

**ROBERTA PETITET**

**IDADE E CRESCIMENTO DA TARTARUGA-  
CABEÇUDA (*Caretta caretta*) NO LITORAL SUL  
DO RIO GRANDE DO SUL**



**Rio Grande  
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**UNIVERSIDADE FEDERAL DO RIO GRANDE  
INSTITUTO DE OCEANOGRAFIA  
PÓS GRADUAÇÃO EM OCEANOGRAFIA BIOLÓGICA**

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CABEÇUDA (*Caretta caretta*) NO LITORAL SUL  
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Dissertação apresentada ao Programa de Pós-graduação em Oceanografia Biológica da Universidade Federal do Rio Grande, como requisito parcial à obtenção do título de MESTRE.

Orientador: Paul G. Kinas

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## RESUMO

A espécie de tartaruga marinha *Caretta caretta* (tartaruga-cabeçuda) utiliza a costa brasileira para desenvolvimento e reprodução, suas praias de desova estão situadas nos estados da Bahia e Espírito Santo. A maioria dos estudos sobre a tartaruga-cabeçuda no Brasil lidam com fêmeas adultas e os estágios de juvenis e sub-adultos são pouco conhecidos. O presente estudo faz uma estimativa da idade de tartarugas-cabeçudas através da técnica de esqueletocronologia por análises do úmero provenientes de ambos os estágios, nerítico e oceânico. E ajusta um modelo de crescimento para a população dessa espécie do Atlântico Sul Ocidental. Baseado na validação de que uma linha de crescimento corresponde a um ano, os números de linhas presentes no úmero correspondem a idade do animal. Para tartarugas de tamanho maior, foi aplicado o fator de correção para o cálculo de linhas perdidas devido à reabsorção óssea e perda das primeiras linhas de crescimento. Esse fator de correção foi baseado em dois modelos, o primeiro denominado “simples” que não incorpora a variação na deposição de linhas de crescimento no animal e entre animais, já o segundo modelo, denominado “hierárquico” faz essa incorporação. O modelo hierárquico obteve melhor ajuste aos dados de tamanho (CCC – comprimento curvilíneo da carapaça) e diâmetro do úmero, provavelmente devido a experiências desses répteis em ambientes com condições estocásticas, portanto alguns indivíduos podem crescer mais do que outros. A estimativa da duração do estágio oceânico foi de 8 a 19 anos (com média de 11,5) e a idade de maturação de 25,7 a 39,2 anos (com média de 31,2 anos). O modelo de crescimento de Schnute se ajustou bem aos dados de tamanho (CCC) e idade, devido sua versatilidade em forma e não requerimento de dados de tamanho de animais neonatais e de adultos próximos ao tamanho assintótico. Entretanto, a “curva” de Schnute foi bastante similar a uma reta, portanto foi ajustada uma regressão linear que obteve um melhor ajuste aos dados, que

por sua vez, é composto por uma “janela de idade” do ciclo de vida das tartarugas marinhas. A “Hipótese de proporcionalidade corporal” foi aplicada para o cálculo das taxas de crescimento. As taxas de crescimento das tartarugas-cabeçudas neríticas foram similares as reportadas para tartarugas-cabeçudas do Atlântico Norte, porém menores do que as tartarugas oceânicas do Atlântico Sul. Sugerindo que as condições ambientais locais podem influenciar na taxa de crescimento da tartaruga marinha, como também, a energia gasta durante migrações, alocação de energia e origem genética.

**Palavras-chave:** *Caretta caretta*, Schnute, crescimento, idade, esqueletocronologia

## **ABSTRACT**

The juvenile and sub-adult stages of loggerhead sea turtles (*Caretta caretta*) are poorly studied in Brazil. We present age estimates and a growth model for loggerhead sea turtles in the South Atlantic Ocean obtained through skeletochronological analysis of humeri obtained from both neritic and oceanic stage individuals. Since it was validated that each increment growth corresponds to one year for loggerhead sea turtle, the number of lines of arrested growth (LAGs) was taken as the age estimated. For larger turtles a correction factor was applied to solve for lost LAGs. This correction factor was based on two models, the first denoted “naïve” makes no distinction between inter- and intra-individual variability and the second denoted “hierarchical”, takes this distinction into account. The hierarchical model had the best fit to the data set, probably because these reptiles experience stochastic conditions through their life cycle, so that some individuals may grow more than others. The estimated ages indicate that the duration of the pelagic stage is 8 to 19 years (average 11.5 years) and the age at maturation ranges from 25.7 to 39.2 years (average 31.2 years). Schnute’s growth model was fit to age-at-length data, due to its

versatility in shape and no requirement of size data for hatchlings up to individuals at old ages with near asymptotic size. However, since the shape of Schnute's curve was almost linear for the age-window comprising our data, a linear regression ultimately yielded a slightly better fit. The "Body Proportional Hypothesis" was incorporated in the calculation of growth rates. Growth rates from neritic stage South Atlantic loggerheads were similar to those reported for neritic loggerhead sea turtles from the North Atlantic, but lower than for oceanic loggerheads from South Atlantic. This finding suggests that local environmental conditions influence turtle's growth rates, as well as, the energy expenditure during migrations, energy allocation and genetic origin.

**Keywords:** *Caretta caretta*, Schnute's growth model, age, growth, skeletochronology

## I. INTRODUÇÃO

### *Caretta caretta*

Esta espécie tem uma distribuição tropical e subtropical, sendo encontrada no oceano índico, Austrália, Japão, Estados Unidos, Mediterrâneo e Brasil. A tartaruga-cabeçuda tem uma dieta carnívora durante todo seu ciclo de vida, se especializando no estágio de sub-adulto e adulto em presas do grupo de invertebrados, com preferência em animais sésseis e corpo rígido (Limpus & Limpus, 2003). Esta espécie ocorre ao longo da costa brasileira, se reproduzindo principalmente nas praias do Estado da Bahia. A tartaruga-cabeçuda tem sido afetada pelo o contato da mesma com a pesca de espinhel pelágico, devido a seus hábitos serem mais oceânicos, esta espécie pode ser encontrada em habitats com profundidades de 60-200m (Hopkins-Murphy et al., 2003). E devido à constante captura incidental em espinhel pelágico na maioria das áreas aonde a tartaruga-cabeçuda é encontrada e a exploração de seus ovos no passado (Limpus & Limpus,

2003), esta espécie se encontra na lista de espécies ameaçadas de extinção classificadas como em “perigo” de extinção (IUCN, 2010).

### **Ciclo de vida**

Todas as sete espécies de tartarugas marinhas compartilham um ciclo de vida comum com poucas diferenças, todas as espécies migram pelo menos distâncias curtas de áreas de alimentação para áreas de reprodução, depois os machos retornam para áreas de alimentação e as fêmeas partem para a postura dos ovos. Após o período reprodutivo de muitos meses, as fêmeas retornam para as áreas de alimentação e começam novamente a se prepararem para a próxima época de reprodução, que será de poucos ou muitos meses depois da primeira (Miller, 1997) (figura 1).

Esses répteis são encontrados em águas tropicais e subtropicais dos oceanos Atlântico, Pacífico e Índico. São animais que passam basicamente toda sua vida em habitats marinhos ou estuarinos, somente retornando para o ambiente terrestre para desovar. Conseqüentemente, adaptações fisiológicas, anatômicas e comportamentais ocorreram em resposta à seleção no ambiente aquático. Baseado nos estágios ontogenéticos, se construiu um modelo generalizado de habitats para as tartarugas marinhas, (1) Habitat pelágico e oceânico, para os primeiros estágios de juvenis; (2) Habitat normalmente demersal e nerítico, para os juvenis em desenvolvimento; (3) Habitats de alimentação para os adultos; e (4) Habitats de cópula e/ou período entre desovas (Musick & Limpus, 1997). Portanto, devido a um ciclo de vida complexo, estes répteis necessitam de uma grande variedade de ecossistemas, desde o estágio da postura de ovos e desenvolvimento embrionário (habitat terrestre) até o estágio de juvenis/adultos (habitats nerítico e oceânico) (Frazier, 1999).



## Esqueletocronologia

Essa metodologia é baseada em marcas de crescimento encontradas em alguma estrutura óssea, o princípio básico desse método é que o crescimento do osso é cíclico e tem uma periodicidade anual em que a formação óssea cessa ou retarda antes de uma nova formação (Snover & Hohn, 2004) (figura 2; figura 4). E em animais mais velhos, as marcas de crescimento são acumuladas na periferia do osso como um resultado de crescimento mais lento (Snover & Hohn, 2004). Essa metodologia ao longo do tempo vem se aperfeiçoando e foi aplicada pela primeira vez por Zug et al. (1986) em tartarugas marinhas, que utilizaram elementos do esqueleto do crânio e o membro dianteiro (úmero) direito de tartarugas-cabeçudas. Constatando assim, que o úmero foi a estrutura óssea mais sensível a esse tipo de análise. Em tartarugas marinhas essa metodologia tem sido validada para algumas espécies, como por exemplo, *Caretta caretta* (Zug et al., 1995; Zug et al., 1986; Parham & Zug, 1998; Klinger & Musick, 1992; Snover e Honh, 2004; Snover et al., 2007), *Chelonia mydas* (Zug & Glor, 1999; Zug et al., 2002; Goshe et al., 2010), *Lepidochelys kempii* (Zug et al., 1997; Snover & Hohn, 2004), *Lepidochelys olivacea* (Zug et al., 2006) e *Dermochelys coriacea* (Zug & Paham, 1996; Avens et al., 2009).

Idade é um dos elementos que influencia a dinâmica populacional de uma dada população. Esse tipo de informação é essencial para o cálculo de taxas de crescimento naturais e idade de maturação sexual, que são necessárias para o desenvolvimento de planos de conservação para espécies de tartarugas marinhas ameaçadas (Bjorndal & Bolten 1988; Zug et al. 2002). Contudo, esse tipo de dado é difícil de coletar devido ao complexo padrão de migração das tartarugas marinhas exibido por todo o seu ciclo de vida (Musick & Limpus 1996) e, portanto, muitas questões relativas a este assunto ainda permanecem desconhecidas.

Estimativas de idade podem fornecer informações sobre as taxas de crescimento, a duração dos estágios do ciclo de vida e idade de maturação sexual, que são críticos para o desenvolvimento do perfil demográfico para as diferentes populações de tartarugas-cabeçudas (Zug et al. 1986). Parâmetros demográficos, como a mortalidade, o recrutamento, a dispersão de habitats, remigração anual, e sexo, tamanho, idade e taxas de crescimento específico pode ser realizada através de dados de marcação-recaptura e utilizado para modelar uma população (Chaloupka & Musick, 1996). Embora este método tem sido utilizado com todas as espécies de tartarugas marinhas em todo o mundo (Bjorndal et al., 2000a;. Chaloupka e Limpus 2002; Revelles et al. 2008; Reisser et al. 2008), isso exige um trabalho intensivo de campo de longa duração (Casale et al., 2007). Conseqüentemente os resultados tornam-se disponíveis apenas em longo prazo.

Em contraste, estudos de esqueletocronologia têm sido validado e aplicado em *Caretta caretta* (Zug et al., 1986; Parham e Zug, 1997; Klinger & Musick, 1992; Snover & Honh, 2004), permitindo a estimativa de idade a partir de incrementos de crescimento formado no úmero (Parham & Zug, 1997). Esta abordagem permite a compreensão de alguns parâmetros com base na idade, semelhante à marcação-recaptura, porém o método de esqueletocronologia tem potencial para produzir resultados mais rapidamente. Além disso, as taxas de crescimento podem ser obtidas a partir de cada linha de crescimento, permitindo estimar as taxas de crescimento de vários anos e detecção de mudanças ontogenéticas (Snover, 2002). Partindo de que cada incremento de crescimento corresponde a um ano, é possível modelar com precisão a relação entre o osso e o crescimento somático (Klinger & Musick 1992; Coles et al., 2001; Snover & Hohn, 2004).

## **Modelo de Schnute**

Independentemente de como as informações de crescimento é obtido, ajustar um modelo de crescimento para os dados de idade é essencial, pois gera um padrão para uma dada população e possibilita estimar a idade de um indivíduo baseado no tamanho do mesmo. Na literatura, há um grande número de modelos de crescimento para contemplar, tais como: Pütter, von Bertalanffy, Richards, Gompertz, ou logístico. No entanto, estes modelos de crescimento exibem um limite ou assíntota (Schnute, 1981) necessitando de uma amostra que abrange todas as idades durante todo o ciclo de vida, caso contrário, não é possível o ajuste aos dados. Em tartarugas marinhas, os modelos de crescimento mais utilizados são os de von Bertalanffy, Gompertz e logístico, porém os autores tiveram que estimar as idades na fase de pós-neonatal, para pequenos juvenis e também para o comprimento assintótico, para gerar uma curva de crescimento razoável (Klinger & Musick 1995; Zug et al., 1995; Bjorndal et al., 2000; Snover, 2002; Zug et al., 2002; Goshe et al., 2010). Schnute (1981) desenvolveu um modelo de crescimento generalizado, que inclui muitos modelos específicos (como os citados acima), como casos especiais, permitindo o ajuste de um modelo de crescimento, mesmo se apenas dados de uma janela de idade do ciclo de vida completo está disponível.

## **II. OBJETIVOS**

Utilizando a metodologia de determinação de idade (esqueletocronologia), os objetivos do presente trabalho são: (1) estimar a faixa de idade de tartarugas-cabeçudas (*Caretta caretta*) encontradas encalhadas mortas no litoral sul do Rio Grande do Sul (zona nerítica) e de tartarugas-cabeçudas capturadas acidentalmente no espinhel pelágico (zona oceânica); e (2) gerar curvas de crescimento para esta espécie de tartaruga marinha baseado no modelo de crescimento de Schnute, a partir dos dados de idade estimada e tamanho.

### III. MATERIAL E MÉTODOS

A área de estudo foi ao longo da costa sul do Rio Grande do Sul, entre a Lagoa do Peixe (31°20'S; 51°05'W) e Arroio Chuí (33°45'S; 53°22'W), totalizando 355 km de praia (figura 3a). Durante monitoramentos de praias foram coletados úmeros das nadadeiras anteriores da espécie de tartaruga marinha, *Caretta caretta*. Além das tartarugas de praia, foi utilizado úmeros da mesma espécie capturada acidentalmente em espinhel pelágico na frota de Rio Grande-RS (figura 3b). Para cada espécime foram feitas duas medidas biométricas, comprimento curvilíneo da carapaça (CCC) e largura curvilínea da carapaça (LCC). Essas medidas foram baseadas em Bolten (1999).

Os úmeros foram dissecados e macerados em água durante 2 a 3 semanas para a possível retirada do tecido mole, e colocado para secar durante 2 semanas aproximadamente. A metodologia histológica foi baseada em Avens & Goshe (2007) para os cortes dos ossos e baseado em Goshe et al. (2010) para criação de um banco de dados para posterior análise dos ossos (maiores detalhes, ver apêndice).

A primeira linha de crescimento (“annulus”) em tartarugas marinhas é depositada diante do centro do osso, enquanto que as linhas de crescimento mais recente ocorrem ao longo da circunferência mais interna (Zug et al. 1986) (figura 4). As tartarugas marinhas podem reter ou não a primeira linha de crescimento, pois esta primeira linha e linhas mais antigas são perdidas devido à reabsorção óssea durante o crescimento da tartaruga (Zug et al., 1986). Para tartarugas que não retinham a primeira linha de crescimento (“annulus”), foi calculado as linhas perdidas baseado no fator de correção demonstrado por Parharm e Zug (1998). Portanto, partindo de que uma linha de crescimento corresponde a um ano (Klinger & Musick, 1992; Coles et al., 2001; Snover & Hohn, 2004), as tartarugas que retinham a “annulus”, a idade era equivalente ao

número de linhas de crescimento observadas e para as tartarugas sem “annulus”, a idade era equivalente ao número de linhas de crescimento observadas adicionada ao número de linhas perdidas. Para esse cálculo foi ajustado dois modelos (regressão linear e função de poder) com dois tipos de erros, simples e hierárquico (Faraway, 2006), o último incorpora a variação na deposição de linhas de crescimento no indivíduo e entre indivíduos (maiores detalhes ver apêndice).

A taxa de crescimento foi calculada a partir da aplicação da técnica de “retro-cálculo”, muito utilizada na área de ictiologia. É uma técnica desenvolvida para estimar o tamanho de um peixe em momentos passados a partir de medidas no momento de sua morte (Francis, 1990). O conjunto de dados é composto de medidas de tamanho em alguma parte dura do animal (geralmente otólitos) e seu tamanho corporal atual (Francis, 1990). A partir desses dados, o comprimento do corpo para qualquer marca de crescimento, é estimado. Em tartarugas marinhas, essa técnica tem sido aplicada e validada para as espécies *Caretta caretta* e *Chelonia mydas* (Snover et al., 2007; Goshe et al., 2010). No presente estudo, foram ajustados quatro modelos aos dados de comprimento (CCC) e diâmetro do úmero, como em Snover et al. (2007) para as tartarugas-cabeçudas do Atlântico Norte. Após ajuste do modelo, foi aplicada a “Hipótese de proporcionalidade corporal” (BPH – “Body Proportional Hypothesis”). Essa hipótese consiste em que a relação do tamanho do animal real ( $L$  = tamanho no momento da morte) e o tamanho estimado pelo modelo do retro-cálculo associado ao diâmetro do úmero ( $\hat{L} = f(D)$ ) será o mesmo valor para todo tamanho estimado a partir do diâmetro das linhas de crescimento ( $f$ ). Portanto, a taxa de crescimento foi calculada subtraindo o tamanho estimado a partir da linha de crescimento mais interna da linha mais externa, e dividindo pelo número de linhas entre as mesmas, somando uma unidade (maiores detalhes ver apêndice).

Após obter a idade de todos os espécimes, foi ajustado o modelo de crescimento de Schnute (1981). O modelo de crescimento de Schnute é um modelo genérico que inclui a maioria dos modelos de crescimento (Schnute, 1981) como casos particulares. Como os dados do presente estudo consistem em uma janela específica de idade do ciclo de vida das tartarugas marinhas, a flexibilidade do modelo de Schnute é uma vantagem.

As inferências foram baseadas no enfoque bayesiano (Ellison, 2004; McCathy, 2007) para todas as análises estatísticas. Simulações de Monte Carlo por cadeias de Markov (MCMC) (Gelman et al., 2003) foram feitas para obter as distribuições posteriores dos parâmetros e foi utilizado *prioris* não informativas. A escolha entre os modelos foi baseada no critério de informação de deviância (DIC) (Spiegelhalter et al., 2002). Os softwares R (R Development Core Team 2008) e Winbugs/Openbugs (Thomas et al. 2006) foram utilizados para todas as análises estatísticas.

#### **IV. RESULTADOS**

Foram coletados no total 64 e 20 úmeros de tartarugas-cabeçudas encontradas mortas e capturadas incidentalmente em espinhel pelágico, respectivamente. Os tamanhos das tartarugas de praia variaram de 45,5 até 102,0 CCL (média de 74,8 e  $sd = 11,59$ ) e das tartarugas do ambiente oceânico variaram de 47,0 até 67,0 (média de 58,92 e  $sd = 5,00$ ). Porém somente 49 úmeros dos animais de praia foram processados e obtiveram suas idades estimadas, 4 úmeros foram danificados ao longo da metodologia de esqueletocronologia e 10 úmeros não possuíam medidas biométricas. Baseado nos tamanhos de fêmeas reprodutivas da área de reprodução mais próxima da área de estudo (83,0-120,0 CCL) (Baptistotte et al. 2003), os indivíduos foram classificados como juvenis e adultos.

Dentre os 69 úmeros de tartarugas-cabeçadas, 13 retinham a primeira linha de crescimento (annulus) (Snover e Hohn, 2004), com deposição de 8 a 13 linhas de crescimento. O modelo hierárquico de função de potência obteve o melhor ajuste para os dados de idade (DIC = -430), portanto foi esse o modelo escolhido para o cálculo das linhas perdidas para as 56 tartarugas restantes. A idade estimada para as tartarugas-cabeçadas capturadas incidentalmente foi de 8 a 19 anos, indicando a duração do estágio oceânico para a população de *C. caretta* do Atlântico Sul Ocidental. Para as tartarugas de praia, as idades compreenderam entre 9 e 24 anos.

Para o retro-cálculo, o modelo que obteve melhor ajuste foi com a incorporação dos intercepts biológicos (DIC = -170,4). A relação entre taxa de crescimento e tamanho bem como idade estimada, foi negativa ( $r = -0.29$ ;  $r = -0.65$ , respectivamente), sugerindo que a taxa de crescimento diminui com o aumento de tamanho e idade. Entretanto a relação da taxa de crescimento e idade estimada foi mais pronunciada, sugerindo que talvez a idade seja um indicador melhor de estágio do ciclo de vida do que o tamanho. Como esperado, a taxa de crescimento das tartarugas oceânicas foram maior do que as tartarugas neríticas, mesmo entre tartarugas do mesmo tamanho.

O modelo de Schnute se ajustou bem aos dados de idade estimada e tamanho (CCC – comprimento curvilíneo da carapaça), porém o modelo gerou uma curva de crescimento similar a uma linha reta, já que os dados cobrem somente uma janela do ciclo de vida das tartarugas marinhas. Portanto, uma regressão linear foi ajustada aos dados, obtendo um melhor ajuste do que o modelo de Schnute (DIC = 499,9 e 502,2, respectivamente). Sugerindo que na janela de idade da amostra, o crescimento é linear. Para a estimativa de idade de maturação sexual, foi utilizado o modelo de regressão linear, baseado na média de tamanho de fêmeas maduras da área

de desova mais perto da área de estudo, resultando em um intervalo de 25,7 a 39,2 anos (com média de 31,2 anos).

## V. CONCLUSÃO

A costa sul do Rio Grande do Sul é uma importante área de desenvolvimento para os juvenis oceânicos (8 a 19 anos) bem como para os juvenis imaturos e adultos neríticos (9 a 24 anos). Devido à relação negativa entre taxa de crescimento e ambos idade e tamanho, conclui-se que tanto mais velho quanto maior o animal, ocorre um decréscimo na taxa de crescimento. E o crescimento é linear ao longo da fase de pequenos juvenis até juvenis tardios, com a idade de maturação sexual em torno dos 30 anos.

A técnica de esqueletocronologia vem se tornando uma poderosa ferramenta para dinâmica de populações de tartarugas marinhas pelo mundo inteiro. Esse estudo foi o primeiro a descrever idade e crescimento para *Caretta caretta* no Atlântico sul, e essa informação será de valor inestimável para a avaliação da dinâmica populacional de tartarugas-cabeçudas na presente área.

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## VII. FIGURAS

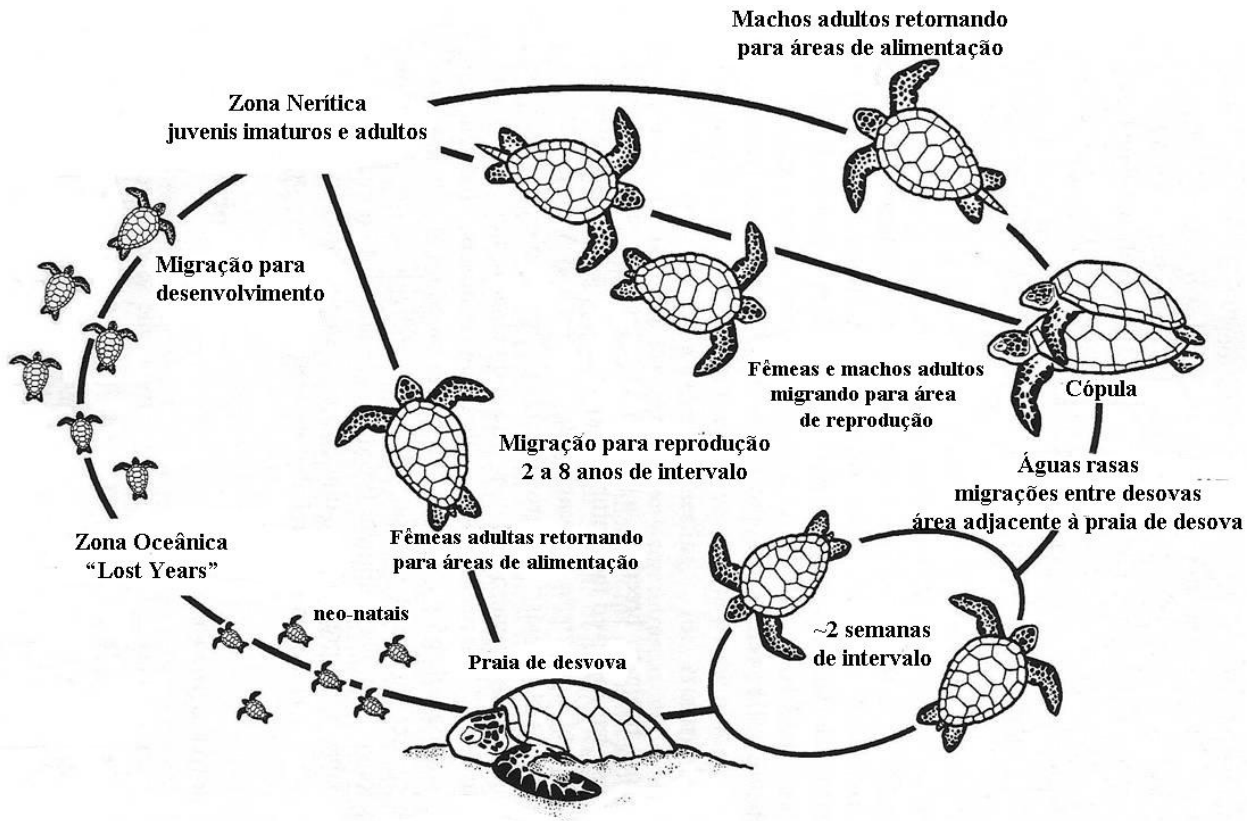
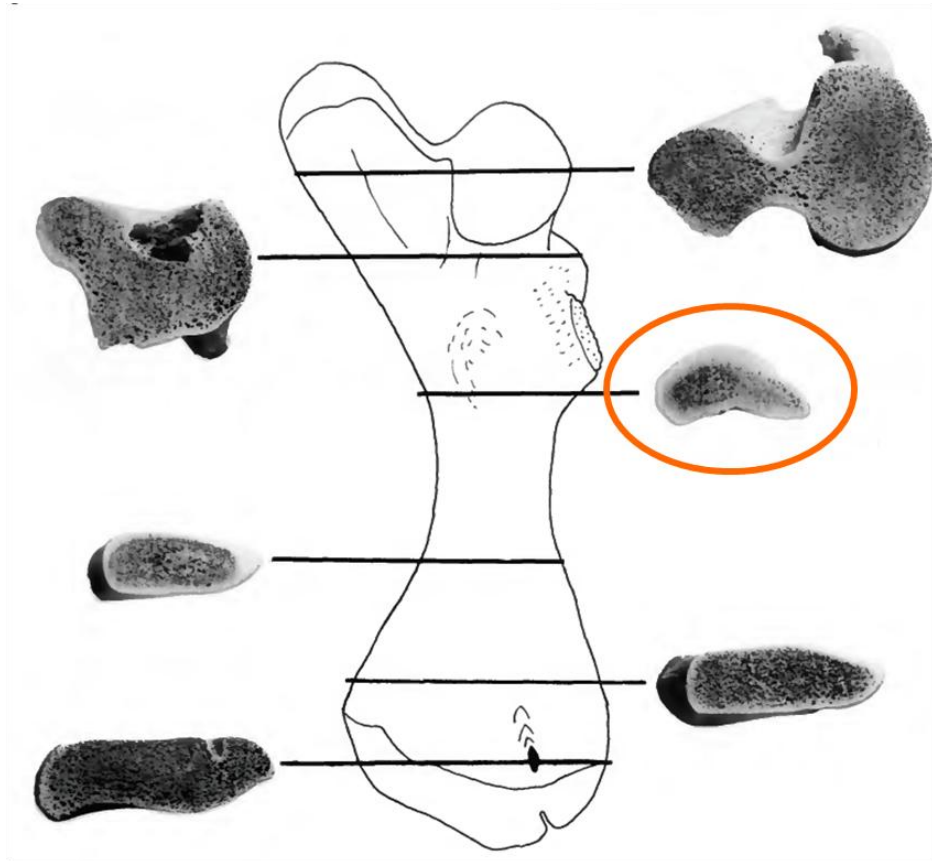
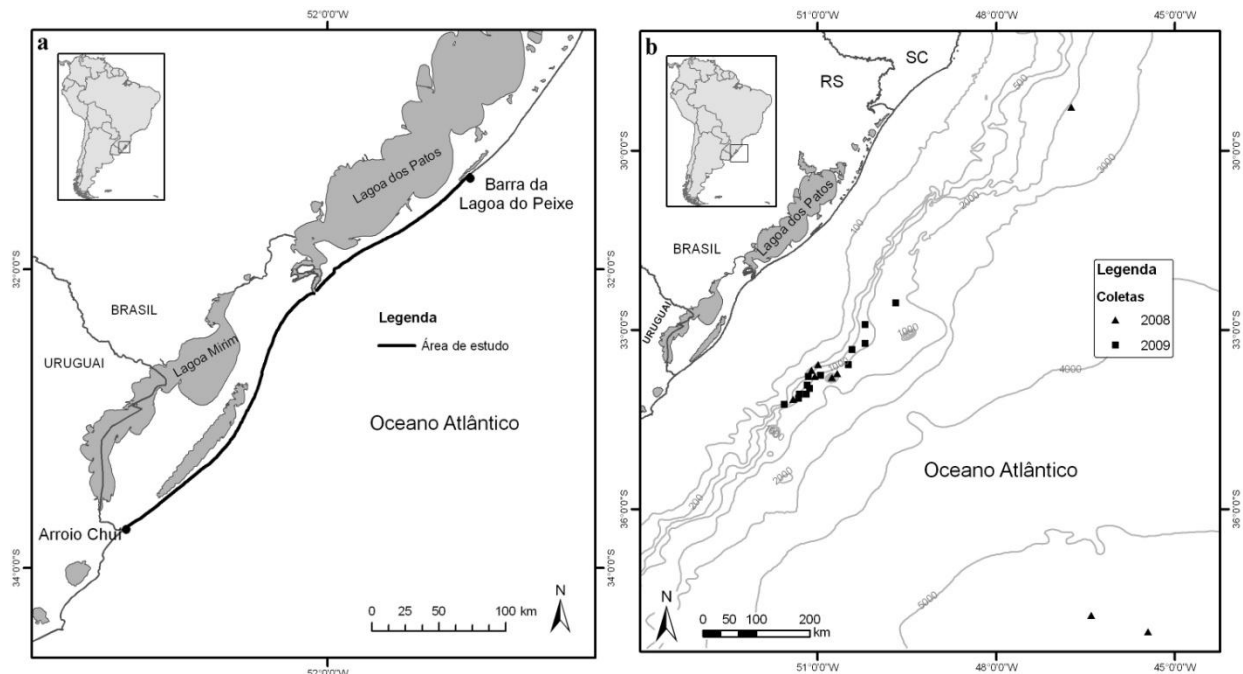


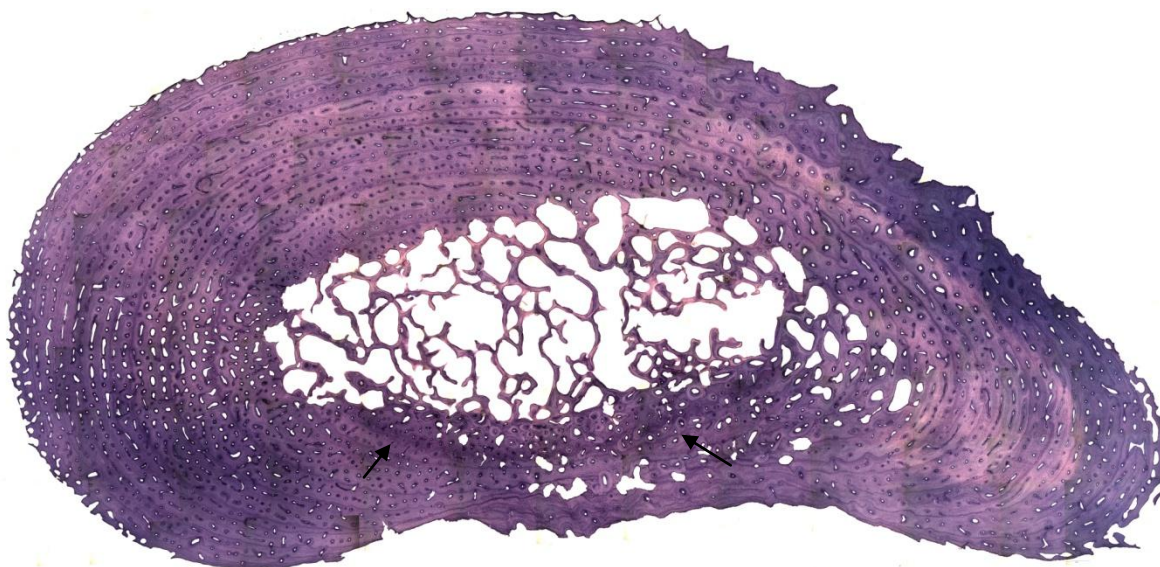
Figura 1: Ciclo geral das tartarugas-marinhas. Adaptado de Miller, 1996.



**Figura 2:** Úmero proveniente de uma tartaruga marinha, e seus cortes em cada local do mesmo. Adaptado de Zug et al. (1986).



**Figura 3:** Localização da área de estudo (a) zona nerítica, amostra provenientes de tartarugas-cabeçadas encontradas mortas no litoral sul do Rio Grande do Sul e (b) zona oceânica, amostra proveniente de tartarugas-cabeçadas capturada acidentalmente pela pesca de espinhel pelágico de Rio Grande, Rio Grande do Sul. Fonte: Barros, 2010.



**Figura 4:** Corte histológico do úmero de uma tartaruga-cabeçada. Setas indicam a primeira linha de crescimento, “annulus”.

## VIII. APÊNDICE: MANUSCRITO: formatado para o periodic Marine Biology

### Age and growth of loggerhead sea turtle (*Caretta caretta*) in southern Brazil

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#### Abstract

The juvenile and sub-adult stages of loggerhead sea turtles (*Caretta caretta*) are poorly studied in Brazil. We present age estimates and a growth model for loggerhead sea turtles in the South Atlantic Ocean obtained through skeletochronological analysis of humeri obtained from both neritic and oceanic stage individuals. The estimated ages indicate that the duration of the oceanic stage is 8 to 19 years (average 11.5 years) and the age at maturation ranges from 25.7 to 39.2 years (average 31.2 years). Schnute's growth model was fit to age-at-length data, due to its versatility in shape and no requirement of size data for hatchlings up to individuals at old ages with near asymptotic size. However, since the shape of Schnute's curve was almost linear for the age-window comprising our data, a linear regression ultimately yielded a slightly better fit. Growth rates from neritic stage South Atlantic loggerheads were similar to those reported for neritic loggerhead sea turtles from the North Atlantic, but were lower than for oceanic loggerheads from South Atlantic. This finding suggests that local environmental conditions influence turtle's growth rates, as well as, the energy expenditure during migrations, energy allocation and genetic origin.



## Introduction

Age is one of the elements which influence the dynamics of a given population. This type of information is essential for calculating natural growth rates and age at sexual maturity, which are needed to develop conservation management plans for endangered sea turtles species (Bjorndal and Bolten 1988; Zug et al. 2002). However these data are challenging to collect due to the complex pattern of migration exhibited by sea turtles throughout their life cycle (Musick and Limpus 1996) and therefore many questions relating to this matter still remain.

The loggerhead turtle (*Caretta caretta*) is one of the seven species of sea turtle and is widely distributed through the oceans. Throughout its range, the loggerhead faces a number of threats to its survival and is therefore classified as “endangered” in the IUCN Red List of Endangered Species of Fauna and Flora (IUCN, 2010). *C. caretta* shares a complex life cycle with the others species of sea turtles, except *Natator depressus* (Musick and Limpus 1996). As soon as they enter the sea, they swim to oceanic zone in offshore waters where they spend the first years of their life (the “lost years”, a time when sea turtles stay away from researchers’ eyes) (Musick and Limpus 1996). Thereafter, when the curve carapace length (CCL) reaches about 46 to 64cm they recruit, as juveniles, to foraging areas in the neritic zone (Bjorndal et al 2000a). Upon maturation, adults then start migrating between these foraging areas and breeding/nesting areas (Bolten et al 2003).

Age estimates can provide information about growth rates, the time span of sea turtle life stages, and age at sexual maturation, all of which are critical for the development of demographic profiles for the different loggerhead sea turtle populations (Zug et al. 1986). Demographic parameters, as mortality, recruitment, inter habitat dispersal, annual remigration, and sex-, size-, and age-specific growth rates can be provided by mark-recapture data and used to model a population (Chaloupka and Musick, 1996). Although this method has been used with all sea turtle species throughout the world (Bjorndal et al. 2000a; Chaloupka and Limpus 2002; Revelles et al. 2008; Reisser et al. 2008), it requires intensive long-lasting field work (Casale et al, 2007). Consequently results became available only in the long-term.

In contrast, skeletochronological studies have been validated and applied to *Caretta caretta* (Zug et al. 1986; Parham and Zug, 1997; Klinger and Musick, 1992; Snover and Honh 2004), allowing estimation of age from growth increments formed in the humerus bone (Parham

and Zug 1997). This approach allows for understanding some age-based parameters, similar to mark-recapture; however the skeletochronological method has the potential to yield results more rapidly. Furthermore, growth rates can be obtained from each growth mark, thus allowing for estimating growth rates from multiple years and detecting ontogenetic changes due to life stage intrinsic dynamics (Snover 2002), provided that each growth increment correspond to one year and that it is possible to accurately model the relationship between bone and somatic growth (Klinger and Musick 1992; Snover and Hohn 2004).

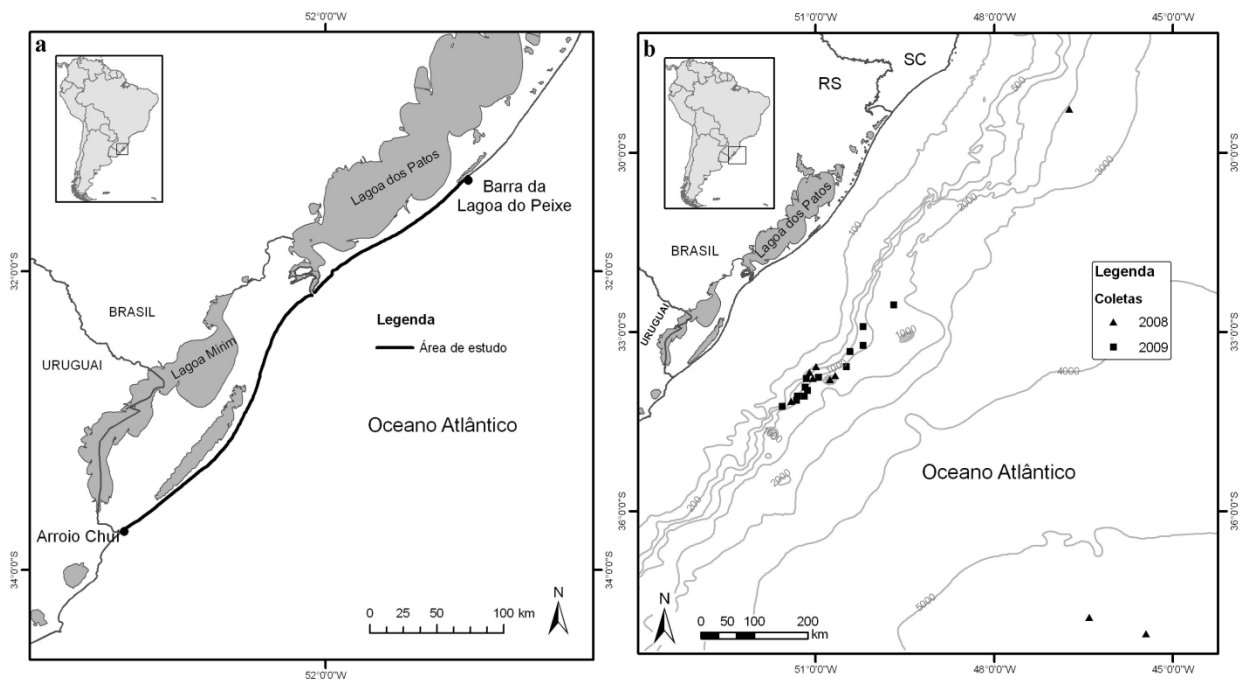
Regardless of how growth information is obtained, fitting a growth model to the age data is essential, to generate a pattern for a given population and to estimate age of individuals based on their size. In the literature, there are an extensive number of growth models to contemplate, such as: Pütter, von Bertalanffy, Richards, Gompertz, or logistic. However, these growth models exhibit a limit or asymptote (Schnute 1981) necessitating that sampling cover all ages throughout the life cycle, otherwise it is not possible to adequately fit these growth models to the data. In sea turtles, the growth models mostly used are the von Bertalanffy, Gompertz and Logistic, but the authors had to estimate ages in the stage of post-hatchling to early juveniles and also the asymptotic length in order to generate reasonable growth curve (Klinger and Musick 1995; Zug et al. 1995; Bjorndal et al. 2000; Snover 2002; Zug et al. 2002; Goshe et al. 2010). Schnute (1981) developed a general growth model which includes many specific models (like those cited above) as special cases, allowing the fit of a growth model even if only data from an age window of the complete life cycle is available.

Along the Brazilian coast, most studies on loggerheads deal with adult females on nesting beaches and it has been found that the majority of nesting occurs in the states of Bahia and Espírito Santo (Marcovaldi and Chaloupka 2007). Although information on immature individuals in their pelagic and neritic stages is fragmentary, it is known that the southern coast of Rio Grande do Sul state, southern Brazil, is an important foraging area to both stages of *Caretta caretta* (Martinez-Souza 2009; Barros 2010). However, virtually nothing is known about age and growth during these stages which are essential to understand the population dynamics of loggerhead in South Atlantic. Although carcasses of loggerheads very often are washed ashore (Monteiro et al. 2006), little is known about the species demography in this area. In this study, skeletochronological data are used to describe growth patterns of loggerheads washed ashore or incidentally caught in pelagic longline fisheries off southern Brazil.

## Material and Methods

### Study area

Sample collection took place on the south coast of Rio Grande do Sul, southern Brazil, between Lagoa do Peixe (31°20'S; 51°05'W) and Arroio Chuí (33°45'S; 53°22'W), spanning 355Km of beach (**Fig. 1a**). This stretch of beach was monitored once a week, between November 2008 and December 2009, to collect humeri from sea turtles washed ashore for the skeletochronology analysis. Humeri collected from loggerheads incidentally caught by the longline fisheries in the oceanic zone of southern Brazil, between 29°/38°S latitude and 45°/51°W longitude (**Fig. 1b**) were also analyzed. For every turtle, the curved carapace length (CCL) and width (CCW) were measured (Bolten, 1999) using a flexible metric tape ( $\pm 0.1$  cm).



**Fig. 1:** Study area of the two sampling locations: (a) neritic zone, sampling of stranded dead loggerhead sea turtles at south coast of Rio Grande do Sul, southern Brazil; (b) oceanic zone, sampling of loggerhead sea turtles caught by the longline fisheries in the south of Rio Grande do Sul, southern Brazil. Adapted from Barros (2010).

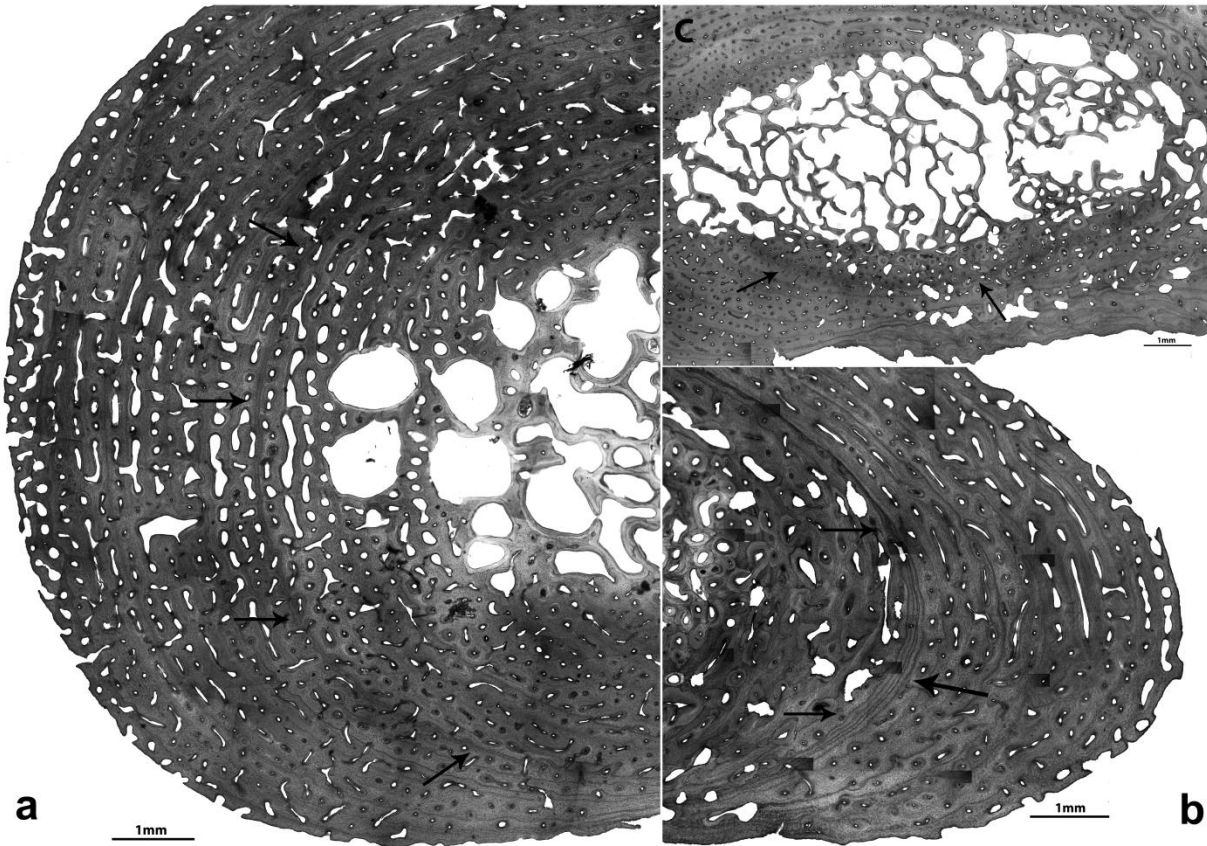
### Sample preparation

Each humerus was dissected and macerated in water during approximately 2 to 3 weeks to remove the soft tissue, and then air-dried for about two weeks more. After cleaning the bone,

some morphometric measurements were recorded using digital calipers ( $\pm 0.1\text{mm}$ ): (1) maximal length, (2) longitudinal length, (3) proximal width, (4) delto-pectoral process width, (5) medial width, (6) distal width, (7) thickness and (8) weight (Zug et al. 1986). The histological methodology was based on Avens and Goshe (2007) for the cross-sections. Due to the fast fading of stain from the histologically processed cross sections, 5x magnified pictures were taken from sequential portions using a SPOT Insight scientific digital CCD camera (Spot imaging solution Inc., Sterling Heights, Miami, USA) fitted to an Zeiss Axiovert 135 binocular inverted microscope (Carl Zeiss, Germany), for archiving and growth marks analysis. Then pictures were put together using Adobe Photoshop Elements 8.0 (Adobe Systems Inc., San Jose, California, USA) resulting in a high resolution composite digital image of each cross-section.

### **Growth layers**

Each digital image from the cross-section was labeled with a random number before growth mark counting. Each section was interpreted by one reader in three independent readings performed in different occasions and later compared to increase the accuracy. Because if the number of growth marks varied between readings, a fourth reading was done. In the cross-sections a growth mark consisted of a light-staining area followed by a dark line of arrested growth (LAG), the LAGs appeared as defined or diffuse lines (Zug et al. 1986). When these layers were continuous along the humerus circumference, the line was counted as one LAG, if there were two dark lines following the same direction closely spaced along the entire circumference, this was counted as a double LAG representing one LAG (**Fig. 2a**). However, if there was a dark line that split into multiple lines in some region of the bone circumference, each multiple line was counted as one LAG (**Fig. 2b**). The interpretation of double and splitting lines was based on Castanet et al. (1990) and Snover and Hohn (2004). The resorption core, each LAG and each humerus diameter were measured along an axis parallel to the dorsal edge of the selection using SPOT Camera 3.5.0.0 software.



**Fig. 2:** Interpretation of lines of arrested growth (LAG) from loggerhead humerus; (a) double line, counted as one LAG; (b) one dark LAG that split into five lines, counted as five LAGs; (c) design of a first year mark (denoted as annulus). Scale 1mm.

### Age estimation

The first growth mark (annulus) appears closest to the center of the bone and later growth marks that are deposited sequentially along the outer circumference (Zug et al. 1986) (**Fig. 2c**). Snover and Hohn (2004) validated that, for Kemp's ridley (*Lepidochelys kempii*), this earliest growth mark is shaped as a diffuse line. We assumed in this study that the pattern holds for loggerhead sea turtles, as well. Accepting that the bone growth is cyclic (Zug et al. 1986) and that, for *Caretta caretta*, each growth mark indicates one year of life (Klinger and Musick 1992, Coles et al. 2001; Bjorndal et al. 2003), the age was defined as the number of LAGs for the turtles that retained an annulus. However, in animals with larger sizes, the early periosteal layers are entirely replaced by remodeling and endosteal growth (denoted "lost LAGs") (Zug et al. 1986).

The number of lost LAGs was calculated based on the age-estimation protocol proposed in Parham and Zug (1997) as a correction factor. According to Zug et al. (2006), age estimation by a correction factor is more plausible biologically because age and size are dissociated. This correction factor derives from a relationship between the number of growth layers ( $x$ ) and the corresponding growth layer diameters ( $y$ ). In a first step, the pairs ( $x, y$ ) were measured for turtles which retained an annulus with numbered lines from the inner to outer edge of the bone. Two models: (1) linear regression  $y = a + bx$  and (2) power function  $y = ax^b$  were fitted to the data set.

To estimate model parameters, two different error structures were assumed (Faraway, 2006). The first, denoted ‘naïve’, assumes that  $y_i = A + bx_i + v_i$  or  $y_i = ax_i^b e^{v_i}$ , where  $v_i$  are independent Normal random variables with mean 0 and variance  $\sigma^2$  for a total of  $n$  pairs of data ( $y_i, x_i$ ),  $i = 1, \dots, n$  and  $a = \ln A$ . The second, denoted ‘hierarchical’, in line with the data collecting process, takes the inter- and intra-individual variability into account. Hence, this error structure assumes that  $y_{ij} = A_i + b_i x_{ij} + v_{ij}$  or  $y_{ij} = a_i x_{ij}^{b_i} e^{v_{ij}}$  where, within individual  $i = 1, \dots, m$ , the variables  $v_{ij}$  are independent Normal random variables with mean 0 and variance  $\sigma^2$  for a total of  $n_i$  pairs of data ( $y_{ij}, x_{ij}$ ),  $j = 1, \dots, n_i$  and  $n = \sum_{i=1}^m n_i$ . Furthermore, the pair of parameters ( $a_i, b_i$ ) are individual specific and modeled as independent Normal random variables with mean and variance  $(\mu_a, \sigma_a^2)$  and  $(\mu_b, \sigma_b^2)$ , respectively. The naïve models have three parameters  $a$  (or  $A$ ),  $b$  and  $\sigma$ , while the hierarchical models have five parameters ( $\mu_a, \mu_b, \sigma_a, \sigma_b$  and  $\sigma$ ).

In a second step, for turtles without an annulus, the resorption core diameters were measured ( $y_{core}$ ), and the corresponding number of lost lines inferred by reverse prediction ( $x_{core}$ ). Therefore, the number of growth layers observed in the outermost region of the bone section ( $x_{obs}$ ) plus the predicted number of resorbed growth layers represented in the resorption core of the humerus, is the turtle’s estimated age ( $x = x_{core} + x_{obs}$ ).

### **Back-calculation and growth rates**

Back-calculation is a technique, developed to estimate the length of a fish at an earlier time, based on measurements made at time of death. The data set is usually composed of the size of marks in hard parts of a fish (usually otoliths) and its current body length. From these data, the

body length for all previously formed marks is estimated (Francis, 1990). Smedstad and Holm (1996) applied and validated the method for cod fish (*Gadus morhua*). In sea turtles, the back-calculation method has been applied and validated for loggerheads and green sea turtles (Snover et al. 2007; Goshe et al. 2010).

In this study, we fitted four models to find the best relationship between curved carapace length and humerus diameter, as did Snover et al. (2007) for North Atlantic loggerheads: (1)  $L = l_{op} + b(D - d_{op})^c$ ; (2)  $L = l_{op} + b(D - d_{op})$ ; (3)  $L = a + bD^c$ ; and (4)  $L = a + bD$ , where  $L$  is curved carapace length (CCL),  $D$  is the diameter of the humerus,  $l_{op}$  is a given CCL of the turtle at hatching,  $d_{op}$  is a given diameter of the humerus at hatching and  $c$  is the allometric coefficient which it is equal to 1 for models 2 and 4. For  $l_{op}$  and  $d_{op}$ , we used the hatchling mean Straight Carapace Length (SCL) (4.6cm) of Snover et al. (2007) converted to CCL based on the linear regression equation in Avens and Goshe (2007) ( $SCL = 0.923(CCL) - 0.189$ ;  $l_{op} = 4.77\text{cm}$ ).

Once the best model is established, back-calculation provides estimates of size (CCL) for growth layer (LAG) diameters within the humerus. Thereafter, the “Body Proportional Hypothesis” (BPH) was applied. This hypothesis says that the ratio between true size ( $L$ ) and model-estimated size  $\hat{L} = f(D)$  for the associated humerus diameter ( $D$ ) and a given model  $f$ , is the same for all values of  $D$  (Francis 1990; Snover et al. 2007). Under BPH, and taking the best fitted model as  $f$ , the back-calculated length ( $L_b$ ) for a given diameter  $D_b$  is:

$$L_b = [f(D_b)][L_{final}][f(D_{final})]^{-1} \quad (1)$$

Where  $L_{final}$  is the CCL of a turtle at death; and  $f(D_{final})$  is the back-calculated CCL, based on humerus diameter.

To calculate the average yearly growth rate for each turtle, the diameter of the innermost LAG was measured and the corresponding CCL back-calculated with equation (1) and then subtracted from the CCL for the outermost LAG; the difference was divided by  $k + 1$ , where  $k$  is the number of LAGs in between.

## Growth model

In the literature, there are a broad number of growth models, including the Pütter, von Bertalanffy, Richards, Gompertz and logistic growth models, among others. All these models

become special cases of a generalized model proposed by Schnute (1981). Logistic and von Bertalanffy growth models have been applied to skeletochronological and mark-recapture growth data for loggerhead sea turtles (Frazer and Ehrhart 1985; Klinger and Musick 1995; Zug et al. 1995; Bjorndal et al. 2000; Snover 2002). However, Schnute's model is fitted here to age-at-length due to its generality in shape. Since the set of data included in the present analysis covers only a specific age window of the turtle's life cycle, this model flexibility is a possible advantage. Schnute's, generic equation with four parameters takes the form,

$$y_{\tau} = \left\{ \gamma_1^b + [\gamma_2^b - \gamma_1^b] * \left[ \frac{1 - e^{-a(\tau - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right] \right\}^{\frac{1}{b}} \quad (2)$$

where  $y_{\tau}$  is the size of the specimen at age  $\tau$ , in this case the size was the curved carapace length (CCL). The parameters  $\tau_1$  and  $\tau_2$  are the ages fixed by the researcher with the restriction  $\tau_2 > \tau_1$ , being usually the youngest and oldest ages present in the sample, respectively. The parameters  $\gamma_1$  and  $\gamma_2$  are the expected sizes at ages  $\tau_1$  and  $\tau_2$ , respectively, with restriction  $0 < \gamma_1 < \gamma_2$ . The parameters  $a$  and  $b$  define the shape of the curve and can be positive, negative or equal to zero. Parameter  $a$  is related to the curve slope and its unit is  $\tau^{-1}$  and parameter  $b$  doesn't have a unit. Specific combinations of these two parameters lead to different growth models; for example, the von Bertalanffy curve when  $a > 0$  and  $b = 1$ . The set of five parameters to be estimated are  $(a, b, \gamma_1, \gamma_2, \sigma)$  where  $\sigma$  is the standard error of residuals.

## Statistical Analysis

Inference was performed within a Bayesian statistical framework. In Bayesian analysis, estimates of unknown parameters are given as probability distributions denoted *posteriors* (Gelman et al. 2003). These posteriors are obtained by the integration of the data likelihood with other relevant information expressed in *prior* probability distributions, using Bayes' Theorem. When analytical solutions are not feasible, posteriors are approximated by random samples taken from it. If the inclusion of external information is not possible or desirable, appropriate non-informative or "open-minded" priors are chosen instead.

We used non-informative priors in all but Schnute's growth model, for which the prior for the parameter vector  $(a, b, \log \gamma_1, \log \gamma_2, \log \sigma)$  was a 5-dimensional Student distribution with 10 degrees of freedom, centered at the mode of the log-likelihood and with scale matrix equal to the inverse-Hessian. Although informative, this prior is considered open-minded, in the sense



that all possible parameter values have positive prior probability. Samples from the posterior distributions were drawn by the method of Markov chain Monte Carlo (MCMC) (Gelman et al. 1995). In MCMC, a Markov chain is set up in such a fashion that the posterior is its long run equilibrium distribution.

Posterior means were used as parameter estimates, unless otherwise stated. Uncertainty about these estimates were expressed in 95% posterior probability intervals with lower and upper limits equal to the quantiles 2.5% and 97.5% of the posterior sample, respectively. A posterior probability interval is the Bayesian analog to conventional confidence intervals (Ellison 1996; McCarthy 2007). Model selection was based on the deviance information criterion (DIC) (Speigelhalter et al. 2002). All analyses were performed using software R (R Development Core Team 2008) and OpenBugs (Thomas et al. 2006) which is an application of BUGS language ([www.mrc-bsu.cam.ac.uk/bugs/](http://www.mrc-bsu.cam.ac.uk/bugs/)) to specify models and perform the Bayesian analysis (Gilks et al 1994). The R-code on all applications can be obtained under request to the first author.

## Results

A total of 64 and 20 humeri were collected from loggerhead turtles washed ashore and incidentally caught in pelagic longline fisheries, respectively. Their sizes ranged from 45.5cm CCL to 102.0cm CCL (mean = 74.81 sd = 11.59) for beach turtles and from size 47.0cm CCL to 66.5cm CCL (mean = 58.92 sd = 5.00) for oceanic animals (**Table 1**). However only 49 humeri from stranded dead loggerhead were processed and had their age estimated, 4 humeri were damaged during age determination procedures and for 11 humeri morphometric data (CCL and CCW) were not available. The oceanic and neritic sea turtles were grouped for growth analysis, because they were considered to be the same population (Reis et al 2010). The individuals were classified as adults and juveniles, based on the range size (83.0-120.0cm CCL) of mature loggerheads from the nearest nesting area (Baptistotte et al. 2003).

**Table 1:** Number of loggerhead sea turtles from neritic (beach coast) ( $n$ ) and oceanic (incidentally caught in pelagic longline fisheries) ( $N$ ) zone with their respective size classes (CCL).

CCL (cm)	Neritic	Oceanic
	$n$	$n$
40.0-49.0	2	1
50.0-59.0	4	10
60.0-69.0	11	9
70.0-79.0	16	--
80.0-89.0	13	--
90.0-99.0	2	--
100.0-109.0	1	--

### Age estimation

Of the 69 loggerhead humeri, only 13 humeri retained a diffuse annulus representing the first year mark (Snover and Hohn, 2004); these turtles retained between 8 to 13 LAGs. The hierarchical power function model provided the best fit to age-at-death data, based on DIC (**Table 2**). With posterior means as parameter point estimates, the equation took the form:

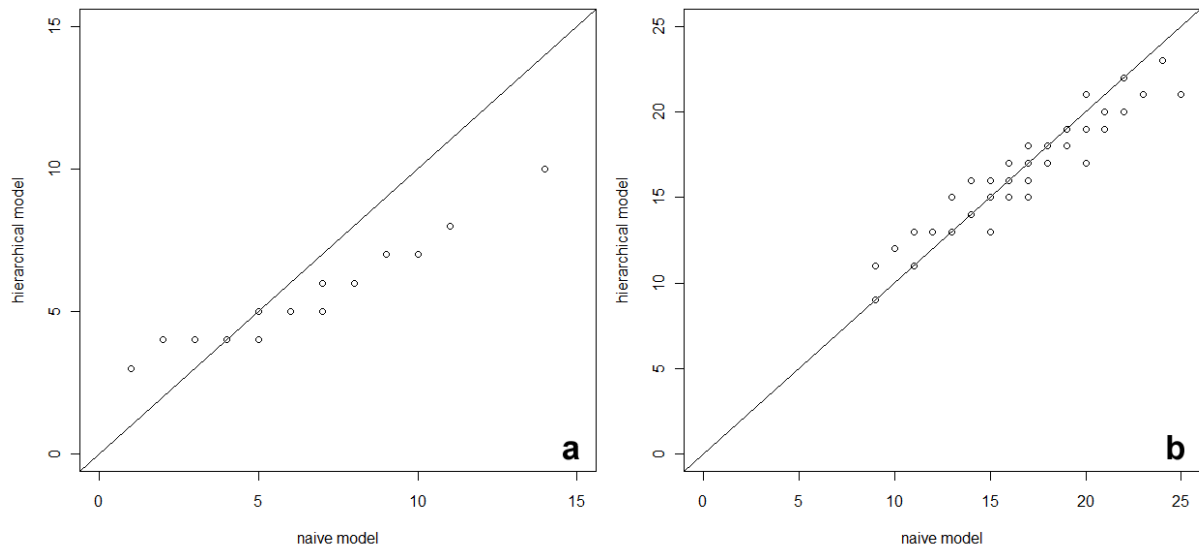
$$\text{LAGdiameter (mm)} = 2.18 * (\text{LAGnumber})^{0.35} \quad (3)$$

For the 56 turtles without an annulus, the LAG diameter ( $y$ ) was replaced by the resorption core diameter ( $y_{core}$ ) and the equation solved for lost LAGs ( $x_{core}$ ). The estimated age for turtles incidentally caught in longline fisheries varied between 8 and 19 years, which indicates the oceanic stage duration for South Atlantic loggerhead. For stranded dead turtles along the coast, estimated ages were between 9 and 24 years.

The comparison in estimated lost LAGs from the naïve and hierarchical power models is displayed in figure 3 and shows an increased over-estimation of the naïve model in comparison to the hierarchical model, for older ages (**Fig. 3a**) and this difference is less pronounced for the overall age estimation (**Fig. 3b**).

**Table 2:** Bayesian fits of the four models for line arrested growth (LAG) vs. line number data. The letters  $a$ ,  $b$  and  $\sigma$  are the posterior mean; values within brackets are the 95% probability intervals. DIC is the deviance information criteria; a smaller DIC indicates a better fit.

Parameters	Naïve model		Hierarchical model	
	$y = a + bx$	$y = ax^b$	$y = a + bx$	$y = ax^b$
$a$	9.11 [8.5;9.7]	2.18 [2.1;2.2]	8.98 [7.8;9.9] ( $\sigma_a = 2.21$ [1.4;3.5])	2.18 [2.0;2.3] ( $\sigma_a = 0.21$ [0.1;0.3])
$b$	1.16 [1.1-1.3]	0.35 [0.3;0.4]	1.18 [1.0;1.3] ( $\sigma_b = 0.27$ [0.2;0.4])	0.35 [0.3;0.4] ( $\sigma_b = 0.08$ [0.05;0.13])
$\sigma$	1.70 [1.5;1.9]	0.12 [0.10;0.13]	0.75 [0.7;0.9]	0.04 [0.03;0.05]
<b>DIC</b>	504.9	-170.7	321.1	-430.0



**Fig. 3:** Estimated lost LAGs (a) and estimated age (b) for turtles without an annulus obtained from the naive model versus hierarchical model. Points on the diagonal line represent some estimates from both models.

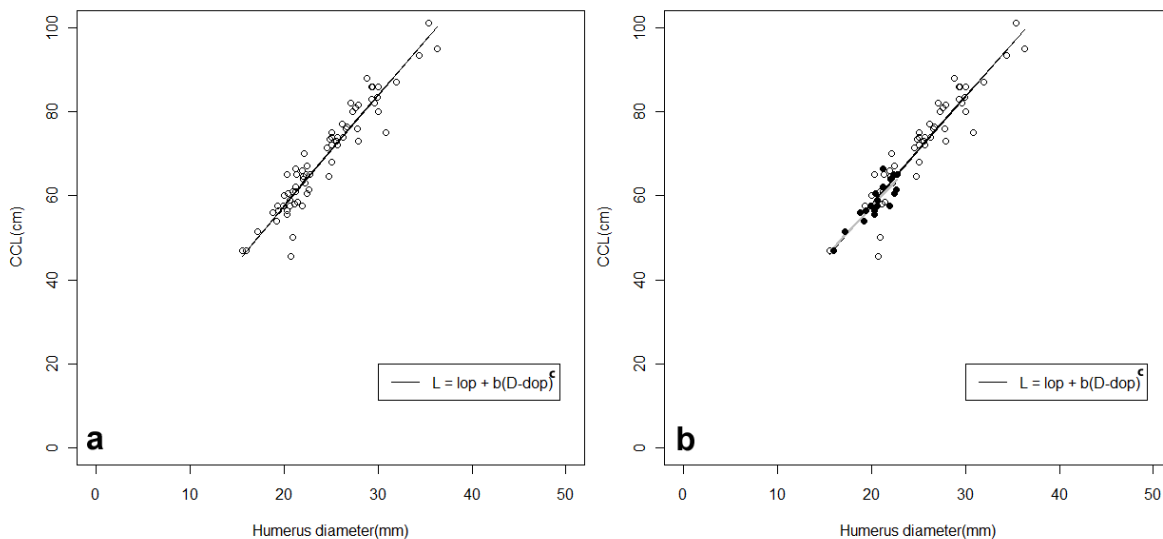
### Back-calculation and growth rates

The best fitted model incorporated the biological intercepts  $l_{op}$ ,  $d_{op}$ , and constant  $c$ . While the other three models provided reasonable fits to the data, the first model obtained the lowest DIC (Table 3; Fig. 4). This model was fitted to the complete age-at-length data set, because when applied separately, the fit was similar for the two samples (Fig. 4). Thus the growth rates were calculated for the clumped data.

The relationships between growth rates and size (CCL), as well as growth rate and estimated age were negative ( $r = -0.29$ ;  $r = -0.65$ , respectively), suggesting that turtle growth rates decrease as age and size increase (Fig. 5). However the relationship between age and growth rate was stronger, since individuals of different sizes may be the same age. This suggests that age may be a better indicator of life stage than size. As expected, the growth rate for oceanic loggerhead was greater than for neritic turtles, even for turtles within the same size range (Table 4).

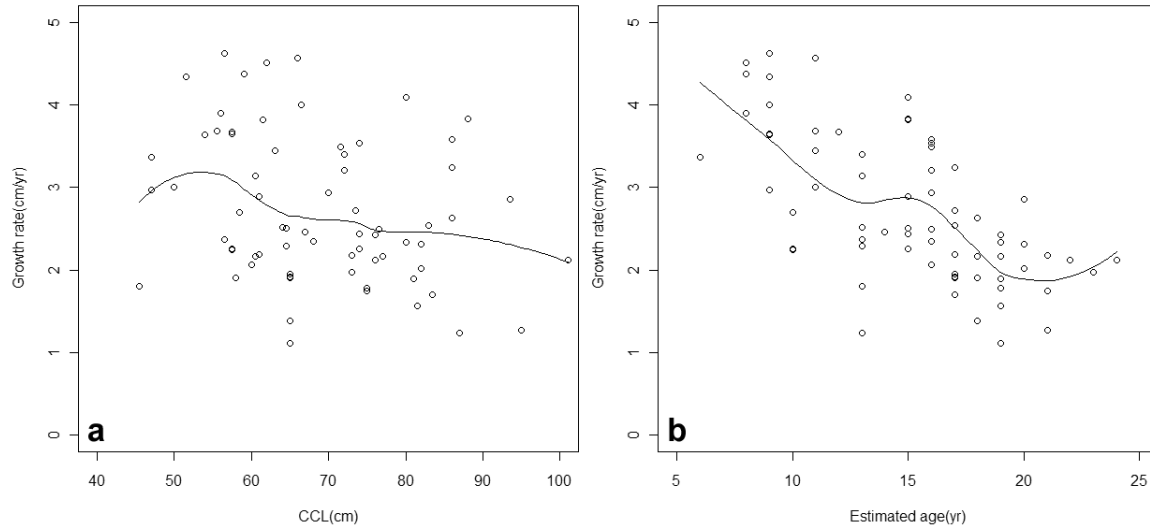
**Table 3:** Bayesian fit of four models for carapace length vs. humerus diameter. In each model  $L$  is carapace length and,  $D$  the humerus diameter;  $lop$  indicates the carapace length at hatching and  $dop$  indicates humerus diameter at hatching. Estimated parameters are posterior means; values within brackets are 95% probability intervals. DIC is the deviance information criterion to select among models. A smaller DIC indicates a better fit.

Model	Parameters estimates				DIC
	$a$	$b$	$c$	$\sigma$	
$L = lop + b(D - dop)^c$	-	1.30 [1.1;1.5]	0.92 [0.8;1.0]	0.07 [0.05;0.08]	<b>-170.4</b>
$L = lop + b(D - dop)$	-	2.86 [2.8;2.9]	-	4.06 [3.5;4.7]	<b>393.9</b>
$L = a + b(D)^c$	0.57 [0.0;4.4]	3.69 [2.8;44]	0.92 [0.9;1.0]	3.90 [3.3;4.7]	<b>391.7</b>
$L = a + b(D)$	5.22 [-0.3;9.7]	2.62 [2.4;2.8]	-	3.91 [3.3;4.6]	<b>393.2</b>



**Fig. 4:** Relationship between CCL and humerus diameter ( $n = 69$ ). (a) All loggerhead from this study (oceanic plus neritic zone), the solid black line is the fitted model  $L = lop + b(D - dop)^c$ ; (b) Grey solid line is the same

model fitted only to oceanic zone data set (solid circles) and black solid line is the model fitted only to neritic turtles data set (open circles).



**Fig. 5:** Relationship between growth rates and **(a)** size (CCL) ( $r = -0.29$ ); **(b)** estimated age ( $r = -0.65$ ). All loggerhead sea turtles are included. The smooth line was obtained by the locally-weighted smoother; function *loess* in R.

**Table 4:** Growth rates - GR ( $\text{cm}\cdot\text{yr}^{-1}$  CCL) of loggerheads from neritic and oceanic zone of western South Atlantic. *n* indicates the sample size and the values between brackets are the range.

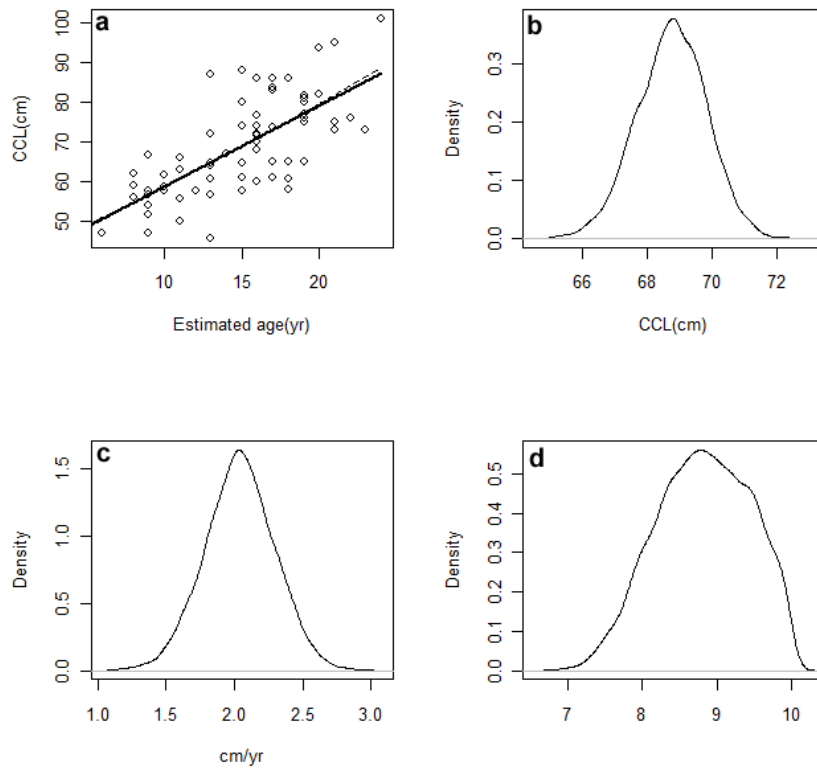
Neritic zone		Oceanic zone	
CCL(cm)	GR( $\text{cm}\cdot\text{yr}^{-1}$ )	CCL(cm)	GR( $\text{cm}\cdot\text{yr}^{-1}$ )
<b>40.0-49.0</b>	2.39 [1.8; 3.0] ( <i>n</i> = 2)	<b>40.0-49.0</b>	3.37 ( <i>n</i> = 1)
<b>50.0-59.0</b>	2.82 [1.9; 3.7] ( <i>n</i> = 4)	<b>50.0-59.0</b>	3.51 [2.2; 4.4] ( <i>n</i> = 10)
<b>60.0-69.0</b>	2.55 [1.4; 4.6] ( <i>n</i> = 11)	<b>60.0-69.0</b>	2.79 [1.1; 4.5] ( <i>n</i> = 9)
<b>70.0-79.0</b>	2.55 [1.7; 3.5] ( <i>n</i> = 16)	-	-
<b>80.0-89.0</b>	2.53 [1.2; 4.1] ( <i>n</i> = 13)	-	-
<b>&gt; 90.0</b>	2.08 [1.3; 2.9] ( <i>n</i> = 3)	-	-

## Growth models

Schnute’s growth model fit well the relationship between estimated age and carapace length (CCL) data; since the data did not cover earlier ages (hatchling and small juveniles) and older adults, Schnute’s curve was almost a straight line (**Fig. 6a**). Thus, a linear regression ( $CCL = A + Bx$ ) was also fitted, where  $x = (age - 15)s_x^{-1}$  is the standardized distance from age 15, the full age closest to the mean age in the sample. Non-informative priors were used for parameters  $A$  and  $B$ . The much simpler linear model fit well to the data (**Fig. 6a**), and had a slightly lower DIC than Schnute’s model (**Table 5**), suggesting, that within this “age window” the growth is nearly linear. Parameter  $A$  is the average size (cm) of an individual at age 15 years (**Fig. 6c; Table 5**). Parameter  $B$  was divided by  $s_x$  to become  $B_y$ , the average yearly growth (cm.yr<sup>-1</sup>), resulting in a posterior mean 2.04 cm.yr<sup>-1</sup>, similar to the average growth rate obtained from back calculation (2.45cm.yr<sup>-1</sup>) (**Fig. 6b; Table 5**).

**Table 5:** Bayesian fit of Schnute’s growth model and linear model for carapace length (CCL) and estimated age data. Estimated parameters are the posterior means; values within brackets are the 95% probability intervals.

<b>Schnute’s model</b>		<b>Linear model</b>	
<b><i>a</i></b>	0.02 [-0.1;0.2]	<b><i>A</i></b>	68.71 [66.5;70.9]
<b><i>b</i></b>	0.04 [-0.7;1.5]	<b><i>B</i></b>	2.04 [1.5;2.5]
<b><math>\gamma_1</math></b>	49.04 [37.6;58.0]	<b><math>\sigma</math></b>	8.81 [7.6;9.9]
<b><math>\gamma_2</math></b>	88.53 [79.3;100.2]	-	-
<b><math>\sigma</math></b>	8.73 [7.2;10.4]	-	-
<b>DIC</b>	<b>502.7</b>	<b>DIC</b>	<b>499.9</b>



**Fig. 6:** (a) Bayesian fit of Schnute's model (dashed line) and linear model (solid line) to estimated age vs. size (CCL); (b) posterior distribution of average CCL (cm) at age 15 years for the linear model; (c) Posterior distribution of parameter  $B_y$  in  $\text{cm}\cdot\text{yr}^{-1}$  for linear model (d) posterior distribution of residual standard deviation  $\sigma$  (cm) for the linear model.

## Discussion

### Age estimation

The size range and age estimates of oceanic loggerheads were lower than for neritic loggerheads. Bjorndal et al. (2000a) suggested that loggerheads from the North Atlantic recruit to the neritic zone at about 46.0 to 64.0cm CCL, similar to our findings for the South Atlantic. Our results showed that oceanic turtles ranged from 47.0 to 65.5cm CCL while those from the neritic area were predominantly larger than 70cm CCL, although a few individuals fell within the size range of oceanic turtles. These small individuals might be new recruits in transition from the oceanic to the neritic zone, as observed by McClellan and Read (2007), or perhaps these smaller turtles might represent discharge from longline fisheries, although this is less likely given that the

fishing ground is at least 150km far from shore. Moreover, Monteiro et al. (2006) reported that most stranded loggerheads (average 74.3cm CCL) showed marks as cuts on the carapace produced by sharp objects, entanglement in fishing lines, hooks and nets, which it is evidences of interactions with fisheries that operate in coastal waters, such as bottom trawling and gillnet. These evidences also support the hypothesis that the smaller loggerheads washed ashore may be new recruits. However, Barros (2010) found three out of 18 turtles (50.0 to 69.9cm CCL) with pelagic items in their stomach, suggesting that the strandings may have another cause.

The age range for the oceanic stage has been previously estimated through skeletochronological analysis between 9 and 24 years for North Atlantic loggerhead (Snover 2002). Here, we estimated the age range of the western South Atlantic loggerhead turtle population incidentally caught in pelagic logline fishery from 8 to 19 years (average 11.5 years). While estimates by Snover (2002) and by the current study are similar, Bjorndal et al. (2000a) estimated ages from 6.5 to 11.5 years using length-frequency analysis in the North Atlantic, suggesting that the methodology may have an influence.

Within skeletochronological analysis there are differences in the calculation of lost LAGs that can explain minor difference that remain between Snover et al. (2007) and our studies. Several methods to calculate the loss of periosteal layers have been applied in skeletochronology studies: correction factor, ranking, and simple deduction based on the smallest turtle (Zug et al. 1997; Parham and Zug 1997; Zug et al 2002; Bjorndal et al. 2003, Zug et al. 2006; Goshe et al. 2010). However, the variation of LAG deposition within a specimen and between specimens from the same population had never been taken into account. This variation is expected due to the stochastic nature of the environmental conditions experienced by turtles during the many years in their oceanic phase until they recruit to neritic habitat (Bjorndal et al. 2003).

The hierarchical power model was more stable in comparison to the naïve alternative, because for larger turtles the estimated ages were lower and for smaller turtles they were higher (**Fig. 3**). Moreover this model had lower residual variance (**Fig. 3; Table 2**) due to the incorporation of  $\sigma_a$  and  $\sigma_b$ , which are related to parameters  $\mu_a$  and  $\mu_b$  respectively, which take into account the variation in LAG deposition. Furthermore, the application of Bayesian inference provided further accuracy to estimated ages because they were based on predictive probabilities over all possible ages given the whole data set (Ellison 1996).



## Growth rate

Growth rates were greater for oceanic than for neritic loggerhead turtles, even for turtles within the same size range. Some neritic turtles within the size range of new recruits presented growth rates similar to oceanic turtles, suggesting that the former could have been on their transition between both zones (**Table 4**). However, it has recently been demonstrated that this ontogenetic shift for loggerheads is not as clear cut, as previously thought (McClellan and Read 2007).

Growth rates can vary significantly between feeding areas, both within and between individual turtles (Bolten 2003; Braun-McNeill et al. 2008), potentially due to a variety of factors such as water temperature, food resource, energy expenditure during migrations, and genetic origin (Goshe et al. 2010). Water temperature influences the physiology of reptiles (Moon et al. 1997), as at high and low extremes feeding behavior, locomotor movements and hormone levels are negatively impacted (Milton and Lutz 2003). Schwartz (1978) reported that turtles halt feeding and start floating when temperatures fall below 10°C, which influences their growth rates. However, the growth rates for neritic loggerheads in the Southwest Pacific (Great Barrier Reef: 1-2cm.yr<sup>-1</sup> CCL/ 15°C in winter and Moreton Bay: 2-3mm.yr<sup>-1</sup> CCL/15°C) (Limpus and Limpus 2003; Read et al. 1996), western North Atlantic (2.1-4.8cm.yr<sup>-1</sup>SCL/ 13.3-28°C) (Snover 2002; Coles and Musick 2000; Braun-McNeill et al. 2008) and western South Atlantic (1.5-4.5cm.yr<sup>-1</sup>CCL/12.5°-23°C), indicate that temperature is not the main factor to explain the difference in growth rates between feeding areas. Turtles have the ability to move into regions of preferred temperature for physiological maintenance (Coles and Musick 2000). Shoop and Kenny (1992) reported by aerial surveys that loggerheads migrate to lower latitude in winter and to high latitudes in summer in the North Atlantic. In contrast, there is no evidence that loggerhead turtles in Moreton bay undertake south-north, summer-winter, non-breeding migrations (Musick and Limpus 1996). Instead, they become lethargic and spend longer time on the bottom, decreasing their growth rates (Limpus and Limpus 2003).

Before recruitment to the neritic zone, loggerheads inhabit extremely stochastically varying environments (Bjorndal et al. 2003) and the growth rates of these turtles may vary between individuals and populations. Bjorndal et al. (2000a) reported growth rates that are higher than the growth rates obtained in the present study (**Table 6**). This variation might be explained by the different environmental conditions, such as water temperature and food

resource, experienced by the turtles in the pelagic habitat of each ocean basin. Loggerheads from the North Atlantic oceanic zone exhibit compensatory growth, which is an increase in growth when the conditions are favorable (Bjorndal et al. 2003).

Migration patterns are little understood of the loggerhead turtle populations in the South Atlantic. Nevertheless, it is possible that the energy expended during seasonal and inter-nesting migration may influence growth rates. The wide seasonal water temperature variation in southern Brazil (Garcia 1998) may induce the northward migration of loggerhead during cold months, as was observed for green sea turtles (*Chelonia mydas*) (unpubl. data, Petit, 2008). Moreover, the turtles within the size range of mature loggerheads along the Brazilian coast (83.0-120.0cm CCL) (Bapitistotte et al. 2003) may perform seasonal migration between foraging (southern Brazil) and nesting grounds (Espírito Santo State), contributing to the slow growth rates of this group (**Table 4**). Satellite telemetry would potentially improve the understanding on the migration and distribution patterns of loggerhead turtles in southern Brazil, an important foraging area for the western South Atlantic population (Martinez-Souza, 2009; Barros, 2010).

Martinez-Souza (2009) and Barros (2010) have observed that oceanic loggerheads feed mostly on salps and pyrosoms and suggested that these turtles feed constantly to balance the low energy budget of this food source. Thus, the difference of growth rates between neritic and oceanic turtles may be due to the amount of food intake. In the oceanic zone the aim may be to grow faster to minimize predation risks (Snover et al. 2007). Although in the neritic zone, the turtles feed upon prey with higher energy content (Barros 2010) but their growth rates are lower in comparison. This might be because: 1) larger turtles direct the energy intake to reproduction (Snover et al. 2007) and; 2) food intake by smaller neritic turtles is low due to the less predictable nature of their prey, which results in a higher energy cost to forage in the benthos and to find their prey.

As it has been reported that larger turtles present lower growth rates (Klinger and Musick 1995; Goshe et al. 2010), the difference between ours and Moreton Bay studies may be due the size range of recruits. In Australia, loggerhead turtles recruit to neritic habitat with an average CCL of 78.62cm (Limpus and Limpus 2003), which is a much larger size than those estimated for the South (~58.9cm CCL – this study) and North Atlantic (~53.0cm CCL; Bjorndal et al. 2000a). The low growth rate for Moreton bay (2.3mm.yr<sup>-1</sup> CCL) may be because the animals are already fairly large when they recruit to the neritic zone.

Different genetic stocks may also influence growth rates (Bjorndal et al 2000b). In the longline fishery from southern Brazil, rookeries from Australia and Greece contribute with 28.5% of all found haplotypes (Reis et al. 2010). However, since African and Indo-Pacific rookeries are poorly known, the haplotypes from Australia and Greece may be derived from them (Reis et al 2010). Haplotypes from the African coast may occur in southern Brazil, as the Agulhas current and the subtropical gyre in the south Atlantic may transport hatchlings in a manner similar to that observed in the North Atlantic (Bolten 2003; Castello et al 1998).

In addition to the various factors described above, growth rates may vary depending on the calculation method. As “Body Proportional Hypothesis” (BPH) method was validated by Snover et al. (2007) for loggerheads, the calculation of growth rates became more accurate (Smedstad and Holm, 1996). The growth rates estimated for pelagic turtles from the North Atlantic, based on mark-recapture studies (Bjorndal et al. 2000a) were greater than our estimates (**Table 6**) obtained from skeletochronology combined with the BPH method. Nevertheless, the growth rates estimated by Snover et al. (2007) for neritic turtles based on skeletochronology were similar to ours but higher than those estimated by Braun-McNeil et al. (2008) based on mark-recapture analysis. Skeletochronological data provide a growth rates for multiple years whereas the mark-recapture studies produce a growth rate estimate related merely to the time interval between capture and recapture.

**Table 6:** Comparative growth rates for loggerhead sea turtle populations (SCL, cm.yr<sup>-1</sup>). RS, BR – Rio do Grande, Brazil; NC – North Carolina; GA – Gerogia; SC – skeletochronology; MR – mark-recapture; LF – length-frequency. The values between brackets represents: (a) 95% probability interval; (b) and (d) 95% confidence interval; (c) and (e) standard error.

SCL(cm)	Pelagic			Neritic			
	S.Atlantic <sup>a</sup>	N.Atlantic <sup>b</sup>		RS, BR <sup>a</sup>	NC, USA <sup>c</sup>	GA, USA <sup>d</sup>	NC, USA <sup>e</sup>
	SC	MR	LF	SC	SC	SC	MR
40-49	3.6 [3.1;4.0]	4.0 [3.4;4.6]	3.9	2.2 [1.7;2.8]	4.7 [±0.37]	3.6 [2.6;4.3]	- -
50-59	3.1 [2.0;4.3]	6.1	3.1	2.4 [1.8;3.4]	3.9 [±0.31]	3.3 [1.7;5.2]	1.81 [±1.15]
60-69	2.1 [1.0;3.7]	2.9 [2.8;3.0]	-	2.4 [1.6;4.2]	3.2 [±0.24]	2.9 [2.2;4.1]	2.16 [±1.61]
70-79	-	-	-	2.3 [1.6;3.8]	2.1 [±0.37]	[1.6;2.4]	2.41 [±0.51]
80-89	-	-	-	2.1 [1.1;3.5]	-	[0.9;3.5]	-
90-100	-	-	-	2.0	-	-	-

<sup>a</sup>This study, CCL converted to SCL, based on Avens and Goshe (2007);

<sup>b</sup>Bjorndal et al 2000;

<sup>c</sup>Snover 2002;

<sup>d</sup>Parham and Zug 1997;

<sup>e</sup>Braum-McNeil 2008.

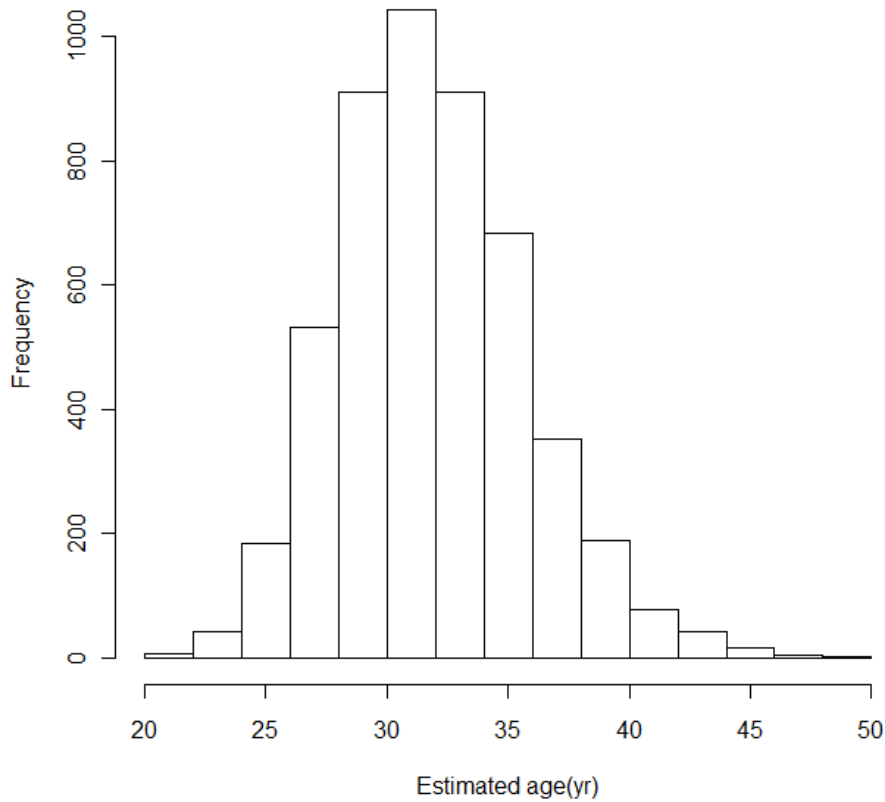
## Growth model

Schnute’s growth model (Schnute 1981) resulted in an almost straight line (figure 4), probably because the data set incorporated only a small “age window” of the sea turtle life cycle. Furthermore, the majority of individuals were classified as juveniles (Limpus and Limpus 2003), a stage when turtles appear to grow faster than adults (Bjorndal et al. 2003) perhaps due to the requirement of size increase to protect from predators (Snover and Hohn, 2004).

An important advantage of Schnute’s growth model is the versatility to adapt its shape according to the age window for which data are available. In contrast, to fit the more conventional von Bertalanffy growth model, a sample from all size classes ranging from hatchlings to old adults encompassing asymptotic size, is required. Such a data set is difficult to gather due to the extensive migration pattern characteristic of the sea turtle life cycle and the

uncertainty remaining in regard to the “lost years” (Carr, 1987). In spite of these difficulties, the logistic or the von Bertalanffy growth models have usually been applied in most sea turtle growth studies (Frazer and Ehrhart 1985; Klinger and Musick 1995; Zug et al. 1995; Bjorndal et al. 2000; Snover 2002). However, because von Bertalanffy’s curve would not fit the data set properly, these authors had to infer the asymptotic length by other means.

Since the much simpler linear model had a lower DIC than Schnute’s model, we used the former for estimating the age distribution of turtles within the size range of mature loggerheads from the Brazilian coast (83.0 to 123.0cm CCL) (Baptistotte et al. 2003). The estimated age distribution was based on the assumption that this size range has an approximate normal distribution with mean equal to 102.5cm and variance equal to  $5.3\text{cm}^2$  and that the linear regression is acceptable up to the maximum size. Uncertainty in the parameter estimates of the linear age-at-size relation was included by use of the posterior distribution. The simulated age distribution resulted in a mean age at maturation for loggerhead sea turtle population at 31.8 years ( $\pm 3.47$ ; 95% Probability Interval: [25.7;39.2]) (**Fig. 7**). Snover (2002) reported a mean of 30.8 years for age at maturation and Bjorndal et al. (2000) estimated 26.5 years to grow from hatchling to a size of 87cm CCL, which is considered as the minimum size of mature loggerhead from the North Atlantic. These estimates and estimates from Klinger and Musick (1995) (22-26 years) are within the credibility interval of ours estimates; however, the estimates strongly depend on the mean estimated size of mature loggerhead turtle in the population.



**Fig. 7:** Estimated age at maturation for South Atlantic loggerhead sea turtle population.

### Conclusions

The south coast of Rio Grande do Sul is an important development area for oceanic juveniles (8 to 19 years) as well as for neritic juveniles/adults (9 to 24 years) of loggerhead sea turtles. Due the difference between growth rates of individuals from oceanic and neritic zone, the growth rates decrease with an increase of both age and size. And the phase of post-hatching until late juveniles, the growth is linear, with an age-at-maturation around 30 years.

Skeletochronological analysis is becoming a powerful tool in sea turtle population dynamics throughout the world. This study is the first to describe age and growth for *Caretta caretta* in the South Atlantic, and provide invaluable information for assessing loggerhead population dynamics in this area.

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