos estáveis funcionem como traçadores naturais, tornando possível acompanhar o ciclo dos diferentes elementos químicos pela biosfera (Fry 2006). Por exemplo, a composição isotópica de carbono ($\delta^{13}\text{C}$) é em geral utilizada para investigar o uso de hábitat, pois pouco varia de um nível trófico para o próximo (Peterson e Fry 1987). Assim, reflete características dos produtores primários de onde se alimentam os animais (e.g., Pinela *et al.*

2010; Botta *et al.* 2012). Já a composição isotópica de nitrogênio ($\delta^{15}\text{N}$) é em geral consideravelmente mais enriquecida (apresenta maior proporção de ^{15}N) em níveis tróficos mais altos devido a maior excreção do isótopo leve (Peterson e Fry 1987). Desta forma, é útil para determinar a posição trófica dos consumidores e suas relações tróficas (e.g., Pinela *et al.* 2010; Botta *et al.* 2012).

Segundo Bearhop *et al.* (2004), o nicho trófico é uma das dimensões de nicho mais palpáveis, e através da utilização de isótopos estáveis é possível obter uma métrica quantitativa comum para sua comparação entre diferentes grupos taxonômicos e níveis de organização (e.g., indivíduos, espécies ou comunidades). Assim, Newsome *et al.* (2007) propuseram o conceito de nicho isotópico, no qual as composições de diferentes isótopos como, por exemplo, os de carbono e nitrogênio ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$), são utilizadas como variáveis para a criação de um δ -espaço comparável ao espaço n-dimensional do conceito de nicho ecológico, o que os autores explicam ser possível devido ao fato de que a composição química dos tecidos de cada organismo advém daquilo que é consumido por cada indivíduo (variáveis bionômicas) e do tipo de habitat onde vivem (variáveis scenopoéticas).

Este tipo de abordagem tem se tornado cada vez mais comum para investigar o nicho ecológico de cetáceos (e.g., Secchi *et al.* 2016; Díaz-Gamboa *et al.* 2018), em especial por serem animais extremamente móveis, difíceis de acompanhar e que habitam ambientes de difícil acesso (Newsome *et al.* 2010). Além disso, a composição isotópica de um indivíduo varia não apenas conforme os recursos ingeridos e a taxa de fracionamento dos isótopos (o quanto de isótopos leves e pesados são de fato assimilados), mas também com o *turnover* (taxa de renovação) de cada tecido. Portanto, a análise de tecidos metabolicamente inertes como os dentes, que são facilmente encontrados em coleções científicas de cetáceos ao redor do mundo, permite investigar variações na dieta e ecologia trófica ao longo da vida de diferentes espécies (Peterson e Fry, 1987; Newsome, *et al.* 2010). Outra vantagem, em especial nos estudos com odontocetos, é o fato de que estes animais possuem uma única dentição ao longo de toda a vida, na qual a polpa do dente é preenchida ano a ano com novas camadas de dentina (Growth Layer Groups – GLG). Através da leitura dessas camadas é possível estimar a idade dos animais (Hohn *et al.* 1989) e ainda, obter amostras em séries temporais da dentina, que permitem investigar variações da dieta ao longo de toda

a vida do animal através de análise de isótopos estáveis (e.g., Newsome et al. 2009).

Espécies amplamente distribuídas têm a tendência de variarem em aspectos morfológicos (Ashton et al. 2000; Jaffe et al. 2016), genéticos (Tezanos-Pinto et al. 2009), comportamentais (Endler e Houd 1995) ou ecológicos (Barros e Odel 1990; Fine 2015). Quando duas populações são diferentes, mas não o suficiente para serem consideradas espécies distintas, termos como *subespécie* e *ecótipo* são utilizados (Brown e Lomolino 1998). O termo ecótipo foi empregado primeiramente por Turesson (1922), que percebeu variações genotípicas em uma espécie de planta quando relacionada com diferentes habitats. Assim, ao falar de ecótipos nos referimos a variações de uma espécie em função do ambiente em que essa se encontra, com variações morfológicas e fisiológicas refletindo diferenças genéticas decorrentes de distintas linhagens adaptativas (Brown e Lomolino 1998). Entre os cetáceos inúmeros exemplos de variações geográficas já foram relatados (e.g., Jefferson e Van Waerebeek 2004; Gilpatrick e Perryman 2008; Jones e Sayight 2002; Bruyn et al. 2013), sendo normalmente relacionados a aspectos ecológicos (Perrin 2008), com o tamanho de corpo e as características cranianas refletindo o hábito alimentar da espécie (e.g., Mead e Potter 1995; McCurry et al., 2017).

O boto-da-tainha ou golfinho-nariz-de-garrafa (*Tursiops truncatus*) é considerada uma espécie cosmopolita, ocorre de águas temperadas a tropicais e ocupa grande variedade de habitats, desde mares interiores, a ecossistemas costeiros e oceânicos (Wells e Scott 1999). Dada a ampla distribuição, ao grande polimorfismo e aos inúmeros registros de hibridização com outras espécies, a taxonomia do gênero ainda é pouco elucidada (Wells e Scott 1999). Cerca de 20 nomes específicos já foram atribuídos a *Tursiops* (Hershkovitz 1966), no entanto, a *Society for Marine Mammalogy* reconhece apenas duas espécies: golfinhos-nariz-de-garrafa do Indo-Pacífico (*Tursiops aduncus*) e golfinho-nariz-de-garrafa-comum (*Tursiops truncatus*) (Committee on Taxonomy 2018). Ainda assim, em diversas regiões do globo, variações genéticas (Segura et al. 2006; Tezanos-Pinto et al. 2009) e morfológicas (Perrin et al. 2011; Costa et al. 2016) entre indivíduos costeiros e oceânicos sustentam a existência de dois ecótipos para a segunda espécie. Esta distinção também é apoiada por análises isotópicas, que evidenciam animais oceânicos com menores valores de $\delta^{13}\text{C}$ típicos de ambientes pelágicos, onde a produção primária é majoritariamente realizada pelo fitoplâncton, e com diferenças também quanto a $\delta^{15}\text{N}$ (Segura et al. 2006; Barros et al. 2010). Desta forma, as

variações nas composições isotópicas sugerem que, além de diferenças morfológicas e genéticas, os ecótipos divergem quanto ao nicho trófico.

No Atlântico Sul Ocidental (ASO) se discute a existência de uma terceira espécie de *Tursiops* ao sul do continente (Barreto 2000; Ott et al. 2016). Evidências morfológicas (Costa et al. 2016; Wickert et al. 2016) e genéticas (Fruet et al. 2017) mostraram diferenças importantes entre as duas formas que ocorrem ao longo da costa brasileira. Com base nas características cranianas, uma das formas está associada a ambientes de maior profundidade e, portanto, é considerada um ecótipo oceânico, enquanto a outra é considerada um ecótipo costeiro (Costa et al. 2016). Os dados de enalhe sugerem que o ecótipo costeiro ocorre do estado de São Paulo, no sudeste do Brasil, até a península Valdés, na Argentina (Toledo 2013), ocupando regiões próximas de desembocaduras de rios, estuários e baías (Di Tullio et al. 2016). Já o ecótipo oceânico é mais amplamente distribuído, tendo sido registrado desde o estado do Pará (Siciliano et al. 2008), no norte do Brasil, até a península Valdés, na Argentina (Goodall et al. 2011; Toledo 2013). Este ecótipo oceânico é observado tanto próximo da costa quanto em águas abertas (Di Tullio et al. 2016; Simões-Lopes et al. no prelo). Assim, ao longo da distribuição de ambos, áreas de potencial co-ocorrência são sugeridas, em especial entre os estados de Santa Catarina e o norte do Rio Grande do Sul (Barreto 2000; Toledo 2013; Simões-Lopes et al. no prelo), no Brasil. No entanto, até o momento nenhum trabalho buscou entender os aspectos ecológicos que permitiriam a co-ocorrência dos dois ecótipos.

Recentemente, no ASO os dois ecótipos foram reconhecidos pela *Society for Marine Mammalogy* como subespécies, sendo o ecótipo oceânico nominalmente referido como golfinho-nariz-de-garrafa-comum (*Tursiops truncatus truncatus*) e o ecótipo costeiro como golfinho-nariz-de-garrafa-de-Lahille (*Tursiops truncatus gephyreus*). No entanto, é importante notar que ainda é evidenciada a necessidade de mais estudos e sob diferentes abordagens para resolver os debates taxonômicos da espécie na região (Committee on Taxonomy 2018). Cada vez mais se reconhece a importância de integrar os conhecimentos advindos de diferentes metodologias e disciplinas (e.g., genética, morfologia, ecologia) para esclarecer a delimitação de espécies e a distinção ou não de novas taxas (Padial et al. 2010; Rosel et al. 2017). Apesar dos recentes avanços nos estudos de genética (e.g., Fruet et al. 2017) e morfologia (Costa et al. 2016; Wickert et al. 2016) comparando os dois ecótipos no ASO serem de extrema importância para esta discussão, a

comparação sob aspectos ecológicos se restringe ainda a estudos de distribuição, tamanho de grupo e uso de habitat (e.g., Di Tullio et al. 2016; Simões-Lopes et al. no prelo).

Estudos sobre a dieta do golfinho-nariz-de-garrafa no ASO são ainda incipientes, a maioria dos trabalhos realizados com a análise de conteúdo estomacal apresenta tamanhos amostrais bastante reduzidos, portanto, reflete pouco da dieta das populações. Além disso, até o momento na região nenhum trabalho de dieta considerou a distinção dos ecótipos (e.g., Di Benedetto et al. 2001; Melo et al. 2010; Milmann et al. 2016). Em uma perspectiva global, o golfinho-nariz-de-garrafa é uma espécie oportunista que se alimenta de grande diversidade de espécies de peixes, cefalópodes e mesmo crustáceos, podendo sua dieta variar entre regiões, com a presença de outras espécies de odontocetos, atividade pesqueira e com a estação do ano (Barros e Odell 1990; Wells e Scott 1999; Bearzi 2005). Entre populações costeiras, diferentes estratégias especializadas de forrageio já foram registradas mundo a fora (e.g., Smolker et al. 1997; Jiménez e Alava 2015) e inclusive no Brasil (Simões-Lopes et al. 1998). Peixes demersais da família Scianidae são as presas mais comumente encontradas nos conteúdos estomacais de animais costeiros (Barros e Odell 1990; Gannon e Waples 2004; Laporta et al. 2016a; Milmann et al. 2016; Secchi et al. 2016). O pouco que se sabe do conteúdo estomacal de espécimes oceânicos indica que se alimentam de peixes pelágicos de águas profundas e de lulas (Barros e Odell 1990; Mead e Potter 1995).

Mudanças na dieta destes animais ao longo da ontogenia já foram sugeridas a partir da análise de conteúdo estomacal (Gannon e Waples 2004) e também por evidências isotópicas, especialmente quando se tratando da transição do consumo de leite maternos para a captura independente de presas, isto é, do período de desmame (Knoff et al. 2008; Fruet et al. 2015). Distintas idades de desmame já foram reportadas para o golfinho-nariz-de-garrafa em diferentes regiões (Cockcroft e Ross 1989; Wells e Scott 1999). Em Shark Bay, na Austrália, a endogamia foi apontada como responsável por períodos de desmame mais prolongados em uma população costeira da espécie, uma vez que reduz o *fitness* da mãe (Frère et al. 2010).

Ao estudar o nicho ecológico de uma espécie é importante ter em conta que o tamanho total do nicho é influenciado pelo nicho de cada indivíduo e pelas diferenças entre os indivíduos que compõem essa população (Roughgarden 1972, Bolnick et al. 2002). Em alguns casos, estas variações podem ser atribuídas a diferentes estágios de desenvolvimento (i.e., nicho ontogenético (Werner e Gilliam 1984)) ou

a outras características de grupos específicos dentro da população (e.g., sexo e fenótipo). No entanto, nos últimos anos, é crescente o interesse em investigar o uso de recursos por cada população sob uma perspectiva individual, buscando-se entender variações que não sejam provenientes de estágios ontogenéticos, sexo ou morfologias específicas, caracterizando assim especializações individuais dentro das populações (Bolnick et al. 2003). Os motivos que levam à especialização individual podem ser inúmero, mas é coerente que sejam investigados sob o entendimento dos *trade-offs* advindos da utilização dos recursos disponíveis, como por exemplo, para evitar a competição intraespecífica (Bolnick et al. 2003). Estudos com este viés são importantes para a compreensão da dinâmica das populações, e tem potencial influencia na estruturação e montagem das comunidades (Miller e Rudolf 2011). Além de que o grau de especialização individual de uma população pode influenciar na ecologia, evolução e conservação das mesmas e, por consequência, das espécies (Bolnick et al. 2003).

Considerando a potencial área de co-ocorrência e a necessidade de maior aporte de informações quanto a ecologia trófica e uso de habitat de ambos ecótipos, o presente trabalho teve por objetivo central investigar as dimensões trófica, espacial e temporal do nicho isotópico (*proxy* do nicho ecológico) dos ecótipos costeiro e oceânico do golfinho-nariz-de-garrafa no sul do Brasil. Mais especificamente, utilizando da análise de isótopos estáveis em amostras sequenciais da dentina de dentes de indivíduos costeiros e oceânicos, buscamos: (1) investigar o nicho isotópico e a variações no uso de habitat e relações tróficas entre os ecótipos; (2) identificar as idades de desmame e outras possíveis mudanças tróficas na ontogenia de cada ecótipo; e, por fim, (3) testar a consistência temporal no uso de recursos e avaliar o grau de especialização individual de cada ecótipo. Nossas hipóteses eram: (1) que o nicho isotópico do ecótipo oceânico seria maior, por ocupar uma área mais extensa (Simões-Lopes et al. no prelo), podendo explorar regiões mais produtivas e diversas, mas que ainda assim fosse verificada uma sobreposição do nicho de ambos ecótipos em função de todo o material analisado ter sido proveniente de uma área de potencial co-ocorrência (Barreto 2000; Toledo 2013), ainda, esperávamos que a distinção dos ecótipos se daria principalmente pelo uso de habitat, com a alimentação dos animais costeiros mais restrita a habitats costeiros e demersais e dos oceânicos a habitats pelágicos (e.g., Pinela et al. 2010; Botta et al. 2012; Secchi et al. 2016; Díaz-Gamboa et al. 2018); (2) que o ecótipo costeiro apresentaria período de desmame mais prolongado,

como reflexo de maior período de cuidado parental para a aprendizagem de técnicas especializadas de forrageio (Simões-Lopes et al. 1998; Cantor et al. 2018) e, também, em função da endogamia já ter sido reportada para uma população costeira da área de estudo (Fruet et al. 2014); e, por fim, (3) esperávamos que o ecótipo costeiro teria maior grau de especialização individual, por formarem populações residentes (Di Tullio et al. 2016; Laporta et al. 2016b; Lodi et al. 2016), em um ambiente heterogêneo (SCBD 2014) e com maior pressão antrópica (Fruet et al. 2014), podendo a especialização ser uma estratégia para evitar a competição intra-específica (Bolnick et al. 2003).

Para responder a tais questões, dentes de 28 indivíduos (15 costeiros e 13 oceânicos) foram selecionados de três coleções científicas ao longo do estado de Santa Catarina: do Laboratório de Mamíferos Aquáticos, Universidade Federal de Santa Catarina (LAMAq/UFSC), do Laboratório de Zoologia, Universidade do Estado de Santa Catarina (UDESC) e do Acervo Biológico Iperoba, Universidade da Região de Joinville (Univille). É importante ressaltar que a costa de Santa Catarina é bastante heterogênea, apresenta diversas baías, ilhas costeiras, e estuários. Além de ser o limite sul de distribuição de costões rochosos no Brasil (Coutinho 2004) e de manguezais no ASO (Schaeffer-Novelli et al. 1990). Ainda, o encontro da corrente do Brasil com as águas subpolares da corrente das Malvinas caracteriza a Convergência Subtropical, que gera na região uma zona de ressurgência bastante produtiva (SCBD 2014).

Os resultados deste trabalho estão apresentados e discutidos em um artigo único em preparação para ser submetido à revista *Oecologia*. Uma breve conclusão com nossos principais achados é apresentada na sequência do artigo.

1.1 REFERÊNCIAS

- Ashton KG, Tracy MC, Queiroz A (2000) Is Bergmann's Rule Valid for Mammals? *The American Naturalist* 156(4):390–415
- Barreto AS (2000) Variação Craniana e Genética de *Tursiops truncatus* (Delphinidae, Cetacea) (Montagu, 1821) na Costa Atlântica da América do Sul. Ph.D. Thesis. Universidade Federal do Rio Grande, Rio Grande, Brasil
- Barros NB, Odell DK (1990) Food Habits of bottlenose dolphins in southeastern United States. In: Leatherwood S, Reeves R (eds.). *The bottlenose dolphin*, Academic Press, pp 309-328

- Barros NB, Ostrom PH, Stricker CA, Wells RS (2010) Stable isotopes differentiate bottlenose dolphins off west-central Florida. *Marine Mammal Science* 26(2):324–336
- Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology* 73(5):1007–1012
- Bearzi M (2005) Dolphin sympatric ecology. *Marine Biology Research* 1(3):165–175
- Begon M, Harper JL, Townsend CR (2007) *Ecologia: De Individuos a Ecosistemas*. 4ª edição. Editora Artmed, 752p.
- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck, R (2002) Measuring Individual-Level Resource Specialization. *Ecology* 83(10):2936–2941
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist* 161(1):1–28
- Botta S, Hohn AA, Macko SA, Secchi ER (2012) Isotopic variation in delphinids from the subtropical western South Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 92(8):1–10
- Brown JH, Lomolino MV (1998) *Biogeography*, 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts
- Bruyn PJN, Tosh CA, Terauds A (2013) Killer whale ecotypes : is there a global model? *Biological Reviews* 88:62–80
- Cantor M, Simões-Lopes PC, Daura-Jorge FG (2018) Spatial consequences for dolphins specialized in foraging with fishermen. *Animal Behaviour* 139:19–27
- Chase JM, Leibold MA (2003) *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago
- Cockcroft VG, Ross GJB (1989) Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the East coast of Southern Africa. *Fishery Bulletin* 88(2):289–302
- Committee On Taxonomy (2018) List of marine mammal species and subspecies. <https://www.marinemammalscience.org/species-information/list-marine-mammal-species-subspecies/>
- Costa APB, Rosel PE, Daura-Jorge FG, Simões-Lopes PC (2016) Offshore and coastal common bottlenose dolphins of the western South Atlantic face-to-face : What the skull and the spine can tell us, (Montagu 1821). *Marine Mammal Science* 32(4): 1433–1457

- Coutinho R (2004) Programa Nacional da Biodiversidade – PRONABIO - Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira – PROBIO Sub-Projeto: Avaliação e Ações Prioritárias para a Zona Costeira e Marinha. Grupo de Ecossistemas: Costões Rochosos. In: Guia para o licenciamento ambiental, Atividades de Sísmica Marítima na Costa Brasileira, Atividades de Perfuração de Óleo e Gás
- Di Benedetto APM, Ramos RMA, Siciliano S, Sanots RADOS, Fagundes-Netto GBAE (2001). Stomach contents of delphinids from Rio de Janeiro, southeastern Brazil. *Aquatic Mammals* 27(1):24-28
- Di Tullio JC, Gandra TBR, Zerbini AN (2016) Diversity and Distribution Patterns of Cetaceans in the Subtropical Southwestern Atlantic Outer Continental Shelf and Slope, 11(5): e0155841
- Díaz-Gamboa RE, Gendron D, Busquets-Vass G (2018) Isotopic niche width differentiation between common bottlenose dolphin ecotypes and sperm whales in the Gulf of California. *Marine Mammal Science* 34(2):440–457
- Elton C (1927) *Animal Ecology*. Sedgwick and Jackson, London.
- Endler JA, Houde AE (1995) Geographic Variation in Female Preferences for Male Traits in *Poecilia reticulata*. *Evolution* 49(3):456-468
- Fine PV (2015) Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics* 46: 369-392
- Frère CH, Krützen M, Kopps AM, Ward P, Mann J, Sherwin WB (2010) Inbreeding tolerance and fitness costs in wild bottlenose dolphins. *Proceedings of the Royal Society B* 277: 2667–2673
- Fruet PF, Secchi ER, Daura-Jorge F, Vermeulen E, Flores PAC, Simões-Lopes PC, Genoves RC, Laporta P, Di Tullio J, Freitas TRO, Rosa LD, Valiati VH, Beheregaray LB, Möller LM (2014) Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. *Conservation Genetics* 15:879–895
- Fruet PF, Genoves RC, Möller LM, Botta S, Secchi ER (2015) Using mark-recapture and stranding data to estimate reproductive traits in female bottlenose dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean. *Marine Biology* 162(3):661-673
- Fruet PF, Secchi ER, Di Tullio JC, Simões-Lopes PC, Daura-Jorge F, Costa APB, Vermeulen E, Flores PAC, Genoves RC, Laporta P, Beheregaray LB, Möller LM (2017) Genetic divergence between two

- phenotypically distinct bottlenose dolphin ecotypes suggests separate evolutionary trajectories. *Ecology and Evolution* 7:9131–9143
- Fry B (2006) *Stable Isotope Ecology*. Springer, New York, NY, USA
- Gannon DP, Waples DM (2004) Diets of coastal bottlenose dolphins from the U. S. Mid-Atlantic coast differ by habitat. *Marine Mammal Science* 20(3):527–545
- Gilpatrick JW, Perryman WL (2008) Geographic variation in external morphology of North Pacific and Southern Hemisphere blue whales (*Balaenoptera musculus*). *Journal of Cetacean Research and Management* 10(1):9–21
- Goodall RNP, Marchesi MC, Pimper LE, Dellabianca N, Benegas LG, Torres MA, Riccialdelli L (2011). Southernmost records of bottlenose dolphins, *Tursiops truncatus*. *Polar Biology*, 34(7), 1085–1090
- Grinnell J (1917) The niche-relationships of the California Thrasher. *The Auk* 34(4):427–433
- Hershkovitz P (1966) Catalog of living whales. US National Museum Bulletin b. 246, 257p.
- Hohn AA, Scott MD, Wells RS, Sweeney JC, Irvine AB (1989) Growth layers in teeth from known-age, free-ranging bottlenose dolphins. *Marine Mammal Science* 5:315–42
- Hutchinson GE (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427
- Jaffe AL, Campbell-Staton SC, Losos JB (2016) Geographical variation in morphology and its environmental correlates in a widespread North American lizard, *Anolis carolinensis* (Squamata: Dactyloidae). *Biological Journal of the Linnean Society* 117(4):760–774
- Jefferson TA, Van Waerebeek K (2004) Geographic variation in skull morphology of humpback dolphins (*Sousa* spp.). *Aquatic Mammals* 30(1):3–17
- Jiménez PJ, Alava JJ (2015) Strand-feeding by coastal bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Guayaquil, Ecuador. *Latin American Journal of Aquatic Mammals* 10(1):33–37
- Jones GJ, Sayigh LS (2002) Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science* 18(2):374–393
- Knoff A, Hohn A, Macko S (2008) Ontogenetic diet changes in bottlenose dolphins (*Tursiops truncatus*) reflected through stable isotopes. *Marine Mammal Science* 24(1):128–137

- Laporta P, Fruet P, Siciliano S, Flores PA, Loudeiro JD (2016a) Report of the Working Group on the Biology and Ecology of *Tursiops truncatus* in the Southwest Atlantic Ocean. *Latin American Journal of Aquatic Mammals* 11(1-2):62-70
- Laporta L, Martins CCA, Lodi L, Domit C, Vermeulen E, Di Tullio JC (2016b) Report of the Working Group on Habitat Use of *Tursiops truncatus* in the Southwest Atlantic Ocean. *Latin American Journal of Aquatic Mammals* 11(1-2):47-61
- Lodi L, Domit C, Laporta P, Di Tullio JC, Martins CCA, Vermeulen E (2016) Report of the Working Group on the Distribution of *Tursiops truncatus* in the Southwest Atlantic Ocean. *Latin American Journal of Aquatic Mammals* 11(1-2):24–28
- McCurry MR, Fitzgerald EMG, Evans AR, Adams JW, McHenry CR (2017) Skull shape reflects prey size niche in toothed whales. *Biological Journal of the Linnean Society* 121(4):936–946
- Mead JG, Potter CW (1995) Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: morphologic and ecologic considerations. *IBI Reports* 5:31-44
- Melo CLC, Santos RA, Bassoi M, Araújo AC, Lailson-Brito J, Dorneles PR, Azevedo AF (2010) Feeding habits of delphinids (Mammalia: Cetacea) from Rio de Janeiro State, Brazil. *Journal of the Marine Biological Association of the United Kingdom* 90(8):1509–1515
- Miller TEX, Rudolf VHW (2011) Thinking inside the box : community-level consequences of stage-structured populations. *Trends in Ecology and Evolution* 26(9):457-466
- Milmann L, Danilewicz D, Machado R, Ott PH (2016) Feeding ecology of the common bottlenose dolphin, *Tursiops truncatus*, in southern Brazil: analyzing its prey and the potential overlap with fisheries. *Brazilian Journal Of Oceanography* 64(4):415–422
- Newsome SD, Del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5(8):429–436
- Newsome SD, Etnier MA, Monson DH, Fogel ML (2009) Retrospective characterization of ontogenetic shifts in killer whale diets via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of teeth. *Marine Ecology Progress Series* 374:229–242
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science* 26(3):509–572

- Ott PH, Barreto AS, Siciliano S, Laporta P, Domit C, Fruet P, Rosa LD, Santos MCO, Meirelles AC, Marchesi MC, Botta S, Oliveira LR, Moreno IB, Wickert J, Vermeulen E, Hoffmann LS, Baracho C, Simões-Lopes PC (2016) Report of the Working Group on Taxonomy and Stock Identity of bottlenose dolphins in the Southwest Atlantic Ocean. *Latin American Journal of Aquatic Mammals* 11(1–2):16–28
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology*, 7, 1–14
- Perrin W (2008) Geographical Variation. In: Perrin W, Wursig B, Thewissen J (Eds.). *Encyclopedia of Marine Mammals*, 2nd edn. Elsevier, San Diego, p. 316-321
- Perrin WF, Thieleking JL, Walker WA, Archer FI, Robertson KM (2011) Common bottlenose dolphins (*Tursiops truncatus*) in California waters: Cranial differentiation of coastal and offshore ecotypes. *Marine Mammal Science* 27(4): 769-792
- Peterson BJ, Fry B (1987) Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics* 18: 293–320
- Pinela AM, Borrell A, Cardona L, Aguilar A (2010) Stable isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. *Marine Ecology Progress Series*, 416:295–306
- Rosel PE, Taylor BL, Hancock-Hanser BL, Morin PA, Archer FI, Lang AR, Mesnick SL, Pease VL, Perrin WF, Robertson KM, Leslie MS, Berta A, Cipriano F, Parsons KM, Viricel A, Vollmer NL, Martien KK (2017) A review of molecular genetic markers and analytical approaches that have been used for delimiting marine mammal subspecies and species. *Marine Mammal Science*, 33, 56–75
- Roughgarden J (1972) Evolution of Niche Width. *The American Naturalist*, 106(952):683–718
- Schaeffer-Novelli Y, Cintrón-Molero G, Adaime RR, Camargo TM (1990) Variability of Mangrove Ecosystems along the Brazilian Coast. *Estuaries*, 13(2):204
- Secretariat of the Convention on Biological Diversity - SCBD (2014) Ecologically or Biologically Significant Marine Areas (EBSAs): Special places in the world's oceans. Volume 2: Wider Caribbean and Western Mid-Atlantic Region. 86 pages
- Secchi ER, Botta S, Wiegand MM, Lopez LA, Fruet PF, Genoves RC, Di Tullio JC (2016). Long-term and gender-related variation in the feeding ecology of common bottlenose dolphins inhabiting a

- subtropical estuary and the adjacent marine coast in the western South Atlantic. *Marine Biology Research*, 13(1):121–134
- Segura I, Rocha-Olivares A, Flores-Ramirez S, Rojas-Bracho L (2006) Conservation implications of the genetic and ecological distinction of *Tursiops truncatus* ecotypes in the Gulf of California. *Biological Conservation*, 133(3): 336–346
- Siciliano S, Emin-lima NR, Costa AF, Rodrigues ALF, Magalhães FA, Tosi CH, Garri RG, Silva CR, Silva JS (2008). Revisão do Conhecimento Sobre os Mamíferos Aquáticos da Costa Norte do Brasil. *Arquivos Do Museu Nacional, Rio de Janeiro*, 66(2), 68912–250381
- Simões-Lopes PC, Fabián ME, Menegheti JO (1998) Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. *Revista Brasileira de Zoologia*, 15(3):709-726
- Smolker R, Richards A, Connor R, Mamm J, Berggren P (1997) Sponge Carrying by Dolphins (Delphinidae, *Tursiops* sp.): A Foraging Specialization Involving Tool Use? *Ethology*, 103:454–465
- Soberón J (2007) Grinnellian And Eltonian Niches And Geographic Distributions Of Species. *Ecology Letters*, 10(12), 1115–1123
- Soberon J, Nakamura M (2009) Niches And Distributional Areas: Concepts, Methods, And Assumptions. *Proceedings Of The National Academy Of Sciences*, 106(2), 19644–19650
- Tezanos-Pinto G, Baker CS, Russell K, Martien K, Baird RW, Hutt A, Stone G, Mignucci-Giannoni AA, Caballero S, Endo T, Lavery S, Oremus M, Olavarría C, Garrigue C (2009) A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. *Journal of Heredity*, 100(1):11–24
- Toledo GAC (2013) Variação geográfica em crânios de golfinhos nariz-de-garrafa, *Tursiops* (Gervais, 1855), no Atlântico Ocidental [Geographic variation in the skulls of bottlenose dolphins, *Tursiops* (Gervais, 1855), in the western Atlantic]. Ph.D. thesis, Universidade Federal da Paraíba, Brazil. 214 pp.
- Turesson G (1922) The species and the variety as ecological units. *Hereditas*, III, 100–113
- Vandermeer JH (1972) Niche Theory. *Annual Review Of Ecology And Systematics*, 3(1), 107–132
- Wells RS, Scott MD (1999) Bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821). In Ridgeway SH, Harrison R (Eds.) *Handbook of marine mammals*. Academic Press, San Diego, CA, p. 137–182

- Wickert JC, Von Eye, SM, Oliveira LR, Moreno IB (2016) Revalidation of *Tursiops gephyreus* Lahille, 1908 (Cetartiodactyla: Delphinidae) from the Southwestern Atlantic Ocean. *Journal of Mammalogy*, 97:1–10
- Werner EE, Gilliam JF (1984) the Ontogenetic Niche, 393–425

2 ARTIGO: “FROM POPULATION TO INDIVIDUALS, A TOOTH TALE: ECOLOGICAL DIFFERENCES BETWEEN COASTAL AND OFFSHORE ECOTYPES OF THE BOTTLENOSE DOLPHIN”

Pereira, L. B.¹; Botta, S.²; Teixeira, C.¹.; Simões-Lopes, P.¹. & Daura-Jorge, F. G.¹

¹Laboratório de Mamíferos Aquáticos (LAMAq), Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Brasil - UFSC; ²Laboratório de Ecologia e Conservação da Megafauna Marinha (ECOMEGA), Instituto de Oceanografia, Universidade Federal do Rio Grande - FURG, Brasil

2.1 INTRODUCTION

Species widely distributed tend to present geographic variation, what is observed in numerous taxa and in different aspects, such as: morphology (Ashton et al. 2000; Jaffe *et al.* 2016), genetic (Tezanos-Pinto et al 2009), behaviour (Endler and Houd 1995) and ecology (Barros e Odel 1990; Fine 2015). When two populations are not distinct enough to be considered different species, terms such as *subspecies* and *ecotypes* are commonly addressed (Brown and Lomolino 1998). For ecotype, we can understand variations of a species regulated by habitats, with morphological and physiological traits reflecting genetic differences due to a distinctive lineage of adaptation (Turesson 1922; Brown and Lomolino 1998).

A key concept to understand the occurrence and distribution of species is that of the ecological niche (Pianka 2000; Chase and Leibold 2003). Carbon and nitrogen stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have been used to estimate the isotopic niche, a *proxy* for the ecological niche and a way to quantify its metrics (Bearhop et al. 2004; Newsome et al. 2007; Newsome et al. 2010). Carbon isotopic values ($\delta^{13}\text{C}$) show little variation along the trophic chain and so reflect the primary producers in a consumer foraging area (Peterson and Fry 1987), thus being useful to understand its habitat use (e.g., Pinela et al. 2010; Botta et al. 2012). Nitrogen isotopic values ($\delta^{15}\text{N}$), on the other hand, are generally enriched in ^{15}N within each trophic step along the food chain due to excretion of the light isotope (Peterson and Fry 1987), what results in higher Trophic Discrimination Factors (TDF – the difference between the isotopic composition of an animal's tissue and its diet (Martinez del Rio et al. 2009)) for these isotopes. Therefore being useful to estimate the trophic position (Post 2002; Vanderklift and Ponsard 2003) and trophic relations (e.g., Secchi et al. 2016). Thus, by plotting the isotopic values as coordinates (e.g., $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) a δ -space comparable to the n-dimensional space of the ecological niche is created, allowing inferences on habitat (scenopoetic variables) and resource (bionomic variables) use (Bearhop et al. 2004; Newsome et al. 2007).

The isotopic niche approach allows the estimation of niche metrics at the community (Layman et al. 2007; Jackson et al. 2011), population (e.g., Rossman et al. 2015a; Albernaz et al. 2017) and even individual level (e.g., Newsome et al. 2009; Rossman et al. 2015b). Recently, increasing interest on population resources use from an individual level is evident (Bolnick et al. 2003), and variations within populations, such as population structure, have been showed to influence even community assemblies, with each ontogenetic stage

affecting the food web in a different way (Miller and Rudolf 2011). Thus, understanding how differences between and within individuals influence the resource use has potential impacts on the ecology, evolution and conservation of population and, consequently, of species (Bolnick et al. 2003). Furthermore, considering that the isotopic composition of a consumer is influenced not only by the resources consumed and the TDFs, but also by the turnover rate of each tissue (Peterson and Fry 1987; Newsome et al. 2010), by analysing metabolically inert tissues such as tooth collagen (Newsome et al. 2009; Evacita et al. 2017), scutes (Vander-Zanden et al. 2013), or baleen plates (Best and Schell 1996), it is possible to obtain time-series data of stable isotope values that allow inference of habitat use and trophic relations along the life of individuals and, consequently, the degree of specialization of a population (Vander-Zanden et al. 2013). Finally, to comprehend what leads to niche individual specialization is important to consider *Trade-offs* associated with resources exploitation, such as the selection of different prey to avoid intra-specific competition (Bolnick et al. 2003).

In cetacean literature many examples of geographic variation exist (e.g., Jones and Sayight 2002; Jefferson and Van Waerebeek 2004; Gilpatrick and Perryman 2008; Bruyn et al. 2013) and are usually related to ecological traits (Perrin 2008), with body size and cranial features indicating feeding habits (e.g., Mead and Potter 1995; McCurry et al. 2017). The bottlenose dolphin (*Tursiops truncatus*) is a widely distributed and ubiquitous species, occurring from temperate to tropical regions in a wide variety of habitats, ranging from sheltered coastal areas to oceanic waters (Wells and Scott 1999). Groups tend to be smaller in estuarine and coastal waters, where resident populations are commonly observed, and larger in offshore waters, where long-distance movements occur (Wells and Scott 1999; Bearzi 2005; Santos-Carvalho et al. 2018), demonstrating great ecological and behavioural plasticity (Scott and Chivers 1990). Given these wide ranges of distribution and habitat occurrence, two distinct ecotypes (coastal and offshore) are recognized worldwide by morphological (e.g., Mead and Potter 1995; Perrin et al. 2011; Costa et al. 2016), genetic (e.g., Segura et al. 2006; Tezanos-Pinto et al. 2009) and even isotopic evidences (e.g., Barros et al. 2010; Díaz-Gamboa et al. 2018).

The diet of the bottlenose dolphin consists of a wide range of fish, cephalopod and crustacean species, that can vary depending on the region and with the presence of other odontocete species, fishing

activities and seasons (Barros and Odell 1990; Wells and Scott 1999; Bearzi 2005). Among coastal individuals specialized foraging tactics are recognized worldwide (e.g., sponge carrying dolphins in Shark Bay, Australia (Smolker et al. 1997); cooperative behavior with artisanal fishermen in southern Brazil (Simões-Lopes et al. 1998); strand-feeding at the Gulf Guayaquil, Ecuador (Jiménez and Alava 2015)). Even so, demersal sciaenid fishes are the prey most frequently observed in the stomach content of coastal individuals (Barros and Odell 1990; Gannon and Waples 2004; Laporta et al. 2016a; Milmann et al. 2016). Diet from oceanic individuals is barely known; however, a few studies have found deep-water pelagic fish and squid in the stomachs of offshore individuals (Barros and Odell 1990; Mead and Potter 1995). Moreover, ontogenetic differences in the diet of bottlenose dolphins have already been suggested from stomach content analysis (Gannon and Waples 2004). Specifically, weaning - the transition between relying on lactation to the ingestion of solids, appears to be a gradual process (Mead and Potter 1990) generally assumed to end around 1–2 years old, when young dolphins are expected to become nutritionally independent (Mead and Potter 1990; Wells and Scott 1999). However, longer lasting periods of milk intake have already been reported (Cockcroft and Ross 1989; Wells and Scott 1999) and have even been related to inbreeding in coastal populations, once it reduces the mother's *fitness* (Frère et al. 2010).

In the western South Atlantic Ocean (wSAO) morphological distinctions between two forms (i.e., coastal and offshore) suggests adaptation to different habitats (i.e., coastal and offshore) (Costa et al. 2016; Wickert et al. 2016; Fruet et al. 2017; Simões-Lopes et al. in press). Recently the Committee on Taxonomy (2018) has recognized these two forms as different subspecies: the Lahille's bottlenose dolphin (*T. t. gephyreus*) being the coastal ecotype, and the common bottlenose dolphin (*T. t. truncatus*) as the offshore ecotype. However, the need for additional independent lines of evidence comparing both is stressed in order to regionally clarify the taxonomic debate on whether it represents two different species or not.

Bottlenose dolphins in the wSAO are observed in a great variety of habitats (Laporta et al. 2016b). Based on stranding reports, the coastal ecotype occurs from the state of São Paulo, southeast Brazil, to Península Valdés, Argentina, (Toledo 2013) usually occupying regions near river mouths, estuaries and bays (Di Tullio et al. 2016), whereas the offshore ecotype is more widely distributed, reported to occur from the state of Pará, north of Brazil (Siciliano et al. 2008), until Península

Valdés, Argentina, with occasional stranding in Tierra del Fuego, Argentina (Goodall et al., 2011; Toledo 2013). This offshore ecotype is observed both near the coast and in open sea areas along the wSAO (Di Tullio et al. 2016; Simões-Lopes et al. in press). Throughout their distribution, potential areas where both ecotypes co-occur are suggested; especially between the states of Santa Catarina and northern Rio Grande do Sul, southern Brazil (Barreto 2000; Toledo 2013; Simões-Lopes et al. in press). Also, in northern Patagonia, Argentina, there are reports of a few offshore individuals sighted with coastal ones (Vermeulen and Cammareri, 2009; Fruet et al. 2017). However, to date no study has attempted to explore the ecological aspects that would allow overlapped distribution of both ecotypes. Ecological studies with bottlenose dolphins in the wSAO are mainly focused on coastal resident populations (e.g., Simões-Lopes et al. 1998; Simões-Lopes and Fabian 1999; Daura-Jorge et al. 2012; Fruet et al. 2015a; Fruet et al. 2015b; Romeu et al. 2017; Cantor et al. 2018), with a few studies presenting data on offshore individuals, such as occurrence, group sizes and genetics (e.g., Wedekin et al. 2008; Di Tullio et al. 2016; Fruet et al. 2017; Simões-Lopes et al. in press). Diet and trophic ecology information are restricted to very few studies and are based on stomach content analysis that does not distinguish between ecotypes (e.g., Di Benedetto et al. 2001; Melo et al. 2010; Milmann et al. 2016). Moreover, information on ontogenetic changes in the diet is still lacking and the weaning age (~2years) was reported only for the coastal ecotype based on the stable isotopic composition of teeth of bottlenose dolphins stranded around the Patos Lagoon Estuary in southern Brazil (Fruet et al. 2015b).

In this study we investigated the trophic, spatial and temporal dimensions of the isotopic niche of coastal and offshore ecotypes of the bottlenose dolphins from an area of potential co-occurrence in the wSAO. Specifically, our goals were: (1) to investigate the isotopic niche, and test for main differences of habitat use and trophic relations between ecotypes; (2) to identify weaning age and other possible ontogenetic trophic shifts within each ecotype; and (3) to investigate temporal consistency on resource use and the degree of individual specialization of each ecotype population. Considering that ecological variability is vital to allow overlapping distributions of two or more taxa/populations (Bearzi 2005), also that both ecotypes have different skull morphologies and body total length (Costa et al. 2016; Wickert et al. 2016) and differ on group size and behavior (Di Tullio et al. 2016;

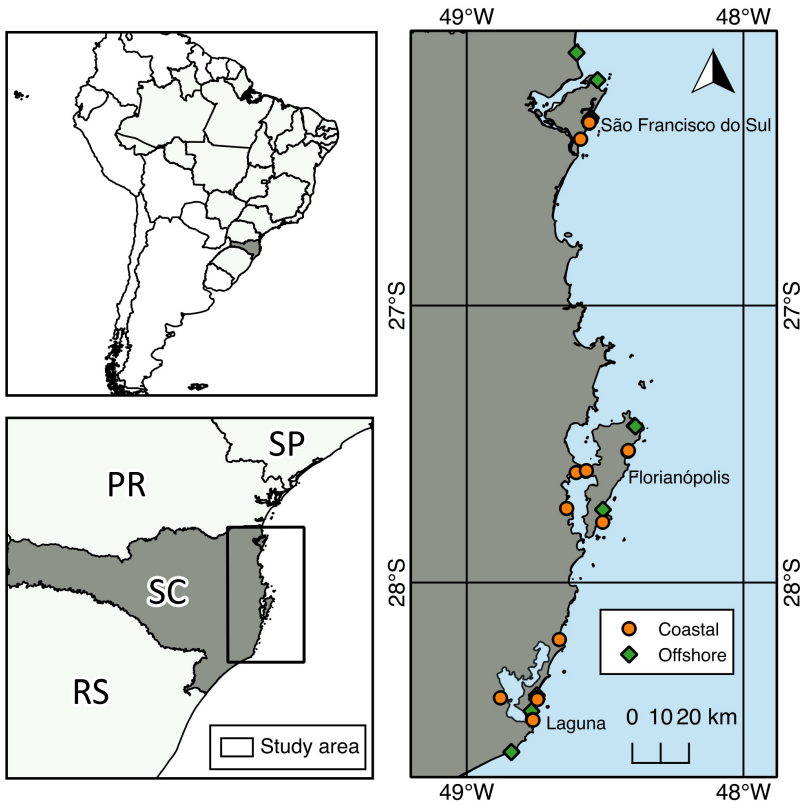
Simões-Lopes et al. in press), we tested the following hypothesis: (1) that isotopic niche is larger in the offshore ecotype as a result of a wider foraging area (Simões-Lopes et al., in press), but that some niche overlap exists given that all individuals analyzed come from a potential co-occurring area (Barreto 2000; Toledo 2013), also that ecotypes vary particularly on habitat use, with the coastal ecotype being more associated with coastal and demersal habitats and the offshore ecotype with pelagic habitats (e.g., Pinela et al. 2010; Botta et al. 2012; Secchi et al. 2016; Díaz-Gamboa et al. 2018); (2) that the coastal ecotypes has prolonged weaning age as a reflection of longer parental carrying to learn specialized foraging tactics (Simões-Lopes et al. 1998; Cantor et al. 2018), and also, given that inbreeding have already been reported for a costal population within the study area (Fruet et al. 2014); and finally, (3) that coastal individuals show a higher degree of individual specialization for presenting a resident behavior (Di Tullio et al. 2016; Laporta et al. 2016b; Lodi et al. 2016) in a heterogeneous habitat (SCBD 2014) with more anthropogenic pressure (Fruet et al. 2014), being the individual specialization an strategy to overcome intra-specific competition (Bolnick et al. 2003).

2.2 MATERIAL AND METHODS

2.2.1 Sample collection and preparation

Teeth of 28 specimens of *Tursiops truncatus* (15 coastal and 13 offshore) were obtained from the scientific collections of Laboratório de Mamíferos Aquáticos, Universidade Federal de Santa Catarina (LAMAQ/UFSC), of Laboratório de Zoologia, Universidade do Estado de Santa Catarina (UDESC) and of Acervo Biológico Iperoba, Universidade da Região de Joinville (Univille). All the animals that compound these collections come from stranded carcasses collected along the coast of Santa Catarina state (26°05'-28°36'S 048°36'-048°50'W), southern Brazil, between 1987 and 2018 (Fig. 1). Because the focus in this study is the ecological features of offshores and coastal dolphins, the term ecotype is addressed; being *Tursiops truncatus* *gephyreus* referred as the coastal ecotype and *Tursiops truncatus truncatus* as the offshore ecotype. To distinguish coastal and offshore ecotypes the skull morphology of all individuals was previously verified, considering features such as the posterior border of the pterygoid (after Costa et al. 2016). The sex of each individual was determined directly from carcasses in the field or during necropsies.

Figure 1 Study area and stranding points of the 28 specimens (15 coastal and 13 offshore) analysed for this study. Some stranding points are overlapped. Skull morphology was used to distinguish ecotypes; orange circles represent stranding of coastal bottlenose dolphins (*T. t. gephyreus*) and green lozenges represent stranding of the offshore bottlenose dolphins (*T. t. truncatus*). The Brazilian states of São Paulo (SP), Paraná (PR), Santa Catarina (SC) and Rio Grande do Sul (RS) are shown at the lower map to the left. The upper map at the left side represents South America.



2.2.2 Age estimation

One tooth from each individual was selected for age estimation (following Hohn et al. 1989). Using a low-speed saw with a diamond-embedded blade sections from both laterals of each tooth were removed to make it thinner. The sliced teeth were then placed into a flask with RDO solution for about 24 hours in order to demineralize it. After, all teeth were washed with abundant running tap water and with the aid of a Leica® freezing microtome serial longitudinal thin sections of approximately 24µm were cut from each tooth. These thin sections were then stained with Mayer's hematoxylin for about 30 minutes, washed with running tap water, drowned in ammonia 0.5% to enhance contrast, rinsed with tap water and stored in 100% glycerine. Tooth sections were mounted in 100% glycerine and photographed with the aid of a stereomicroscope. Three different researchers estimated ages by counting dentine Growth Layer Groups (GLGs) and considering each as representing one year of life (Hohn et al. 1989).

2.2.3 Stable Isotope Analysis (SIA)

The straightest tooth was selected and, whenever possible, with lesser signs of tooth wear. All teeth were cleaned with distilled water and then sectioned longitudinally with the aid of a low-speed saw with a diamond-embedded blade. The dentine surface was then polished with water sand paper and soaked into 25% formic acid for approximately 1 hour and 30 minutes to expose the GLGs. After, the tooth was cleaned with distilled water and let dry naturally (Albernaz et al. 2017). Using a drill bit of 0.3mm the powder from the external surface of each layer was removed, in order to avoid the influence of the formic acid on Stable Isotope Analysis (SIA), and then sequential dentin samples from the GLGs were collected, grouping layers whenever it was not possible to collect it separately. The powder of each sample was then stored into separate silver capsules and exposed to a vaporous 30% hydrochloric acid in a desiccator for 24h to remove biogenic carbonates (Knoff et al. 2008). At last, the acidified samples were dried for 2h at 60°C and each capsule was enclosed with approximately 1 mg.

The samples were analyzed for stable isotope composition of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) at the Center for Stable Isotopes, New Mexico University, Albuquerque, NM, USA, using a Costech (4010) elemental analyzer coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer. Isotope ratios are expressed in delta (δ) notation, meaning parts per thousand (‰) relative to an international standard:

$$\delta = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,$$

where R_{sample} and R_{standard} represent the ratio of heavy and light isotopes ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) of the sample and in the international standard, respectively, for each isotope. The standards are Vienna Pee Dee Belemnite (V-PDB) limestone for carbon and atmospheric N_2 for nitrogen. The analytical precision, based on the standard deviation of the laboratory standard replicas was $< 0.1\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Considering that this study's samples were collected from 1987 to 2018, a correction factor of 0.022‰ was applied per year to all sample carbon isotope values to account for the Suess effect (Francey et al. 1999; Indermühle et al. 1999). Additionally, 111 samples with C:N > 3.5 were normalized for lipid content (mean_C:N = 3.6 ± 0.3) (following Post et al. 2007).

2.2.4 Data Analysis

2.2.4.1 Isotopic niche and ontogeny

Prior to the analysis, to assess data normality and homogeneity in variance, data exploration was carried out by well-established protocols (cf. Zuur et al. 2010). Initially, to check for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between ecotypes and among age classes within each ecotype Student's t tests were applied. Two age classes were defined: calf, represented by the isotopic values of the 3rd GLG given that in this region young dolphins tend to stay with their mothers until about 3 years old (Bezamat et al. in prep) and weaning apparently occurs around 2 years old (Fruet et al. 2015b); and young/adult, represented by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values of GLGs > 3 .

To identify isotopic changes related to weaning age and other possible ontogenetic shifts, generalized additive mixed models (GAMM, Wood 2006), with a Gaussian distribution and identity link function, were applied to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data. GLGs and ecotype were included as fixed factors and the dolphin ID as a random factor to account for a dependence structure. The models were fitted in R with package *mgcv*, and curves were smoothed by GLGs.

Mean isotopic values of each individual were used to delineate standard ellipses corrected for small samples sizes (SEAc) for each ecotype and to calculate the overlap between them through SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). The first and the second GLGs were discarded for these analyses as they

reflect the consumption of milk. Ellipses by sex and age class were also generated to further investigate the total isotopic niche of each ecotype.

2.2.4.2 Temporal consistency and individual specialization

Each individual tooth GLG isotopic values were used to infer its history of resource and habitat use and the population's feeding strategy (Vander-Zanden et al. 2013), by testing the temporal consistency and the degree of individual specialization within the population (Bolnick et al. 2002). Firstly, to test for temporal consistency within each ecotype, young/adult isotopic values were modeled as a function of its calf values by fitting linear regressions. By doing that, it is possible to discuss if foraging habits used as a calf, predispose an individual to exploit the same foraging habits as an adult (Rossman et al. 2015a).

The total niche width (TNW) of a population can be divided into two components: the within-individual component (WIC, or within-phenotype component by Roughgarden 1972), meaning the variance on resource use by each individual; and the between-individual component (BIC, or between-phenotype component by Roughgarden 1972), which is the variation on resource use between individuals (Bolnick et al. 2002). If the proportion of TNW explained by WIC is close to 1 ($WIC/TNW \sim 1$) it means that there is little variation between individuals and the population is composed of generalists; otherwise it is composed of specialists. Therefore, $\delta^{13}C$ and $\delta^{15}N$ values beginning from the third GLG of each individual were used to calculate the degree of individual specialization by WIC, BIC and TNW, using the ANOVA framework. The mean sum of squares within individuals were assumed as equivalent of WIC and the mean sum of squares between individuals as a proxy of BIC; the indices were then tested for statistical significance by a bootstrapping with 1000 replicates (adapted from Vander-Zanden et al. 2013).

2.3 RESULTS

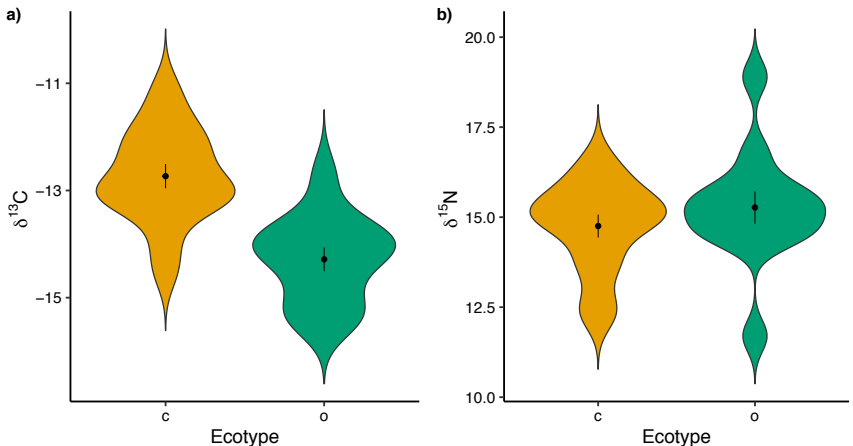
2.3.1 Variation of $\delta^{13}C$ and $\delta^{15}N$

A total of 195 GLG samples were analyzed, being 108 from coastal specimens and 87 from offshore specimens. The number of samples obtained per individual varied from four samples from a young offshore dolphin to nine samples obtained from four different individuals (three from the coastal ecotype and one from the offshore ecotype). Values of $\delta^{13}C$ ranged from -14.5‰ to -11.1‰ among coastal individuals and from -15.4‰ to -12.7‰ among offshore individuals.

$\delta^{15}\text{N}$ values ranged from 12.3‰ to 16.6‰ among coastal dolphins and from 11.7‰ to 18.9‰ among offshore dolphins.

Mean $\delta^{13}\text{C}$ values were higher for the coastal ecotype ($\delta^{13}\text{C}_c = -12.7$ ‰ and $\delta^{13}\text{C}_o = -14.3$ ‰; $t = 4.8677$, $df = 26$, $p\text{-value} < 0.0001$). $\delta^{15}\text{N}$ values were not significantly different between ecotypes ($\delta^{15}\text{N}_c = 14.7$ ‰ and $\delta^{15}\text{N}_o = 15.3$ ‰; $t = -0.95$; $df = 26$, $p\text{-value} = 0.35$) (Fig. 2). When comparing isotopic values between age classes no significant differences were detected for both coastal ($\delta^{13}\text{C}_{\text{calf}} = -12.7$ ‰ and $\delta^{13}\text{C}_{\text{young/adult}} = -12.7$ ‰, $t = -0.04$, $df = 28$, $p\text{-value} = 0.97$; $\delta^{15}\text{N}_{\text{calf}} = 14.8$ ‰; and $\delta^{15}\text{N}_{\text{young/adult}} = 14.7$ ‰, $t = -0.22$, $df = 28$, $p\text{-value} = 0.83$) and offshore ($\delta^{13}\text{C}_{\text{calf}} = -14.3$ ‰ and $\delta^{13}\text{C}_{\text{young/adult}} = -14.3$ ‰, $t = 0.08$, $df = 24$, $p\text{-value} = 0.94$; $\delta^{15}\text{N}_{\text{calf}} = 15.3$ ‰; and $\delta^{15}\text{N}_{\text{young/adult}} = 15.2$ ‰, $t = -0.05$, $df = 24$, $p\text{-value} = 0.96$) ecotypes.

Figure 2 Violin-plot with distribution of (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ values for coastal [c] and offshore [o] ecotypes of bottlenose dolphin. Points represent mean values with standard deviation. Difference between mean values was only significant for $\delta^{13}\text{C}$ values ($p < 0.0001$)



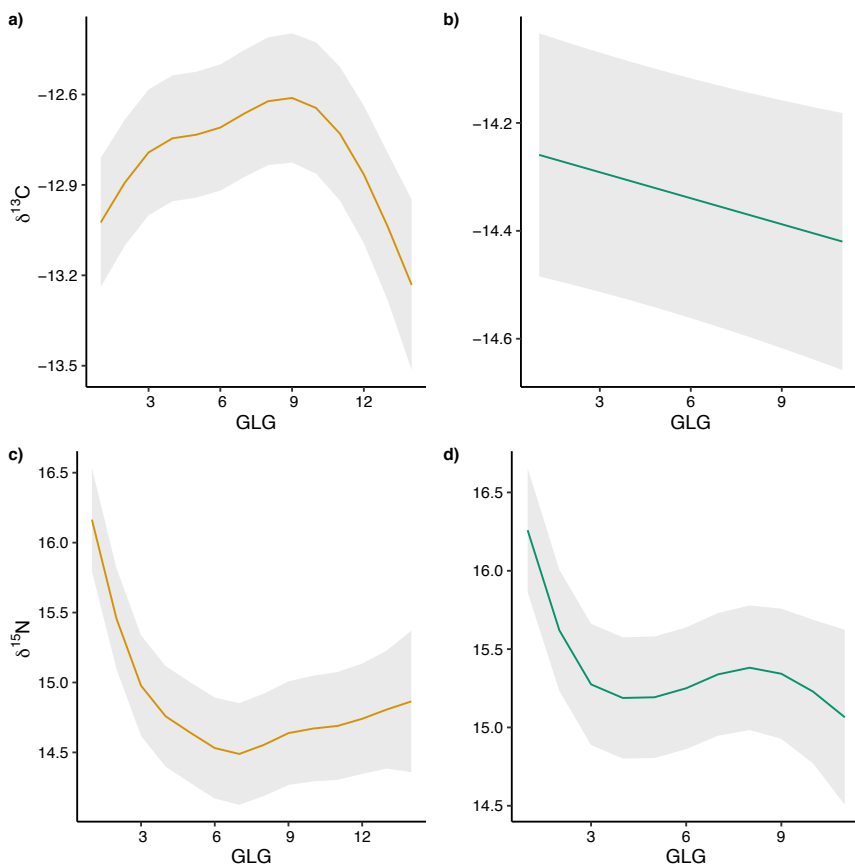
2.3.2 Ontogenetic variation in isotopic composition

The estimated smoothers of the GAMM models highlight a non-linear relationship with age for $\delta^{13}\text{C}$ in the coastal, and for $\delta^{15}\text{N}$ in both ecotypes. Carbon isotopic values were significantly smoothed by the GLGs only for the coastal ecotype (Adjusted- $r^2 = 0.454$, $p < 0.0001$).

The offshore ecotype presented a linear pattern for this isotope. Graphically, an increase of $\delta^{13}\text{C}$ values during the first three years of life, and another increase around eight years of age could be observed, especially for the coastal ecotype (Fig. 3 **a** and **b**).

Nitrogen isotopic values were significantly smoothed by GLGs for both ecotypes (for coastal: Adjusted- $r^2 = 0.104$, $p < 0.0001$; for offshores: Adjusted- $r^2 = 0.104$, $p < 0.0001$). A sharp decline in $\delta^{15}\text{N}$ could be observed for both ecotypes from the first until the third year of age; further on the decline continues with a softer inclination until seven and four years old for the coastal and offshore ecotypes, respectively. The predicted values (Fig. 3 **c** and **d**) indicate that the decrease starts immediately after the first GLG for both ecotypes ($\delta^{15}\text{N}_{\text{GLG1}_c} = 16.2\text{‰}$ and $\delta^{15}\text{N}_{\text{GLG1}_o} = 16.3\text{‰}$) and reaches the lowest value at the 7th ($\delta^{15}\text{N}_{\text{GLG7}_c} = 14.5\text{‰}$) and 4th ($\delta^{15}\text{N}_{\text{GLG7}_o} = 15.2\text{‰}$) GLG for coastal and offshore ecotypes, respectively, representing an average change of 1.7‰ for the coastal and 1.1‰ for the offshore ecotype.

Figure 3 Predicted $\delta^{13}\text{C}$ (above) and $\delta^{15}\text{N}$ (below) values in tooth GLGs of the coastal and offshore bottlenose dolphin's ecotypes based on a fitted generalized additive mixed model. Graphs a) and c) represent the coastal ecotype (orange line) and graphs b) and d) represent the offshore ecotype (green line). Coloured lines are the predicted curve, while grey limits represent the approximated 95% point-wise confidence intervals. The approximate significance of smooth terms for coastal ecotype was $F = 7.076$, offshore ecotype was $F = 1.487$



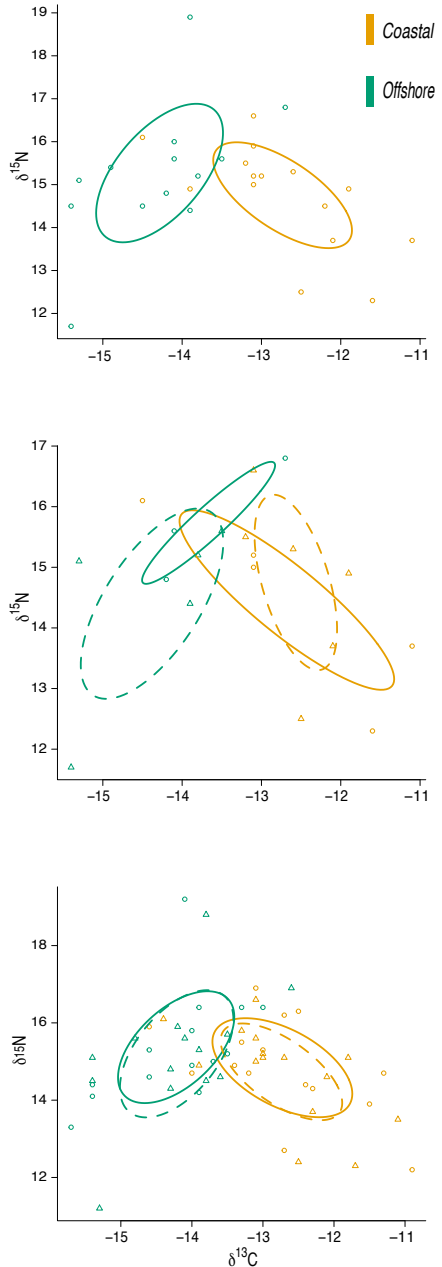
2.3.3 Isotopic niche variation

The standard ellipse area for the offshore ecotype was larger ($\text{SEAc}_o = 3.60\text{‰}^2$) than for the coastal ecotype ($\text{SEAc}_c = 2.73\text{‰}^2$) (Fig.

4a). A small overlap between coastal and offshore forms could be observed, representing 2.43% of the coastal ecotype area and 1.84% of the offshore ecotype area.

When analyzing the isotopic niche by sex, standard ellipses of males and females within ecotypes were overlapped and apparently the overlap between ecotypes occurred mainly due to coastal females, as the ellipse of coastal males was completely apart from the offshore ones (Fig. 4b). It is important to note, however, that only nineteen individuals of our sample had their sex determined (five females and six males from the coastal ecotype; and three females and five males from the offshore ecotype). The SEAc areas of females were 3.99‰^2 for the coastal ecotype and 1.81‰^2 for the offshore ecotype, whereas the SEAc of males were 2.49‰^2 for the coastal ecotype and 4.20‰^2 for the offshore ecotype. Ellipses for calves and young/adults were similar between each other among ecotypes (Fig. 4c). The SEAc of calves were 3.63‰^2 for the coastal ecotype and 3.39‰^2 for the offshore ecotype, whereas the SEAc of young/adults were 2.77‰^2 for the coastal ecotype and 3.77‰^2 for the offshore ecotype.

Figure 4 Isotopic Standard Ellipses adjusted for small sample sizes (SEAC) representing the isotopic niche for coastal and offshore ecotypes of bottlenose dolphins, generated with individual's mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values excluding GLGs 1 and 2, considering all individuals sampled (a), separated by sex (b) and separated by age class (c). In (b), female's ellipses (solid lines) are defined by circles and male's ellipses (dashed lines) are defined by triangles; In (c), calves ellipses (solid lines) are defined by circles and young/adults ellipses (dashed lines) are defined by triangles



2.3.4 Temporal consistency and individual specialization

Results on temporal consistency showed that young/adult $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly explained by calf values for both ecotypes (Fig. 5).

Carbon and nitrogen isotopic values through lifetime showed some individual variation within both ecotypes (Fig. 6 **a** and **b**). The within-individual component (WIC), calculated by the ANOVA framework, was higher in the coastal ecotype for $\delta^{13}\text{C}$ ($\text{WICc} = 0.13$ and $\text{WICo} = 0.07$) and also for $\delta^{15}\text{N}$ ($\text{WICc} = 0.25$ and $\text{WICo} = 0.13$) values. However, the metric for individual specialization (WIC/TNW) was very similar between ecotypes for both $\delta^{13}\text{C}$ ($\text{WIC/TNWc} = 0.04$ and $\text{WIC/TNWo} = 0.01$) and $\delta^{15}\text{N}$ ($\text{WIC/TNWc} = 0.02$ and $\text{WIC/TNWo} = 0.04$) values.

Even though numerical differences were observed in WIC values between ecotypes, no significant difference was observed between both ecotypes indexes of WIC and WIC/TNW for data of carbon (WIC: p-value = 0.08; WIC/TNW: p-value = 0.09) and nitrogen (WIC: p-value = 0.13; WIC/TNW: p-value = 0.6) (Fig. 6 **c** and **d**).

Figure 5 Individual bottlenose dolphin's $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) values as young/adult plotted against its isotope values as a calf. Calf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are represented by the isotopic values of the 3rd GLG, while young/adult values are represented by the mean isotopic values of GLGs >3 (4th GLG upwards). Ecotypes are differentiated by colour, orange for coastal (left) and green for offshore (right). The r^2 , the F-statistics and p-values are shown on top of each graph

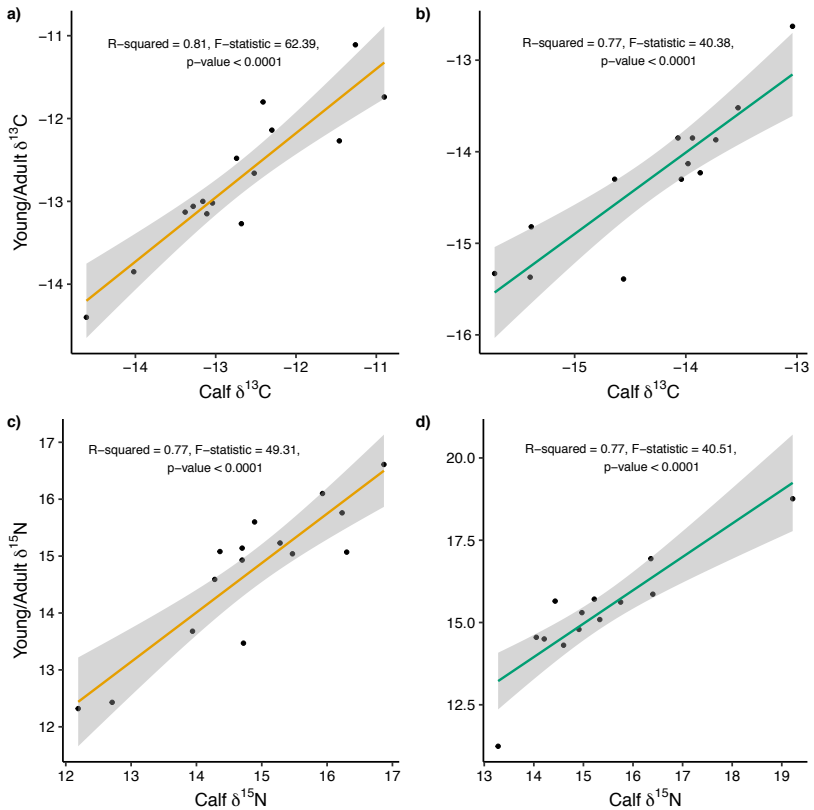
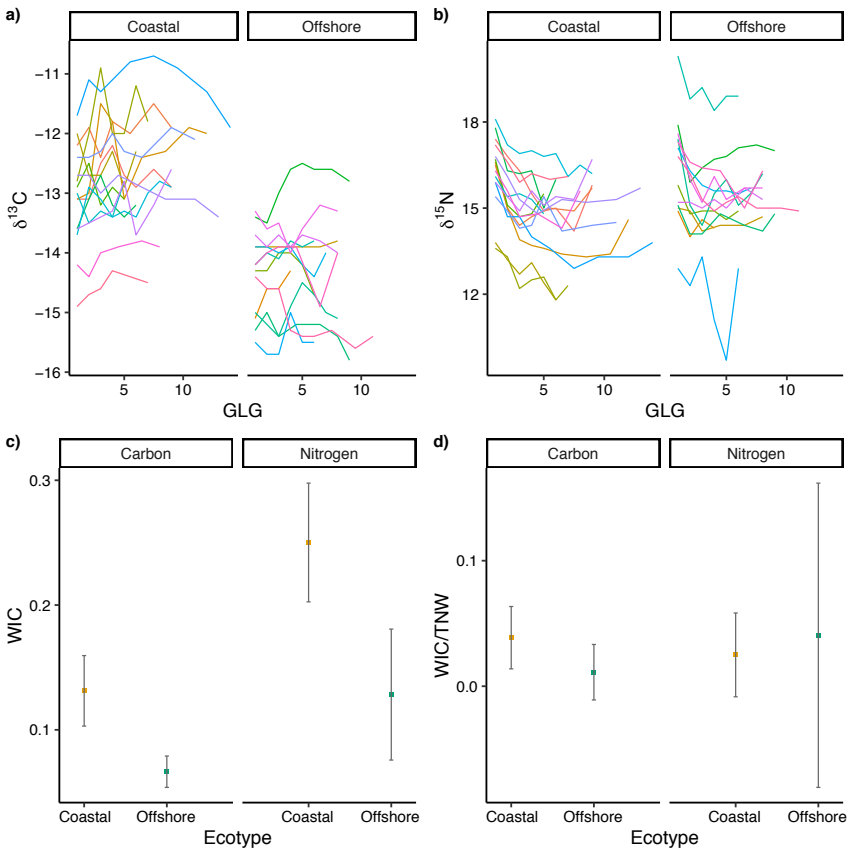


Figure 6 Individual carbon (a) and nitrogen (b) isotopic ontogenetic profiles from coastal ($n = 15$) and offshore ($n = 13$) bottlenose dolphins (each line represents all samples for an individual). And within individual component (WIC) (c) and the degree of individual specialization (WIC/TNW) (d), calculated for carbon and nitrogen isotope compositions in both bottlenose dolphin's ecotypes. WIC/TNW ratio range from 0 when all individuals are specialists to 1 when all are generalist. Squares represent mean \pm SD. Pairwise comparisons of WIC and WIC/TNW were conducted separately for $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values by a bootstrap with 1000 replicates; no significant difference was observed between ecotypes



2.4 DISCUSSION

This is the first study to investigate resources use in the ontogenetic development of two ecotypes of bottlenose dolphins in an area of co-occurrence in the western South Atlantic. The data analyzed here demonstrates that both ecotypes diverge in their trophic ecology, especially due to their habitat use. The weaning process seems to last longer in the coastal ecotype, and some degree of specialization in resource use is observed within both ecotypes.

Stable carbon isotope values were consistently higher in the coastal ecotype, a result that we expected due to the typical inshore – offshore pattern of decreasing $\delta^{13}\text{C}$ values found in marine environments (Hobson et al. 1999). Although analyzing material from primary producers and potential prey (e.g., Pinela et al. 2010), or combining isotope analyses with other methodologies (e.g., stomach content (e.g., Barros et al. 2010); contaminants (e.g., Wilson *et al.* 2012); or compound specific stable isotope analysis (e.g., Nelson et al. 2018)) would be desirable to better understand the regional scenario in which these animals forage, many studies have already shown a trend for higher values of $\delta^{13}\text{C}$ near shore and in estuarine habitats than in offshore and pelagic habitats where the primary production is based on phytoplankton (e.g., Segura et al. 2006; Newsome et al. 2010; Botta et al. 2012; Bisi *et al.* 2013; Díaz-Gamboa et al. 2018). As the samples analyzed here were collected from animals of unknown origin and from different years, the lower $\delta^{13}\text{C}$ values found in individuals classified as belonging to the offshore ecotype, based on cranial morphology (Costa et al. 2016), confirm the pelagic/offshore feeding habit of this ecotype (Hobson 1999).

Although a small isotopic niche overlap was observed between these ecotypes, mainly due to the isotopic niche of coastal females, a niche partitioning is evident between ecotypes in this area of overlapped distribution. The coast of this sampling-region is very heterogeneous (SCBD 2014), with many different bays, coastal islands and estuaries. It is also the southernmost distribution of rocky shores in Brazil (Coutinho 2004) and mangroves in the western South Atlantic (Schaeffer-Novelli et al. 1990). Moreover, the encounter of warm waters from the Brazil current with the cold and nutrient-rich subpolar waters characterizes the Subtropical Convergence, which combined with the coastal features enumerated above makes this an upwelling and a very productive area (SCBD 2014). Therefore, even though the offshore ecotype is observed close to the coast along the study area (Simões-Lopes et al. in press), the

isotopic data indicates that it feeds mainly on different prey when compared to the coastal ecotype. Along southern Brazil different populations of the coastal ecotype show resident behavior and are associated with estuarine systems (Di Tullio et al. 2016; Laporta et al. 2016b; Lodi et al. 2016), mainly preying upon demersal fish (Secchi et al., 2016). Prey preferences of the offshore ecotype are not known, but our results indicate that the coastal sightings of these individuals probably result from an occasional and opportunistic behavior of expanding its distribution into the coastal areas when advantageous. This could include, for example, when foraging upon catadromous fish species that spawn off Santa Catarina's coast during winter, such as mullet (Lemos et al. 2014), a frequently observed item in the stomach content of bottlenose dolphins across regions (Barros and Odell 1990; Mead and Potter 1990; Well and Scott 1999; Milmann et al. 2016; Secchi et al. 2016).

The isotopic niche overlap between females from both ecotypes together with males from the offshore ecotype is intriguing but needs to be evaluated with caution. As four parameters are needed to build convex hulls and SIBER ellipses, only sample sizes equal or larger than five should be used (Jackson et al. 2011). Only three samples from the offshore ecotype were known to be from female dolphins, therefore, any conclusion about their isotopic niche would be doubtful and probably biased by outliers. However, it is interesting to note that offshore males also show some more ^{13}C -enriched $\delta^{13}\text{C}$ values than females and the largest ellipse area, suggesting that this group is foraging in a wider area around this sampling-region.

The difference between coastal females and males might be confusing at first, as the lowest values of $\delta^{13}\text{C}$ among coastal individuals were detected in the former and we would expect from photo-ID studies that males are the ones to disperse more along the coast and to explore pelagic habitats (Möller et al. 1994; Simões-Lopes and Fabian 1999). However, ^{13}C depleted $\delta^{13}\text{C}$ values are common in freshwater in comparison to other coastal habitats (e.g., Garcia et al. 2007). Considering that some freshwater fishes explore estuarine and coastal areas, and also that estuarine resident/dependent fishes can disperse into freshwater areas for feeding (e.g., Garcia et al. 2007), the fact that coastal bottlenose dolphins are associated with different coastal habitats (e.g., estuaries, coastal lagoons, bays) and that females tend to be more resident makes it possible for the consumption of fishes dispersing from nearby freshwater habitats. Furthermore, Milmann et al. (2016) have found Atlantic sabretooth anchovy (*Lycengraulis grossidens*) in the

stomach content of three bottlenose dolphins from southern Brazil, and, even though this is an estuary-resident species, Garcia et al. (2007) have collected specimens in freshwater areas. ^{13}C -depleted values of $\delta^{13}\text{C}$ have also been found on the teeth of beluga whales, being associated with feeding from freshwater sources (Nelson et al. 2018). Therefore, the apparent overlap between coastal females with individuals from the offshore ecotype, due to similar $\delta^{13}\text{C}$ values, does not necessarily imply that these females are feeding away from the coastline, but rather that they might be eating freshwater prey. Additionally, three out of five coastal females analyzed in this study were stranded inside a coastal bay, and the other two were stranded close to estuary complexes (Laguna and São Francisco do Sul), demonstrating that these coastal individuals can be strongly influenced by freshwater environments. The plasticity of feeding habits among coastal females (Rossman et al. 2015a), and the wider isotopic niche on coastal females in comparison to coastal males have also been reported for Sarasota Bay, USA (Rossman et al. 2015b).

From an age class perspective, the isotopic niche results show that regardless of age class, ecotypes diverge on habitat use throughout their lives. This can be observed also in the results on temporal consistency, that show young/adult isotopic values of both carbon and nitrogen being explained by its calf value, and, likewise, the low values of WIC indicate little variation within each individual lifetime. These results reinforce the fact that individuals tend to keep similar foraging habits to those learned as a calf with their mothers (Sargeant and Mann 2009) or with other possible role models within the population (Sheppard et al. 2018).

When analyzing samples per GLG, we noticed that higher values of $\delta^{15}\text{N}$ (for both ecotypes) and lower values of $\delta^{13}\text{C}$ (for the coastal ecotype) are evident during the first year of life in agreement with a diet based on milk, a product metabolized from the mothers' tissue and rich in lipids, respectively (Newsome et al. 2009). Even though both ecotypes seem to start the weaning process at a similar age, between two and three years old, from the $\delta^{15}\text{N}$ predicted values (Fig. 5) it appears that for the coastal ecotype it lasts longer, what can be a reflection of a prolonged mother-calf association in order to learn specialized behaviors such as feeding tactics associated with a more heterogeneous habitat (Cantor et al. 2018). Furthermore, the continuous decline of $\delta^{15}\text{N}$ values and the second increase of $\delta^{13}\text{C}$ values until approximately seven years old observed for the coastal ecotype may reflect a rapid growth rate

stage between the post-weaning period and the age of sexual maturity. During a stage of rapid growth, the rate of nitrogen assimilation tends to be higher than that of excretion provoking a diminishment of the fractionation of this isotope, therefore, resulting in lower values of $\delta^{15}\text{N}$ (Newsome et al. 2009; Evacita et al. 2017). Finally, the weaning age at 2–3 years old agrees with a previous study made exclusively with coastal individuals from southern Brazil (Fruet et al. 2015b), nevertheless, for large-bodied animals weaning seems to vary greatly within and between populations (Lee 1996), thus the longer weaning process observed in the coastal ecotype could be due to higher variability within these individuals.

The results of individual specialization (WIC/TNW) indicate that both ecotypes are composed by specialist individuals (Bolnick et al. 2002). We expected this result in the case of the coastal ecotype, as individuals live in a quite heterogeneous habitat (SCBD 2014). Moreover, coastal populations of the bottlenose dolphin are known to develop many different foraging tactics, from following fishing trawlers to catch discarded bycatchs (Corkeron et al. 1990) to performing intentional stranding in order to corral its prey (Jiménez and Alava 2015). In Shark Bay, Australia, for example, individuals vary in at least 13 different foraging strategies (Whitehead 2008). In Laguna, southern Brazil, a subset of a bottlenose dolphin population (coastal ecotype) specialized in foraging in cooperation with artisanal fisherman (Simões-Lopes et al. 1998; Daura-Jorge et al. 2012); as specialized dolphins reduce their home range, this foraging tactic seems to be a solution to avoid competition in a heterogeneous habitat (Cantor et al. 2018).

On the other hand, we did not expect the individual specialization for the offshore ecotype, as animals live in an unrestricted area and tend to form larger groups (Wells and Scott 1999; Bearzi 2005; Santos-Carvalho et al. 2018). However, considering the long distances movements already noted for a few individuals, the site fidelity to oceanic islands demonstrated by some populations, and the seasonal residency observed in the north of the state of Santa Catarina and in northern regions of Brazil (Laporta et al. 2016b), it is possible that the isotopic variation observed in offshore individuals is due to the potential heterogeneous origin of the specimens analysed, which might include animals feeding in isotopically distinct areas. Indeed, a latitudinal gradient in basal isotopic values due to oceanographic features and the availability of nutrients in the water column is present in the wSAO (Graham et al. 2010; McMahan et al. 2013). Additionally, freshwater inputs from estuaries can influence pelagic food webs around Santa

Catarina's state (Lemos et al. 2017), and the presence of the Brazil current and subpolar waters varies seasonally (SCBD 2014). Therefore, a heterogeneous isoscape might be expected around Santa Catarina's coast.

The use of the isotope values from different perspectives allowed us to infer about a few aspects of the ecotypes habitat use and ecological niche partition. For instance, in northern Chile, the isotopic niche of resident bottlenose dolphins is completely overlapped by that of transient bottlenose dolphins (Santos-Carvalho et al. 2015). The fact that the isotopic niche of coastal and offshore ecotypes analyzed in the present study differ greatly, supports the adaptation of each to different habitats, also the small overlap observed between them reinforces the hypothesis of a parapatric distribution with a "contact zone" in southern Brazil, suggested in previous studies (e.g., Costa et al. 2016; Fruet et al. 2017). Furthermore, ecotypes seem to differ in resource use throughout the ontogenetic development. Future studies with stable isotope mixing models and compound specific isotopic analysis should help elucidate the diet composition and trophic relations of each ecotype. Finally, the results of individual specialization, although preliminary, give rise to important considerations on how the bottlenose dolphins utilize the habitat. Nevertheless, further time-series investigations on coastal resident populations that consider demographic structure, and a better characterization of the offshore population should be carried out in order to clarify such queries.

2.5 REFERENCES

- Albernaz TL, Secchi ER, Oliveira LR, Botta S (2017) Ontogenetic and gender-related variation in the isotopic niche within and between three species of fur seals (genus *Arctocephalus*). *Hydrobiologia* 787:123–139
- Ashton KG, Tracy MC, Queiroz A (2000) Is Bergmann's Rule Valid for Mammals? *The American Naturalist* 156(4):390–415
- Barreto AS (2000) Variação Craniana e Genética de *Tursiops truncatus* (Delphinidae, Cetacea) (Montagu, 1821) na Costa Atlântica da América do Sul. Ph.D. Thesis. Universidade Federal do Rio Grande, Rio Grande, Brasil
- Barros NB, Odell DK (1990) Food Habits of bottlenose dolphins in southeastern United States. In: Leatherwood S, Reeves R (eds.). *The bottlenose dolphin*, Academic Press, pp 309-328

- Barros NB, Ostrom PH, Stricker CA, Wells RS (2010) Stable isotopes differentiate bottlenose dolphins off west-central Florida. *Marine Mammal Science* 26(2):324–336
- Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology* 73(5):1007–1012
- Bearzi M (2005) Dolphin sympatric ecology. *Marine Biology Research* 1(3):165–175
- Best P, Schell D (1996) Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Marine Biology* 124:483–494
- Bisi TL, Dorneles PR, Lailson-Brito J, Lepoint G, Azevedo AF, Flach L, Malm O, Das K (2013) Trophic relationships and habitat preferences of delphinids from the southeastern Brazilian coast determined by carbon and nitrogen stable isotope composition. *PLoS One* 8(12):e82205
- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck, R (2002) Measuring Individual-Level Resource Specialization. *Ecology* 83(10):2936–2941
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The Ecology of Individuals: Incidence and Implications of Individual Specialization. *The American Naturalist* 161(1):1–28
- Botta S, Hohn AA, Macko SA, Secchi ER (2012) Isotopic variation in delphinids from the subtropical western South Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 92(8):1–10
- Brown JH, Lomolino MV (1998) *Biogeography*, 2nd ed. Sinauer Associates, Inc., Sunderland, Massachusetts
- Bruyn PJN, Tosh CA, Terauds A (2013) Killer whale ecotypes: is there a global model? *Biological Reviews* 88:62–80
- Cantor M, Simões-Lopes PC, Daura-Jorge FG (2018) Spatial consequences for dolphins specialized in foraging with fishermen. *Animal Behaviour* 139:19–27
- Chase JM, Leibold MA (2003) *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago
- Cockcroft VG, Ross GJB (1989) Age, growth, and reproduction of bottlenose dolphins *Tursiops truncatus* from the East coast of Southern Africa. *Fishery Bulletin* 88(2):289–302

- Committee On Taxonomy (2018) List of marine mammal species and subspecies. <https://www.marinemammalscience.org/species-information/list-marine-mammal-species-subspecies/>
- Corkeron PJ, Bryden MM, Hedstrom KE (1990) Feeding of bottlenose dolphins in association with trawling operation in Moreton Bay, Australia. In: Leatherwood S, Reeves RR (Eds.). *The Bottlenose Dolphin*, Academic Press, p. 329-336
- Costa APB, Rosel PE, Daura-Jorge FG, Simões-Lopes PC (2016) Offshore and coastal common bottlenose dolphins of the western South Atlantic face-to-face: What the skull and the spine can tell us, (Montagu 1821). *Marine Mammal Science* 32(4): 1433–1457
- Coutinho R (2004) Programa Nacional da Biodiversidade – PRONABIO - Projeto de Conservação e Utilização Sustentável da Diversidade Biológica Brasileira – PROBIO Sub-Projeto: Avaliação e Ações Prioritárias para a Zona Costeira e Marinha. Grupo de Ecossistemas: Costões Rochosos. In: Guia para o licenciamento ambiental, Atividades de Sísmica Marítima na Costa Brasileira, Atividades de Perfuração de Óleo e Gás.
- Daura-Jorge FG, Cantor M, Ingram SN, Lusseau D, Simões-Lopes PC (2012) The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. *Biology Letters* 8(5):702-705
- Di Benedetto APM, Ramos RMA, Siciliano S, Sanots RADOS, Fagundes-Netto GBAE (2001). Stomach contents of delphinids from Rio de Janeiro, southeastern Brazil. *Aquatic Mammals* 27(1):24-28
- Di Tullio JC, Gandra TBR, Zerbini AN (2016) Diversity and Distribution Patterns of Cetaceans in the Subtropical Southwestern Atlantic Outer Continental Shelf and Slope, 11(5): e0155841
- Díaz-Gamboa RE, Gendron D, Busquets-Vass G (2018) Isotopic niche width differentiation between common bottlenose dolphin ecotypes and sperm whales in the Gulf of California. *Marine Mammal Science* 34(2):440–457
- Endler JA, Houde AE (1995) Geographic Variation in Female Preferences for Male Traits in *Poecilia reticulata*. *Evolution* 49(3):456-468
- Evacita FC, Kao WY, Worthy GAJ, Chou, LS (2017) Annual variability in dentin $\delta^{15}N$ and $\delta^{13}C$ reveal sex differences in weaning age and feeding habits in Risso's dolphins (*Grampus griseus*). *Marine Mammal Science* 33(3):748–770

- Fine PV (2015) Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics* 46: 369-392
- Francey RJ, Allison CE, Etheridge DM, Trudinger CM, Enting IG, Leuenberger M, Langenfelds RL, Michel E, Steele LP (1999) A 1000-year high precision record of $\delta^{13}\text{C}$ in atmospheric CO_2 . *Tellus B: Chemical and Physical Meteorology* 51(2):170-193
- Frère CH, Krützen M, Kopps AM, Ward P, Mann J, Sherwin WB (2010) Inbreeding tolerance and fitness costs in wild bottlenose dolphins. *Proceedings of the Royal Society B* 277: 2667-2673
- Fruet PF, Secchi ER, Daura-Jorge F, Vermeulen E, Flores PAC, Simões-Lopes PC, Genoves RC, Laporta P, Di Tullio J, Freitas TRO, Rosa LD, Valiati VH, Beheregaray LB, Möller LM (2014) Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. *Conservation Genetics* 15:879-895
- Fruet PF, Daura-Jorge FG, Möller LM, Genoves RC, Secchi ER (2015a) Abundance and demography of bottlenose dolphins inhabiting a subtropical estuary in the Southwestern Atlantic Ocean. *Journal of Mammalogy* 96(2):332-343
- Fruet PF, Genoves RC, Möller LM, Botta S, Secchi ER (2015b) Using mark-recapture and stranding data to estimate reproductive traits in female bottlenose dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean. *Marine Biology* 162(3):661-673
- Fruet PF, Secchi ER, Di Tullio JC, Simões-Lopes PC, Daura-Jorge F, Costa APB, Vermeulen E, Flores PAC, Genoves RC, Laporta P, Beheregaray LB, Möller LM (2017) Genetic divergence between two phenotypically distinct bottlenose dolphin ecotypes suggests separate evolutionary trajectories. *Ecology and Evolution* 7:9131-9143
- Gannon DP, Waples DM (2004) Diets of coastal bottlenose dolphins from the U. S. Mid-Atlantic coast differ by habitat. *Marine Mammal Science* 20(3):527-545
- Garcia AM, Hoeninghaus DJ, Vieira JP, Winemiller KO (2007) Isotopic variation of fishes in freshwater and estuarine zones of a large subtropical coastal lagoon. *Estuarine, Coastal and Shelf Science* 73(3-4):399-408
- Gilpatrick JW, Perryman WL (2008) Geographic variation in external morphology of North Pacific and Southern Hemisphere blue

- whales (*Balaenoptera musculus*). *Journal of Cetacean Research and Management* 10(1):9-21
- Goodall RNP, Marchesi MC, Pimper LE, Dellabianca N, Benegas LG, Torres MA, Riccialdelli L (2011). Southernmost records of bottlenose dolphins, *Tursiops truncatus*. *Polar Biology*, 34(7), 1085–1090
- Graham BS, Koch PL, Newsome ND, McMahon KW, Aurioles D (2010) Using Isoscapes to Trace the Movements and Foraging Behavior of Top Predators in Oceanic Ecosystems. In: *Isoscapes Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping*. Springer, New York
- Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314–326
- Hohn AA, Scott MD, Wells RS, Sweeney JC, Irvine AB (1989) Growth layers in teeth from known-age, free-ranging bottlenose dolphins. *Marine Mammal Science* 5:315–42
- Indermühle A, Stocker TF, Joos F, Fischer H, Smith HJ, Wahlen M, Deck B, Mastroianni D, Tschumi J, Blunier T, Meyer R, Stauffer B (1999) Holocene carbon-cycle dynamics based on CO₂ trapped in ice at Taylor Dome, Antarctica. *Nature* 398:121–26
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80(3):595–602
- Jaffe AL, Campbell-Staton SC, Losos JB (2016) Geographical variation in morphology and its environmental correlates in a widespread North American lizard, *Anolis carolinensis* (Squamata: Dactyloidae). *Biological Journal of the Linnean Society* 117(4):760–774
- Jefferson TA, Van Waerebeek K (2004) Geographic variation in skull morphology of humpback dolphins (*Sousa* spp.). *Aquatic Mammals* 30(1):3-17
- Jiménez PJ, Alava JJ (2015) Strand-feeding by coastal bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Guayaquil, Ecuador. *Latin American Journal of Aquatic Mammals* 10(1):33-37
- Jones GJ, Sayigh LS (2002) Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Marine Mammal Science* 18(2):374-393

- Knoff A, Hohn A, Macko S (2008) Ontogenetic diet changes in bottlenose dolphins (*Tursiops truncatus*) reflected through stable isotopes. *Marine Mammal Science* 24(1):128–137
- Laporta P, Fruet P, Siciliano S, Flores PA, Loudeiro JD (2016a) Report of the Working Group on the Biology and Ecology of *Tursiops truncatus* in the Southwest Atlantic Ocean. *Latin American Journal of Aquatic Mammals* 11(1-2):62-70
- Laporta L, Martins CCA, Lodi L, Domit C, Vermeulen E, Di Tullio JC (2016b) Report of the Working Group on Habitat Use of *Tursiops truncatus* in the Southwest Atlantic Ocean. *Latin American Journal of Aquatic Mammals* 11(1-2):47-61
- Layman CA, Arrington DA, Montana CG, Post DM (2007a) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- Lee PC (1996) The meanings of weaning: Growth, lactation, and life history. *Evolutionary Anthropology: Issues, News, and Reviews* 5(3):87–98
- Lemos VM, Varela AS, Schwingel PR, Muelbert JH, Vieira JP (2014) Migration and reproductive biology of *Mugil liza* (Teleostei: Mugilidae) in south Brazil. *Journal of Fish Biology* 85(3):671–687
- Lemos VM, Monteiro-Neto C, Cabral H, Vieira JP (2017) Stock identification of tainha (*Mugil liza*) by analyzing stable carbon and oxygen isotopes in otoliths. *Fishery Bulletin* 115(2):201–205
- Lodi L, Domit C, Laporta P, Di Tullio JC, Martins CCA, Vermeulen E (2016) Report of the Working Group on the Distribution of *Tursiops truncatus* in the Southwest Atlantic Ocean. *Latin American Journal of Aquatic Mammals* 11(1-2):24–28
- Martinez Del Rio C, Wolf N, Carleton SA, Gannes LZ (2009) Isotopic ecology ten years after a call for more laboratory experiments. *Biological Reviews* 84(1):91–111
- McCurry MR, Fitzgerald EMG, Evans AR, Adams JW, McHenry CR (2017) Skull shape reflects prey size niche in toothed whales. *Biological Journal of the Linnean Society* 121(4):936–946
- McMahon KW, Hamady LL, Thorrold SR (2013) Ocean ecogeochemistry: a review. *Oceanography and Marine Biology* 51:327–374
- Mead JG, Potter CW (1990) Natural history of bottlenose dolphin along central atlantic coast of the United States. In: Leatherwood, S.; Reeves, R. R. (Eds.). *The Bottlenose Dolphin*, Academic Press, p. 165-195

- Mead JG, Potter CW (1995) Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: morphologic and ecologic considerations. *IBI Reports* 5:31-44
- Melo CLC, Santos RA, Bassoi M, Araújo AC, Lailson-Brito J, Dorneles PR, Azevedo AF (2010) Feeding habits of delphinids (Mammalia: Cetacea) from Rio de Janeiro State, Brazil. *Journal of the Marine Biological Association of the United Kingdom* 90(8):1509–1515
- Miller TEX, Rudolf VHW (2011) Thinking inside the box : community-level consequences of stage-structured populations. *Trends in Ecology and Evolution* 26(9):457-466
- Milmann L, Danilewicz D, Machado R, Ott PH (2016) Feeding ecology of the common bottlenose dolphin, *Tursiops truncatus*, in southern Brazil: analyzing its prey and the potential overlap with fisheries. *Brazilian Journal Of Oceanography* 64(4):415–422
- Möller LM, Simões-Lopes PC, Secchi ER, Zerbini AN (1994) Uso da fotoidentificação no estudo do deslocamento de botos *Tursiops truncatus* (Cetacea, Delphinidae) na costa sul do Brasil. In: *Proceedings of the VI Reunião de Trabalhos de Especialistas em Mamíferos Aquáticos da América do Sul*, 24–28 October 1994, Florianópolis, p. 5–8
- Nelson MA, Quakenbush LT, Mahoney BA, Taras BD, Wooller MJ (2018) Fifty years of Cook Inlet beluga whale feeding ecology from isotopes in bone and teeth. *Endangered Species Research*, 36: 77–87
- Newsome SD, Del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5(8):429–436
- Newsome SD, Etnier MA, Monson DH, Fogel ML (2009) Retrospective characterization of ontogenetic shifts in killer whale diets via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of teeth. *Marine Ecology Progress Series* 374:229–242
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science* 26(3):509–572
- Perrin W (2008) Geographical Variation. In: Perrin W, Wursig B, Thewissen J (Eds.). *Encyclopedia of Marine Mammals*, 2nd edn. Elsevier, San Diego, p. 316-321
- Perrin WF, Thieleking JL, Walker WA, Archer FI, Robertson KM (2011) Common bottlenose dolphins (*Tursiops truncatus*) in

- California waters: Cranial differentiation of coastal and offshore ecotypes. *Marine Mammal Science* 27(4): 769-792
- Peterson BJ, Fry B (1987) Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics* 18: 293–320
- Pianka ER (2000) *Evolutionary ecology*, 6th edn. Benjamin-Cummings, Addison-Wesley-Longman, San Francisco, CA
- Pinela AM, Borrell A, Cardona L, Aguilar A (2010) Stable isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. *Marine Ecology Progress Series*, 416:295–306
- Post DM (2002) Using Stable Isotopes To Estimate Trophic Position: Models, Methods, And Assumptions *David. Ecology*, 83(3):703–718
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, 152(1):179–189
- Romeu B, Cantor M, Bezamat C, Simões-Lopes PC, Daura-Jorge FG (2017) Bottlenose dolphins that forage with artisanal fishermen whistle differently. *Ethology*, 123(12):906-915
- Rossmann S, McCabe EB, Barros NB, Gandhi H, Ostrom PH, Stricker CA, Wells RS (2015a) Foraging habits in a generalist predator: Sex and age influence habitat selection and resource use among bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 31(1):155–168
- Rossmann S, Ostrom PH, Stolen M, Barros NB, Gandhi H, Stricker CA, Wells RS (2015b) Individual specialization in the foraging habits of female bottlenose dolphins living in a trophically diverse and habitat rich estuary. *Oecologia*, 178(2):415–425
- Roughgarden J (1972) Evolution of Niche Width. *The American Naturalist*, 106(952):683–718
- Siciliano S, Emin-lima NR, Costa AF, Rodrigues ALF, Magalhães FA, Tosi CH, Garri RG, Silva CR, Silva, JS (2008). *Revisão do Conhecimento Sobre os Mamíferos Aquáticos da Costa Norte do Brasil*. Arquivos Do Museu Nacional, Rio de Janeiro, 66(2), 68912–250381
- Santos-Carvalho M, Pérez-Alvarez MJ, Muniain V, Moraga R, Oliva D, Sepúlveda M (2015) Trophic niche overlap between sympatric resident and transient populations of bottlenose dolphins in the Humboldt Current System off north-central Chile. *Marine Mammal Science*, 31(2):790–799

- Santos-Carvalho M, Sepúlveda M, Moraga R, Landaeta MF, Oliva D, Pérez-Alvarez MJ (2018) Presence, Behavior, and Resighting Pattern of Transient Bottlenose Dolphins (*Tursiops truncatus*) in the Humboldt Current System off North-Central Chile. *Pacific Science*, 72(1):41–56
- Sargeant BL, Mann J (2009) Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour*, 78(3):715–721
- Schaeffer-Novelli Y, Cintrón-Molero G, Adaime RR, Camargo TM (1990) Variability of Mangrove Ecosystems along the Brazilian Coast. *Estuaries*, 13(2):204
- Scott MD, Chivers SJ (1990) Distribution and herd structure of bottlenose dolphins in Eastern Tropical Pacific Ocean. In: Leatherwood, S.; Reeves, R. R. (Eds.). *The Bottlenose Dolphin*, Academic Press, p. 387–402.
- Secchi ER, Botta S, Wiegand MM, Lopez LA, Fruet PF, Genoves RC, Di Tullio JC (2016). Long-term and gender-related variation in the feeding ecology of common bottlenose dolphins inhabiting a subtropical estuary and the adjacent marine coast in the western South Atlantic. *Marine Biology Research*, 13(1):121–134
- Secretariat of the Convention on Biological Diversity - SCBD (2014) Ecologically or Biologically Significant Marine Areas (EBSAs): Special places in the world's oceans. Volume 2: Wider Caribbean and Western Mid-Atlantic Region. 86 pages
- Segura I, Rocha-Olivares A, Flores-Ramirez S, Rojas-Bracho L (2006) Conservation implications of the genetic and ecological distinction of *Tursiops truncatus* ecotypes in the Gulf of California. *Biological Conservation*, 133(3): 336–346
- Sheppard CE, Marshall HH, Inger R, Thompson FJ, Vitikainen EIK, Barker S, Nichols HJ, Wells DA, McDonald RA, Cant MA (2018) Decoupling of Genetic and Cultural Inheritance in a Wild Mammal. *Current Biology*, 28(11):1846–1850
- Simões-Lopes PC, Fabián ME, Menegheti JO (1998) Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. *Revista Brasileira de Zoologia*, 15(3):709-726
- Simões-Lopes PC, Fabian ME (1999) Residence patterns and site fidelity in bottlenose dolphins, *Tursiops truncatus* (Montagu) (Cetacea, Delphinidae) off southern Brazil. *Revista Brasileira de Zoologia*, 16(4):1017-1024

- Smolker R, Richards A, Connor R, Mamm J, Berggren P (1997) Sponge Carrying by Dolphins (Delphinidae, Tursiops sp.): A Foraging Specialization Involving Tool Use? *Ethology*, 103:454–465
- Tezanos-Pinto G, Baker CS, Russell K, Martien K, Baird RW, Hutt A, Stone G, Mignucci-Giannoni AA, Caballero S, Endo T, Lavery S, Oremus M, Olavarría C, Garrigue C (2009) A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. *Journal of Heredity*, 100(1):11–24
- Toledo GAC (2013) Variação geográfica em crânios de golfinhos nariz-de-garrafa, *Tursiops* (Gervais, 1855), no Atlântico Ocidental [Geographic variation in the skulls of bottlenose dolphins, *Tursiops* (Gervais, 1855), in the western Atlantic]. Ph.D. thesis, Universidade Federal da Paraíba, Brazil. 214 pp.
- Turesson G (1922) The species and the variety as ecological units. *Hereditas*, III, 100–113
- Vander-Zanden HB, Bjørndal KA, Bolten AB (2013) Temporal consistency and individual specialization in resource use by green turtles in successive life stages. *Oecologia*, 173(3):767–777
- Vanderklift MA, Ponsard, S (2003) Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: A meta-analysis. *Oecologia*, 136(2):169–182
- Vermeulen E, Cammareri A (2009) Variation in external morphology of resident bottlenose dolphins in Bahia San Antonio, Patagonia, Argentina. *Journal of Marine Animals and Their Ecology*, 2(2):3–6
- Wedekin LL, Daura-Jorge FG, Rossi-Santos MR, Simões-Lopes PC (2008) Notas sobre a distribuição, tamanho de grupo e comportamento do golfinho *Tursiops truncatus* (Cetacea: Delphinidae) na Ilha de Santa Catarina, sul do Brasil. *Biota Neotropica*, 8(4):225-229
- Wells RS, Scott MD (1999) Bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821). In RIDGEWAY, S. H.; HARRISON, R. (Eds.) *Handbook of marine mammals*. Academic Press, San Diego, CA, p. 137–182
- Whitehead H (2008) Culture in whales and dolphins. In: PERRIN, W., WURSIG, B. & THEWISSEN, J. (Eds.). *Encyclopedia of Marine Mammals*, 2nd edn. Elsevier, San Diego, p. 292-293
- Wickert JC, Von Eye, SM, Oliveira LR, Moreno IB (2016) Revalidation of *Tursiops gephyreus* Lahille, 1908 (Cetartiodactyla: Delphinidae) from the Southwestern Atlantic Ocean. *Journal of Mammalogy*, 97:1–10

- Wilson RM, Kucklick JR, Balmer BC, Wells RS, Chanton JP, Nowacek DP (2012) Spatial distribution of bottlenose dolphins (*Tursiops truncatus*) inferred from stable isotopes and priority organic pollutants. *Science of the Total Environment*, 425:223–230
- Wood SN (2006) *Generalized Additive Models: An Introduction with R*. Boca Raton, FL: Chapman and Hall/CRC press.
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, 1(1), 3-14

3 CONSIDERAÇÕES FINAIS

Este é o primeiro estudo a avaliar a ecologia trófica de ecótipos costeiro e oceânico do golfinho-nariz-de-garrafa em uma área de co-ocorrência e, ainda, sob uma perspectiva ontogenética. O uso dos valores isotópicos de carbono e nitrogênio ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) para analisar o nicho isotópico sob diferentes perspectivas permitiu inferir sobre diversos aspectos da ecologia trófica dos ecótipos na região.

Constatamos que os ecótipos diferem seu nicho isotópico principalmente em função das composições isotópicas de carbono, o que indica que se alimentam em ambientes distintos. A dieta dos animais do ecótipo oceânico é sustentada aparentemente por presas pelágicas, enquanto a dos animais do ecótipo costeiro é bastante associados a habitats demersais, em ambientes estuarinos ou próximo de desembocaduras de rios.

Verificamos haver consistência temporal no uso de recursos para ambos ecótipos, evidenciada por meio dos valores isotópicos dos dois elementos analisados, carbono e nitrogênio. Isto pode indicar que tanto animais costeiros quanto oceânicos tendem a manter sua estratégia de forrageio ao longo da vida conforme a aprendida com suas mães ou com outros indivíduos-modelo na população quando eram jovens.

Tanto para o ecótipo costeiro quanto para o oceânico a idade de desmame se inicia entre os dois e três anos de idade, aparentemente perdurando por mais tempo no ecótipo costeiro, o que pode estar relacionado com a aprendizagem de técnicas especializadas de alimentação e/ou com a endogamia já reportada para uma população da área de estudo.

Os dados analisados sugerem que tanto as populações do ecótipo costeiro quanto do oceânico são compostas por indivíduos especialistas. Para os primeiros, isto pode ser explicado pelo fato de formarem populações residentes em um ambiente bastante heterogêneo. Já para os últimos, dado que todo o material utilizado é proveniente de encalhes, isto pode ser reflexo de diferentes origens dos indivíduos analisados e, conseqüentemente, de uma variação latitudinal da paisagem isotópica.

Por fim, com os dados obtidos neste trabalho reforça-se a ideia de que as duas populações ocorrem em parapatria, com uma zona de contato de distribuição que parece ser majoritariamente espacial. A diferença no uso de habitat para alimentação indica que os ecótipos estão sujeitos a diferentes realidades ambientais e pressões antrópicas, o que deve ser levado em consideração no gerenciamento de áreas costeiras para a conservação de ambos.

Trabalhos futuros com a composição isotópica das presas para a construção de modelos de mistura e com séries temporais que levem em consideração a estrutura das populações de cada ecótipo devem auxiliar a esclarecer algumas das questões aqui levantadas

APÊNDICE A

Tabela 1 Informações de tombamento de cada indivíduo utilizado para a realização deste estudo. ID representa o número de registro do espécime.

ID	Ecótipo	Idade	Sexo	Procedência	Nº de amostras	Data encalhe	Lat	Long
UDESC_000851/ 4041829	oceânico	4	Ind.	Praia do Sol – Laguna/SC	4	26/mar/16	-28.41	-48.74
UDESC_000865/ 4041836	costeiro	19	Macho	Praia do Mar Grosso (molhes) – Laguna/SC	8	14/abr/16	-28.49	-48.76
UDESC_001605/ 432776	costeiro	20	Macho	Praia D'água - Imbituba - SC	9	13/jan/17	-28.20	-48.66
UDESC_0029/ 9472	oceânico	6	Macho	Praia da Cigana – Laguna/SC	6	24/abr/13	-28.61	-48.83
UDESC_9419	costeiro	>9	Macho	Pescaria Brava – Laguna/SC	7	30/out/13	-28.41	-48.87
UFSC_1077	costeiro	7	Macho	Praia do Pântano do Sul – Florianópolis/SC	6	16/abr/89	-27.78	-48.50
UFSC_1089	costeiro	>11	Fêmea	Praia do Mar Grosso (molhes) – Laguna/SC	7	22/fev/90	-28.49	-48.76
UFSC_1099	oceânico	6	Fêmea	Praia dos Ingleses – Florianópolis/SC	6	20/fev/91	-27.43	-48.39

UFSC_1116	costeiro	5	Fêmea	Aterro da Baía Sul, próximo à Capitania dos Portos – Florianópolis/SC	5	28/jan/93	-27.59	-48.56
UFSC_1209	oceânico	17	Fêmea	Praia do Sol – Imbituba/SC	8	24/dez/94	-28.40	-48.74
UFSC_1249	costeiro		Ind.	Laguna/SC	6	16/jul/98	-28.41	-48.74
UFSC_1252	oceânico	12	Ind.	Praia de Itaguaçu – São Francisco do Sul/SC	7	22/ago/98	-26.18	-48.52
UFSC_1299	oceânico	>8	Ind.	Praia Grande - São Francisco do Sul/SC	8	31/mar/01	-26.32	-48.55
UFSC_1317	oceânico	>6	Ind.	Praia dos Ingleses – Florianópolis/SC	6	09/out/03	-27.43	-48.39
UFSC_1349	costeiro	7	Fêmea	Praia de Fora de Baixo – Palhoça/SC	5	05/jan/07	-27.73	-48.63
UFSC_1395	costeiro	>9	Macho	Praia do Moçambique – Florianópolis/SC	9	14/out/11	-27.52	-48.41
UFSC_1398	oceânico	15	Fêmea	Praia do Iró – Laguna/SC	7	05/dez/11	-28.46	-48.76
UFSC_1415	oceânico	13	Macho	Praia da Armação – Florianópolis/SC	6	21/ago/14	-27.73	-48.50
UFSC_1420	costeiro	>14	Fêmea	Beira-Mar de São José – São José/SC	9	21/out/14	-27.60	-48.60

UFSC_1489	costeiro	>11	Ind.	Praia do Mocambique – Florianópolis/SC	8	15/mar/17	-27.52	-48.41
UFSC_1501	costeiro	12	Ind.	Baía Norte (embaixo da ponte) – Florianópolis/SC	9	22/ago/17	-27.59	-48.56
UNE_002646	costeiro	14	Macho	Praia Grande - São Francisco do Sul/SC	8	15/set/15	-26.33	-48.55
UNE_23841	oceânico	18	Macho	Praia Grande - São Francisco do Sul/SC	7	21/out/16	-26.33	-48.55
UNE_28614	oceânico	16	Macho	Praia Grande - São Francisco do Sul/SC	7	02/dez/16	-26.33	-48.55
UNE_317	costeiro	>8	Ind.	Praia Grande - São Francisco do Sul/SC	6	21/set/11	-26.33	-48.55
UNE_325	oceânico	>8	Ind.	Praia Grande - São Francisco do Sul/SC	6	13/ago/12	-26.33	-48.55
UNE_412	oceânico	>11	Macho	Balneário Paes – Itapoá/SC	9	02/mar/13	-26.08	-48.60
UNE_43	costeiro	>7	Fêmea	Praia do Ervino - São Francisco do Sul/SC	6	13/jan/16	-26.39	-48.58