UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS

Estudo sobre os Siriboias (Ordem Stomatopoda): análises morfométricas entre as espécies mais abundantes do litoral norte de São Paulo

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Orientador: Prof. Dr. Antonio Leão Castilho

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SUMÁRIO

Considerações Iniciais

Esta presente dissertação teve como foco de estudo a morfometria de duas espécies da ordem Stomatopoda, pertencente ao subfilo Crustacea, utilizando ferramentas alométricas afim de se obter maiores conhecimentos sobre elas. Os membros desta ordem, conhecidos popularmente como camarão louva-a-deus, tamburutaca ou siriboia, são predadores ativos e carnívoros obrigatórios que desempenham um importante papel ecológico (Ahyong & Harling 2000), podendo ser encontrados principalmente em regiões tropicais e subtropicais (Schram *et al*. 2013). São bentônicos, habitando tocas e fendas nas regiões de médio e infralitoral em todos os tipos de substrato, utilizando-as para abrigo durante o dia, apresentando períodos mais ativos durante a noite (Caldwell 1991).

Figura 1: *Squilla brasiliensis* (Referência métrica: 10 mm.). Acervo Pessoal.

Stomatopoda possui importância econômica para alguns países da Ásia, como a Malásia, China e Japão (Kodama *et al.* 2004; Antony *et al.* 2010), onde é utilizado na culinária, especialmente a *Oratosquilla oratoria* (De Haan 1844). Recentes estudos indicam a produção de quitina através de espécies do gênero *Oratosquilla* (Thirunavukkarasu *et al*. 2011), ampliando ainda mais seu uso e importância em algumas regiões do Oriente.

Porém para o Ocidente, a captura dos membros desta ordem não é esperada se tornando indesejada, quando é descartado possivelmente morto (Najiah & Lee 2008). Estes animais são desprezados pelos pescadores devido a principal característica desta ordem, um apêndice que pode causar graves acidentes para os pescadores que estiverem triando a fauna coletada pelas redes de arrasto (Haddad Jr. 2000, 2008). Este apêndice é o segundo par de maxilípodos, modificados em garras raptoriais, adaptação esta que os torna competidores e predadores muito eficientes (Ahyong & Jarman 2009). As garras raptoriais são utilizadas durante combates intra e interespecíficos, na obtenção de fêmea para a cópula, na manutenção e aquisição de tocas ou defesa (Caldwell & Dingle, 1975).

Estas garras contém um mecanismo elástico que é a fonte da força característica do camarão louva-a-deus, podendo variar em duas formas principais de acordo com o dáctilo (porção terminal do apêndice raptorial) (Fig. 2): “perfuradores” com dáctilos espinhosos ou “esmagadores” tendo a forma de martelo na base do dáctilo (Caldwell & Dingle 1975; Ahyong & Harling 2000; Ahyong 2001). Estas formas da garra raptorial geralmente estão relacionadas com o comportamento de predação do animal: “perfuradoras” usam tipicamente uma estratégia de predação passiva (“senta-e-espera”) (deVries *et al*. 2012) ou ativa de alcançar e reter a presa (Wal, Van Der *et al.* 2017), enquanto as “esmagadoras” estão associadas à predação de presas com conchas ou qualquer envoltório externo bem espessos (moluscos e crustáceos) e também à captura de peixes (Patek & Caldwell 2005; Weaver *et al*. 2012; de Vries *et al*. 2016).

Figura 2: Garra Raptorial *Squilla brasiliensis* (Referência métrica: 10 mm). Acervo Pessoal.

Os Stomatopoda possuem uma carapaça larga e o seu corpo é alongado e dorsalmente achatado. O segmento torácico possui os 5 primeiros pares de apêndices denominados maxilípodos, sendo estes subquelados (Caldwell & Dingle, 1975). Já os 3 últimos pares de pernas torácicas são os pereiópodos, que são birremes e vibratórios (Caldwell & Dingle, 1975). Esta ordem possui uma estrutura chamada de télson, usada para receber golpes de adversários, em disputas territoriais ou por fêmeas (Green & Patek 2015), também funcionando como um emissor de sinais de luz circular polarizada, sendo que, esta emissão captada unicamente pelos indivíduos desta ordem, pode ser útil para evitar tocas que já estejam ocupadas, logo, um maior télson refletiria em uma maior sinalização, diminuindo as chances de encontros agonísticos (Gagnon *et al*. 2015). O urópodo, junto com o télson, é utilizado como um aparato de investida em relações agonísticas, visto que a estrutura possui espinhos proeminentes (Caldwell, 1975).

Os sexos entre as espécies são facilmente distinguíveis, pois os machos possuem um par de gonópodios longos e finos, localizados na base do terceiro par de pereiópodos enquanto os gonóporos femininos se encontram entre os primeiros pereiópodos. Na maioria das espécies o dimorfismo sexual está presente, sendo evidente para a garra raptorial, que em machos é mais desenvolvida e a largura do télson é maior (Ahyong & Lowry 2001).

Divididos entre 3 subordens, Palaeostomatopodea (Devoniano – Carbonífero), Archaestomatopodea (Carbonífero), e Unipeltata (Jurássico – Recente), os Stomatopoda possuem apenas uma ordem vivente. Unipeltata está dividida em 7 superfamílias, 17 famílias e mais de 100 gêneros, sendo que a grande maioria pertencente às superfamílias Gonodactyloidea, Lysiosquilloidea e Squilloidea (Ahyong & Harling 2000; Ahyoung & Jarman 2009). Estas superfamílias se distinguem morfologicamente, podendo variar entre o formato do apêndice raptorial, o sistema ocular, ornamentação do télson e o padrão de cores (Ahyong & Harling 2000; Ahyong 2005); e ecologicamente quanto ao habitat residente, distinguindo o tipo do substrato, disponibilidade de luz e abrigo (Ahyong 1997; Porter *et al*. 2010).

Na fauna brasileira são registradas seis superfamílias de Stomatopoda: Lysiosquilloidea, Gonodactyloidea, Eurysquilloidea, Squilloidea, Bathysquiloidea e Parasquilloidea (Lucatelli, 2012). Segundo Lucatelli (2012), existem registros de 42 espécies distribuídas amplamente por todo litoral brasileiro, desde o Amapá (latitude 03° N) até o Rio Grande do Sul (latitude 30°S). Porém, um estudo recente de Amaral (2020), confirma a existência de 43 espécies distribuídas no território brasileiro, sendo que dentre estas espécies 34 possuem garras do tipo perfuradoras, 8 do tipo esmagadores e uma do tipo intermediária.

A superfamília com a maior diversidade brasileira é a Squilloidea, sendo representada por apenas uma família, Squillidae, contendo o maior número de espécies descritas no mundo, possuindo mais de 180 divididas em 46 gêneros (Ahyong 2001). Já na fauna brasileira foram registradas 16 espécies, distribuídas em apenas 6 gêneros: *Alima, Cloridopsis, Gibbesia, Meiosquilla, Rissoides* e *Squilla* (Amaral 2020). Todas as espécies desta família possuem a característica de “perfuradores”

(Caldwell & Dingle 1976). Os Squilloidea são diferenciados dos demais Stomatopoda por possuírem: télson com quatro ou mais dentículos intermédios; o terceiro e o quarto maxilípodo com um própodo ovalado; a garra com uma articulação terminal com 3 espinhos retráteis na parte proximal, com um dáctilo com 4 ou mais espinhos; o télson com uma carena média com mais 4 dentículos, sendo que no protopodito do urópodo possui mais 2 espinhos primários, porém podendo possuir só um; e uma articulação dos segmentos do exopodito sempre de tipo terminal (Salgado-Barragán & Hendrickx, 2010).

No litoral do estado de São Paulo existe a ocorrência de 13 espécies, sendo que 11 delas são perfuradoras, uma esmagadora e uma intermediária (Amaral, 2020). As espécies que possuem registros no litoral de São Paulo são: *Pseudosquilla ciliata* (Fabricius, 1787) *, Lysiosquillina glabriúscula* (Lamarck, 1818)*, Lysiosquilla scabricauda* (Lamarck, 1818)*, Alachosquilla digueti* (Coutière, 1905)*, Bigelowina biminiensis* (Bigelow, 1893)*, Coronis scolopendra* Latreille, 1828*, Alima hildebrandi* (Schmitt, 1940)*, Cloridopsis dúbia* (H. Milne Edwards, 1837)*, Gibbesia neglecta* (Gibbes, 1850)*, Gibbesia prasinolineata* (Dana, 1852)*, Squilla brasiliensis* Calman, 1917*, Neogonodactylus oerstedii* (Hansen, 1895) e *Hemisquilla braziliensis* (Moreira, 1903).

Presente estudo visa identificar os padrões morfométricos nos indivíduos analisado. A relação linear entre duas variáveis diferentes pode ser verificada por meio de estudos alométricos, possibilitando dividir a alometria em três diferentes tipos: a positiva (a variável resposta se desenvolve mais em relação à variável preditora); negativo (a variável de resposta se desenvolve menos do que a variável de previsão); e isométrica (indica que ambas as variáveis se desenvolvem em uma proporção semelhante) (Hartnoll, 1982). A partir da análise do crescimento relativo de uma espécie, é possível determinar através da morfometria linear o tipo de alometria que se estabelece entre as estruturas relacionadas (Huxley, 1950), e os dimorfismos entre tamanho e forma podem culminar em diferentes pressões seletivas (Eberhard, 2008).

Outra análise que esta dissertação também explora é o uso da morfometria geométrica. A partir de arquivos fotográficos das estruturas desejadas dos organismos, esta análise permite verificar, baseada no plano cartesiano, as orientações das coordenadas chamadas de *landmarks*, gerando assim informações geométricas destas estruturas. Com esta verificação é possível avaliar a forma destes animais, ajudando a identificar as distinções e nuanças dentre as estruturas exploradas (Slice, 2007)

A região do litoral norte do estado de São Paulo, Brasil, apresenta um clima subtropical, com um litoral bem recortado. A Serra do Mar nesta região se estende de maneira muito estreita a planície costeira e também muito próxima ao mar. Juntamente com a ocorrência dos espigões, esta topografia possibilitou a formação de inúmeras pequenas praias arenosas em meia-lua, tornando esta região espacialmente diversa e complexa. Esta variedade de ambientes costeiros, acaba por propiciar ótimas condições para que se sustente uma alta diversidade biológica (Amaral & Nallin 2011).

A pesca é muito presente e importante para as regiões do litoral norte do estado de São Paulo, tanto quanto a aspectos econômicos, culturais e turísticos. Portanto, tal atividade tende a impactar muitos

os locais onde ela é realizada, sendo que através de métodos de captura não-seletivos que gera uma exploração de recursos indiscriminada (Saila 1983; Broadhurst & Kennely 1996). Como exemplo, podemos citar a pesca de arrasto que tem como objetivo capturar camarões ou peixes com valor comercial. Mesmo que o esforço pesqueiro seja voltado a uma espécie-alvo (ou mais espécies), a capturas de espécies não desejadas é iminente (Slavin, 1983), denominadas como "*by-catch*" (fauna acompanhante) por Alverson *et al.* (1994). Por falta de interesse econômico e/ou tecnológico, parte deste *by-catch* é devolvido ao mar já mortos, o que se denomina de descarte ou rejeição (Alverson *et al*., 1994; Graça Lopes *et al*. 2002). Sendo assim, este tipo de pesca pode representar um potencial risco para o equilíbrio ambiental (Alverson *et al.,* 1994), inclusive quando é empregada em regiões costeiras ou estuarinas, áreas reconhecidas como berçários para diversas espécies (Lazzari *et al*., 2003; Branco & Fracasso 2004).

Em adição, os crustáceos são frequentemente capturados de tais atividades, seja como espécie-alvo ou como *by-catch*. Tal grupo representa um importante papel ecológico nos oceanos, onde a diversidade de hábitos de vida reflete positivamente no seu papel nas teias alimentares. Diversos estudos buscam quantificar e relatar as espécies de crustáceos *by-catch*, podendo citar os estudos de Cutrim *et al*. (2001); Silva *et al*. (2002a); Serejo *et al*. (2006); Serejo *et al*. (2007); Cintra *et al*. (2017); e Bochini *et al*. (2019). Dentre todos os crustáceos encontrados em tais estudos, pode-se notar a presença dos membros da ordem Stomatopoda.

Desta maneira, considerando que algumas espécies da ordem Stomatopoda fazem parte da fauna acompanhante nas pescas de arrasto e que pouco se conhece sobre esses animais, estudos que tragam mais conhecimento são essenciais para melhor entendimento da biologia do animal. Com isso, este trabalho contou com uma parcela do acervo de coletas realizadas pelo programa BIOTA / FAPESP – Bentos Marinho (Processo no. 1998/07090-3), que se encontravam disponíveis na coleção do setor Zoologia, Instituto de Biociências de Botucatu (UNESP). Com este acervo, pode-se analisar indivíduos da ordem Stomatopoda coletados no litoral norte do estado de São Paulo.

Estudos que visam compreender aspectos morfológicos de espécies de crustáceos, servem de respaldo para estratégias de conservação ambiental e a preservação de tais espécies. Além disso, com resultados obtidos e discussões levantadas, ferramentas que elaboram modificações tecnológicas para que se possam gerar uma BRD ("*Bycatch Reduction Devices*") podem ser incrementadas, cujo o principal objetivo é manter a captura das espécies-alvo, reduzindo a captura e o descarte de fauna acompanhante (Davies *et al*. 2009). Conhecimento da biologia e ecologia das espécies aliado as BRDs possuem um grande potencial para a preservação do ecossistema marítimo.

O trabalho está formatado em dois capítulos. Cada capítulo está em Inglês devido a formatação solicitada pelas revistas: Capítulo I foi de acordo com a formatação da Thalassas e o Capítulo II de acordo com a revista Reproduction Biology.

Objetivo geral

O objetivo da presente dissertação é analisar a morfometria de duas espécies da ordem Stomatopoda. Parte do trabalho tem como objetivo verificar a diferenciação morfométrica (linear e geométrica) entre as espécies *Squilla brasiliensis* e *Gibbesia neglecta,* e outra parte tem como objetivo verificar o dimorfismo sexual morfométrica linear da espécie *S. brasiliensis*.

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Capítulo I: Revealing the allometry of the mantis shrimp *Squilla brasiliensis* (Crustacea: Stomatopoda)

Abstract: Stomatopods are active predators known for using their raptorial claws in agonistic and reproductive behaviour or to deal an extremely fast blow to their prey, throughout the lifespan, starting at the larval stage. The objective of this study was to analyse the allometry of *Squilla brasiliensis* Calman, 1917 collected in the São Paulo state littoral (Brazil), in order to investigate, size class, sex ratio and sexual dimorphism. It was found that the sexes did not differ significantly in the dispersion between size classes, but it can be observed that males had larger sizes. The allometric models showed differences in relation to some structures, like the total length of the raptorial claw, which females obtained a significantly higher value than males. Otherwise, the merus width was much greater in males than in females, which is indicative of the frequency of strikes. These findings can highlight different survival strategies and reproductive strategies, like the attacks by males in agonistic clashes.

Key Words: Active predator, Growth, Morphometry, Raptorial claw

Introduction

The crustacean Stomatopoda is active predator and obligatory carnivore, popularly named in Brazil tamarutaca or siriboia (Caldwell and Dingle 1975; Ahyong and Harling 2000). They can be found mainly in tropical and subtropical regions (Schram et al. 2013), inhabiting burrows and crevices in mid- and infralittoral regions in all types of substrates and sheltering during the day since they are more active at night (Caldwell 1991; Ahyong 2001).

The main feature of this order is the shape of the second pair of maxillipeds which are modified into raptorial claws. These claws contain an elastic mechanism located in the merus region, which is the origin of the characteristic force of the mantis shrimp (Patek et al. 2004; Patek et al. 2007). There are three main dactyl-type claws, each generating distinct predatory behaviours: “spearers”, use a sit-and-wait tactic (deVries et al. 2012) which are an asset in reaching and holding their prey (Van Der et al. 2017); “smashers”, associated with predation of prey with very thick shells or carapace (molluscs and crustaceans) and also with the capture of fish (Patek and Caldwell 2005; Weaver et al. 2012; deVries et al. 2016); and "intermediates" (most represented by *Hemisquilla spp*.), which use the thin appendage to dislodge hard-shelled prey.

These claws are the key adaptation that makes them predators and specialized competitors during intra and interspecific agonistic encounters, mating behaviour, maintenance and acquisition of burrows or defence behaviour for males and females (Caldwell and Dingle 1975; Ahyong and Jarman 2009). Besides that, sexual dimorphism is common in crustaceans, with different adaptations between males and females to achieve better fitness, such as the overdevelopment of organs or structures related to combat or display in males. To evaluate these parameters, the study of sexual dimorphism proved to be efficient in identifying such adaptations in different species of the order Stomatopoda, as in *Harpiosquilla raphidea* (Fabricius 1798) (Antony et al. 2014), and in Rissoides pallidus (Giesbrecht 1910) (Mori et al. 2009), where the distinct development between males and females was identified, showing that females acquire more developed raptorial claws.

One of the methods that aims to identify sexual dimorphism is the use of allometries studies, which deal with the relationship between two distinct variables, which may be categorized as ontogenetic (growth of structure changes relative to the total size of individuals at different stages of development, i.e., young and adult), statistic (growth of structure changes relative to the size of individuals of the same species at the same stage of development) and phylogenetic (growth of structure changes relative to the size of individuals of different species at the same stage of development) (Shingleton 2010). Allometry can be divided into three different types: negative (response variable develops at a lower intensity than the predictor variable); positive (response variable develops at a higher intensity than the predictor variable); and isometric (both variables develop in a similar proportion) (Hartnoll 1982). From analysis of the relative growth, it is possible to determine the type of allometry that is established between related structures (Huxley 1950), and the dimorphism between size and shape may culminate in different selective pressures between males and females (Eberhard 2008). Such analysis can also bring new knowledge about the species, besides contributing to the construction of an appropriate theoretical foundation of the Brazilian fauna, which can bring useful information to

understand the habit occupation, feeding and ecology of species, providing theoretical references for species management.

Studies addressing the population characteristics of the mantis shrimp are scarce, mainly of species sampled on the Brazilian coast, such as *Squilla brasiliensis* Calman, 1917. This species is characterized by having a "spearer" claw type and a distribution from Cabo Frio, Rio de Janeiro, Brazil, to Uruguay, being found at a depth of 19 – 285 meters (Manning 1969; Tommasi and Bordin 1987). The few studies mention its occurrence in the trawl-accompanying fauna (Severino-Rodrigues 2007) and indicate that it is part of the diet of the shark *Mustelus schmitti* Springer, 1939 in the coastal region of Rio Grande do Sul, Brazil (Capitoli 1995). Considering that such a species is not the target of the Brazilian fishing activity, which characterizes it as by-catch (incidental capture of non-target species), it is extremely important to acquire knowledge about it. It is known that the collection of species by-catch can immensely affect biodiversity and also disturb the marine ecosystem by discarding these species on the surface of the water, which ends up disrupting biomass in water levels (Hill and Wassenberg 1990).

Thus, the objective of this study is to analyse the allometry and morphometric maturity through relative growth of morphological characteristics of *S. brasiliensis* collected from the coast of São Paulo state, Brazil. Therefore, we tested the hypotheses: male and female have different growth, as well as a different maturity size; and males have the raptorial claw bigger than the female because the agonistic behaviour. This study of *S. brasiliensis* in Brazil bring information on intersexual variations of morphology and body design as a tool to determine how these individuals develop allometrically.

Materials and Methods

The individuals studied were collected in 2001 by a commercial bottom-trawl boat along the coast of the state of São Paulo, Brazil: Ubatuba (23°30'S/44°54'W), Caraguatatuba (23°44'S/45°04'W) and São Sebastião (23°50'S/45°20'W) littorals (Fig. 1). Samples was collected in 90 sites of different depths, covering around 18,000 m² of sampled area. At the end of each trawl, the specimens were sorted on deck, properly separated into plastic bags, packaged in cool boxes with ice and then identified according to Manning (1969).

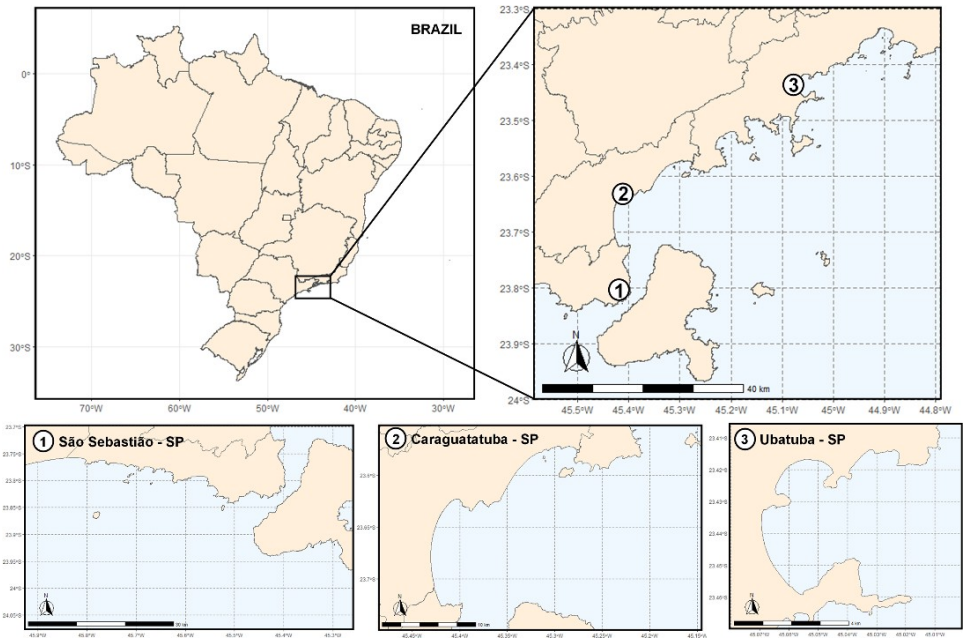

Figure 1. Sampling areas in the coast of São Paulo state, Brazil: 1) São Sebastião; 2) Caraguatatuba; 3) Ubatuba.

Individuals were measured using a digital caliper (0.01 mm), and the structures chosen for growth characterization in accordance with Manning (1969): total length (TL) from the end of the rostrum to the final portion of the telson; abdomen width (AW) in third abdominal segment; telson length (TeL); telson width (TW); merus width (MW); propodus width (PW); propodus length (PL); dactyl length (DL); and raptorial claw length (RCL) (Figs. 2a, b).

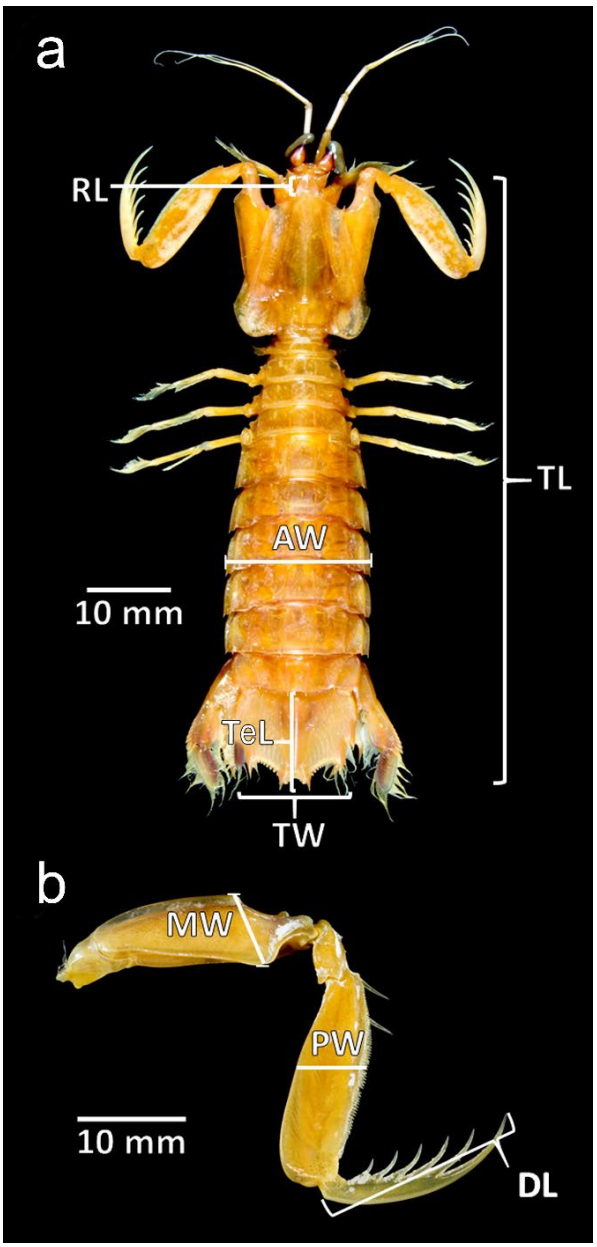

Figure 2. *Squilla brasiliensis* Calman, 1917. Main measures used for this study: a) RL - rostrum length; TL - total length; AW - abdomen width; TeL - telso length; TW - telso width. b) Raptorial claw with the measures taken: MW - merus width; PW - propodus width; DL - dactyl length.

From the size of the individuals, a verification of the size classes between the sexes was carried out, where each class has an interval of 9.9 cm of total length. From this separation, the sex ratio among each size class was evaluated, in order to determine the proportions of these animals in the environment in which they live considering their size. Subsequently, the total number of males and females collected was analyzed so that the general sex ratio is ascertained, based on the expected value and the actual collected. For these analyzes, a chi-square (χ^2) test with a significance level of 5% was be performed.

An estimated major axis regression (MA) was performed, also called "model II regression", for the analysis of relative growth. This model estimates the "line of best fit" for relationships between two variables and was found to be much more satisfactory in allometric contexts than linear regression analysis (Warton *et al*. 2006). The data were logarithmized to better express linear relations between

variables (Hartnoll 1969). Through the logarithmized allometric relationship (Harvey and Pagel 1991), expressed by log (y) = log (γ) + β.log (x), MA regression tests the allometry and verifies the differentiation between the intercept and angulation between groups (all males and all females/young and adult for each sex) (Warton and Weber 2002), considering a significance interval of 5%. A T-test (α=0.05) was done to verify the hypothesis of the existence of heterochely (the difference between cheliped sizes), between the highest and lowest length of the raptorial claws of each individual, for both males and females. To increase the reliability of the results, the values obtained through the total length were subjected to an empirical bootstrap analysis (Efron 1979) to define the 80% confidence interval (bootstrap interactions: 100 000). All analyses were performed by R software (R Development Core Team, 2012, version 3.5.1), using the "readxl", "stats" and "smatr" packages.

Results

A total of 75 individuals (37 males, 38 females) were analyzed, that was separated in 7 size class (Fig. 3). The total length mean of the specimens was 73.94 mm ± 16.61 mm (minimum 43.74 mm and maximum 104.3 mm) for males and 72 mm ± 13.12 mm (minimum 48.5 mm and maximum 101 mm) for females. Sex ratio for total males and females did not indicate a significant difference (χ^2; $p > 0.5$), presenting a ratio of 1: 1.027 (males: females). Also, in the 7 different size classes have not significant difference between the sexes, except in the last size class (107.95 mm, range of 103.1 mm and 113 mm), where 100 % of males was collected (χ^2, $p = 0.157$) (Fig. 3).

The average length for males and females was within the 80% confidence interval. In analyzes of heterochely, the results did not indicate significant differences between the left and right sides of the raptorial claws, both for male (T test, $t = 0.203$, $p = 0.839$) and females (T test, $t = -0.054$, $p = 0.956$).

Through morphometric analysis, a relationship of growth was found between the total length (predictor variable) and the other measured structures (response variables) ($r^2 > 0.75$). Allometry of *S. brasiliensis* showed differences between sexes for different structures (Table 1). For males, the structures that presented positive allometry were TL, ML and PL. For females the structures that presented positive allometry were AL, TL, TW, PL, DL and RCL, meaning that these structures grow more than the predict variable (TL). Furthermore, other structures presented isometry (Table 1). Comparative analysis between the sexes indicated that TeL, along with the raptorial claw variables RCL, ML (but not PL) have significant differences ($P<0.05$, Table 1), as shown in Figure 4, i.e., this structure is different between the sexes.

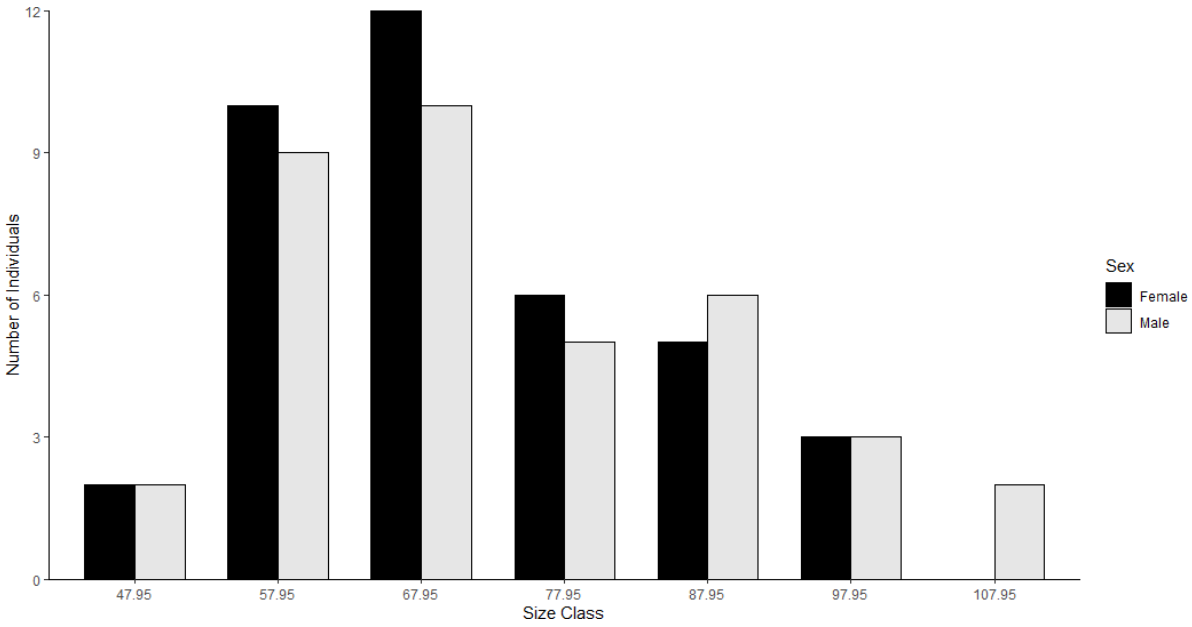

Figure 3. Distribution of the sex ratio between the size classes of *Squilla brasiliensis* Calman, 1917.

Table 1. *Squilla brasiliensis* Calman, 1917. Analysis of relative growth for males (♂) and females (♀). TL, total length; AW, abdomen width; TeL, Telson length; TeW, Telson width; RL, Rostrum length; MW, Merus width, PW, Propodus width; PL, propodus length; DL, Dactyl length; RCL, Raptorial claw length; Category, Juvenile and Adults groups; a, linear coefficient; b, angular coefficient; r^2, coefficient of determination; p (slope), differences between slopes ($\alpha \leq 5\%$); Allometry: isometry (0), negative (-) and positive (+) allometry, among groups. Analyzes of *a* and *b* between the sexes; Factor, (*a*) elevation and (*b*) slope; p, significant for $\alpha \leq 5\%$; sig, Significant (*).

			Regression: log(y)=log(γ)+β.log(x),								
Relation	Sex	N	*a*	*b*	r^2	p (slope)	Allometry	Among groups	Factor	p	sig
Total Length *vs* Abdomen Width	♀	38	-0.870	1.108	0.93	0.019	+	Female *vs* Male	*b*	0.120	
	♂	37	-0.704	1.022	0.96	0.467	0	Female *vs* Male	*a*	0.152	
Total Length *vs* Telson Length	♀	38	-1.089	1.187	0.94	0.00	+	Female *vs* Male	*b*	0.035	*
	♂	37	-0.872	1.068	0.97	0.02	+	Female *vs* Male	*a*	0.543	
Total Length *vs* Telson Width	♀	38	-0.962	1.131	0.97	0.00	+	Female *vs* Male	*b*	0.253	
	♂	37	-0.852	1.072	0.95	0.075	0	Female *vs* Male	*a*	0.799	
Total Length vs Merus Width	♀	24	-1.405	1.056	0.94	0.29	0	Female *vs* Male	*b*	0.018	*
	♂	28	-1.687	1.251	0.94	0.00	+	Female *vs* Male	*a*	0.00	*
Total Length *vs* Propodus Width	♀	38	-1.312	1.05	0.94	0.22	0	Female *vs* Male	*b*	0.632	
	♂	37	-1.35	1.076	0.96	0.03	+	Female *vs* Male	*a*	0.017	*
Total Length *vs* Propodus Length	♀	38	-0.833	1.067	0.97	0.025	+	Female *vs* Male	*b*	0.074	
	♂	37	-0.703	0.996	0.97	0.89	0	Female *vs* Male	*a*	0.929	
Total Length *vs* Dactyl Length	♀	38	-0.961	1.12	0.96	0.00	+	Female *vs* Male	*b*	0.026	*
	♂	37	-0.71	0.979	0.92	0.68	0	Female *vs* Male	*a*	0.116	
Total Length *vs* Raptorial Claw Length	♀	38	-0.589	1.09	0.97	0.005	+	Female *vs* Male	*b*	0.012	*
	♂	37	-0.387	0.978	0.97	0.477	0	Female *vs* Male	*a*	0.274	

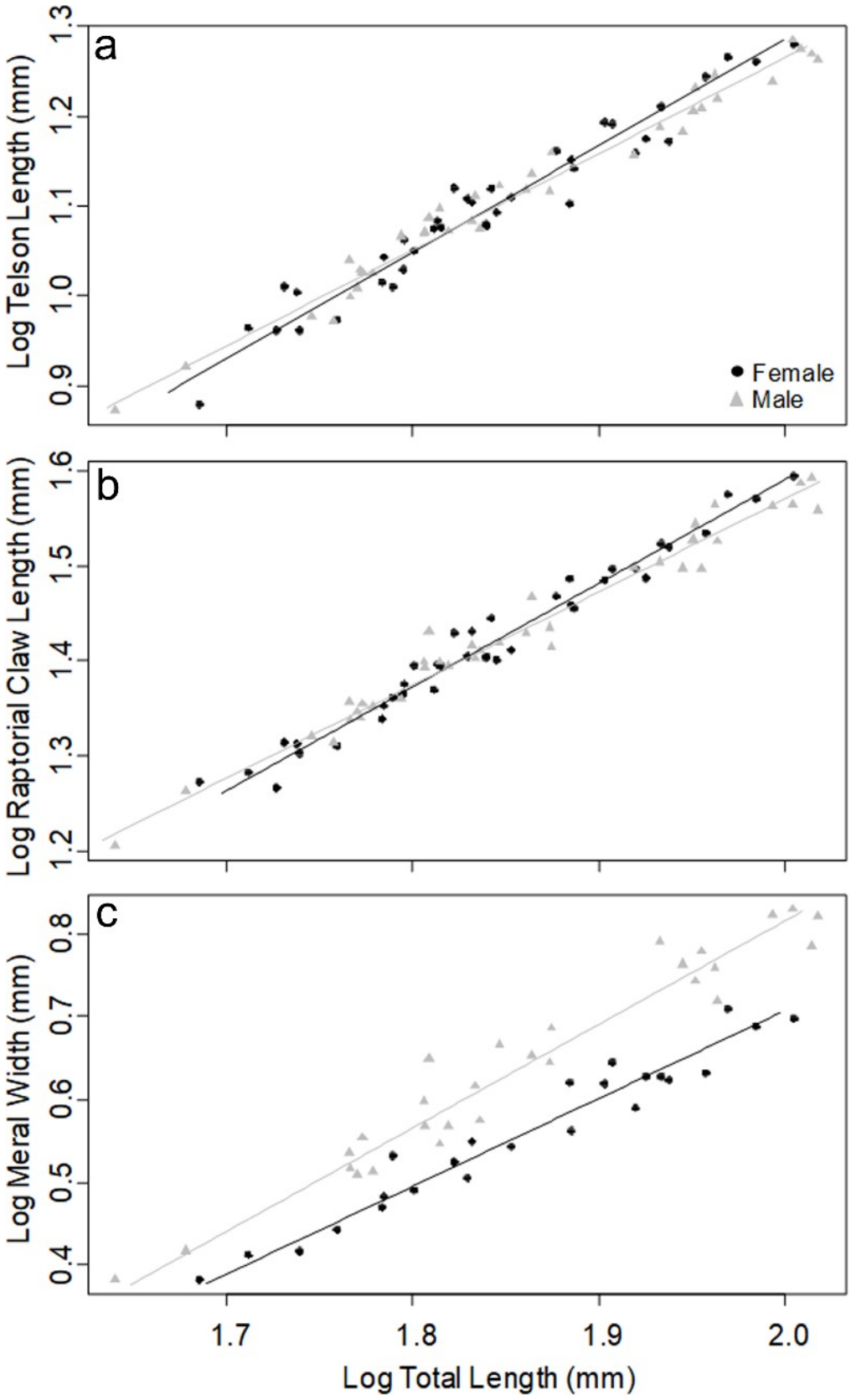

Figure 4. *Squilla brasiliensis* Calman, 1917. Comparison between males and females for the relationship between the total length and the structures: a) telson length, b) raptorial claw length and c) merus width.

Discussion

This study revealed important information about *Squilla brasiliensis*, being one of them the sexual frequency of this species no differs between the sexes, the higher abundance of females was in size class small than males. This may be due to the fact that the growth of females is delayed after sexual maturity, a phase in which there is a great directing of energy for reproduction and not for growth, whereas for males there is the possibility of having superior growth (Hartnoll, 1985).

The present study shows that the relative growth of *S. brasiliensis* females in relation to the width of the abdomen is allometric positive when compared with males and isometric in the adult phase, similar to that reported for Antony *et al*. (2014), a positive allometry related to abdomen width for *H. raphidea*, attributed to the maturation of these individuals (Kodama 2004). Females of species such as *H. raphidea* and *Oratosquilla oratoria* (De Haan, 1844) invest in reproduction with the allometric development of abdomen width factor that directly determining the number of eggs produced (Hartnoll 1985; Kodama *et al.* 2009). Such evidence in these studies helps to identify that such patterns occur frequently in females of the order Stomatopoda, since females *S. brasiliensis* presented a distinct morphometry for the abdomen region when compared to males. There is a greater requirement for energy in females, given that growth and reproduction tend to "compete" for energy in crustaceans (Hartnoll 1985).

The larger claw size of the females of *S. brasiliensis* when compared to the males in the present study, possibly is associated with a reproductive strategy. According to Thomas (2002), females in this group tend to have this characteristic, especially during reproductive periods, in order to obtain better foraging success, as a result of greater reproductive fitness due to greater energy demand for reproduction and childcare. This result was also evidenced for *Squilla mantis* (Linnaeus 1758) (Piccinetti and Piccinetti 1970) and *H. raphidea* (Antony *et al*. 2014), which females also have larger raptorial claws than males.

Females' length in our results showed positive allometric growth in relation to telson development (width and length), with females having greater telson than males, possibly indicating that this structure was used protection, related to offspring protection, as the telson for the spearers type is often used to block their burrows, protecting their entry against any kind of threat (Caldwell and Dingle 1975). Additionally, stomatopod's female incubates their embryos within the tunnels, avoiding predators and possible injuries (Hamano and Matsuura 1984). The telson is also a signal emitter of circularly polarized light, with is extremely rare underwater, and this emission is only discriminated by the eyes of stomatopods members, being useful in avoiding burrows that are already occupied, since larger telson would reflect in greater signalling, reducing the chances of agonists encounters (Gagnon *et al.* 2015).

As for males, there was a positive allometric development of the propodus and merus width compared to females that showed isometry in our results. The merus contains the elastic system known as V-meral, responsible for the impact of the claw due to relaxation of the muscles located in this region. This system releases the stored elastic energy and has great importance in the claw force-speed trade-off, improving the frequency of attacks, especially in the spearers (Blanco and Patek 2014). The potential

energy for the spearer group is not fully utilized in foraging, indicating that investment in merus robustness may be mainly related to agonistic relationships (deVries *et al*. 2012). These distinction between sexes may be related to the fact that males have more frequent agonistic relationships than females, leading to a greater need for robustness of the merus and the propodus (Ahyong and Jarman 2009), influencing the intraspecific selection of the species.

The analysis of the results obtained through the relative growth of *S. brasiliensis* indicated different patterns for males and females, which according to Fairbairn (1997) this can evidence different strategies to achieve high fitness, such as parental investment or even positive allometry related to the growth of associated structures with agonistic combat between males. Given this, it can also be observed that studying the allometric growth of such structures made it possible to observe the differences between the sex of *S. brasiliensis*, that generate different behaviour responses between the sex, which can be used not only to be incorporated in the information about the Brazilian marine fauna trying understand more about reproduction, behaviour and also the involvement of these specie in the trophic web being a predator, but also in the general knowledge about this magnificent order of crustaceans.

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Data availability

All the data set used in this work is available in: Melo dos Santos, Pedro (2021), “Morphometric data of *Squilla brasiliensis* Calman, 1917”, Mendeley Data, V1, doi: 10.17632/kmdgnv32x6.1

Interest Statement

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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Capítulo II: Allometry and interspecific dimorphism on two species of mantis-shrimp: *Squilla brasiliensis* and *Gibbesia neglecta*

Abstract: Stomatopoda order is comprised of active carnivorous and territorialist crustacean, which have raptorial claws capable of delivering extremely fast blows to their prey. The predation strategy of these animals varies according to the type of the raptorial claw, generating habits of foraging, like sit and wait or active search. In this way, allometric studies bring knowledge to explain morphological variations, even to indicate possible traits that are being selected, however, are less studied about Stomatopoda species. Thus, the aim of this study was to morphologically compare the spearers species *Gibbesia neglecta* and *Squilla brasiliensis*, collected on the coast of the state of São Paulo, in order to investigate the allometry, dimorphism and the shape difference between them. Tested models showed that the species have a distinct development in relation to all structures analysed (MA test, $P < 0.05$), as in the raptorial claw length relation, where *G. neglecta* presented a positive allometry and *S. brasiliensis* an isometry, however even with this allometric difference, *S. brasiliensis* has a larger claw pattern. It is noteworthy that mere width showed similar allometric patterns for both species, that is, positive allometry. *Gibbesia neglecta* showed nevertheless a greater mere width, even having a relatively smaller claw than *S. brasiliensis*. Considering that greater lengths of the raptorial claw reflect an increased ability to capture prey, and the morphology of the merus is closely related to the efficiency of the raptorial claw, that is, the speed and frequency of attacks, it can be inferred that such differences between the claws of *S. brasiliensis* and *G. neglecta* indicate different prey capture strategies.

Key Words: Foraging**,** Morphometry, Prey capture, Raptorial claw, Stomatopoda

Introduction

One of the main characteristics of the Stomatopoda order is the raptorial claws, a modification of the second pair of maxillipods that makes them predators and specialized competitors (Ahyong & Jarman, 2009) during intra and interspecific interactions. Popularly known as mantis shrimps, tamarutaca or siriboia (Amaral *et al.*, 2021), these territorial benthic marine crustaceans (Caldwell & Dingle, 1975; Ahyong & Harling, 2000; Amaral *et al.,* 2021) can deal a massive smash on their pray, and moreover, they use this structure also in the dispute to obtain females, also in the maintenance and acquisition of burrows or defense (Caldwell & Dingle, 1975).

The raptorial claws contain an elastic mechanism in the mere region, which is the source of the strength of the mantis shrimp (Patek *et al.*, 2004; Patek *et al.*, 2007). There are three main types of claw related to the type of dactyl (terminal region of the claw), what generating distinct predation behaviours: "smashers" associated with the predation of the prey that have thick shells or carapace (Patek & Caldwell, 2005; Weaver *et al.*, 2012; deVries *et al.*, 2016); "spearers" which can be passive predators ("sit-and-wait") (deVries *et al.*, 2012) or can be active in a behavior in which the claw is used to reach and retain prey (Wal, Van Der *et al.*, 2017); and "undifferentiated", who use their pointed dactyl to remove their prey from their shells (Patek *et al.*, 2012).

The present study will focus on the species *Squilla brasiliensis* Calman, 1917 and *Gibbesia neglecta* (Gibbes, 1850), being both characterized as spearer, according to its claw morphology. Both species are sympatric in southeastern Brazilian coast (Lucatelli et al. 2012). There are records that *S. brasiliensis* is distributed from the region of Espírito Santo, Brazil, to northeast of Argentina, being found at a depth of 19 to 285 meters, preferably between 100 and 150 meters (Manning, 1969; Tommasi & Bordin, 1987). The species *G. neglecta* has records from the South Carolina, USA, to Rio Grande do Sul, Brazil, found at a depth of 15 to 540 meters (Severino-Rodrigues, 2007). Reports of occurrence have been published for both species, also, a study which cites *S. brasiliensis* as by-catch to the commercial shrimp (Severino-Rodrigues, 2007) and part of the diet of the shark *Mustelus schmitti* Springer, 1939 (Capitoli *et al.*, 1995). But the studies about morphological features of these species are scarce, only *S. brasiliensis* has information about its biology (Melo dos Santos *et al*., In press), however *G. neglecta* does not have records of studies involving any characteristics.

In order to improve the knowledge of both species the present study aims to characterize the morphometric growth of *G. neglecta* and *S. brasiliensis* through linear measures of different body parties and geometric morphometric tools in order to assess their morphologic shape differences in claw and telson of these sympatric species and be able to evidence their possible difference in energy expenditure and biology features. Knowledge about the morphology with different tools would enable us to better understand these species and preserve their populations, since this species has suffered by the indirect exploitation as a shrimp fishing in São Paulo littoral regions.

Materials and Methods

Biological sampling

The individuals studied were sampled with an artisanal fishing boat equipped with “double-rig” nets along the coast of the state of São Paulo, Brazil, in the cities of: 1) São Sebastião (23 ° 50'S / 45 ° 20'W), 2) Ubatuba (23 ° 30'S / 44 ° 54'W) and 3) Caraguatatuba (23 ° 44'S / 45 ° 04'W) and, as shown in Figure 1. The specimens were properly separated into plastic bags, packaged in cool boxes with ice and then identified according to Manning (1969) in the laboratory.

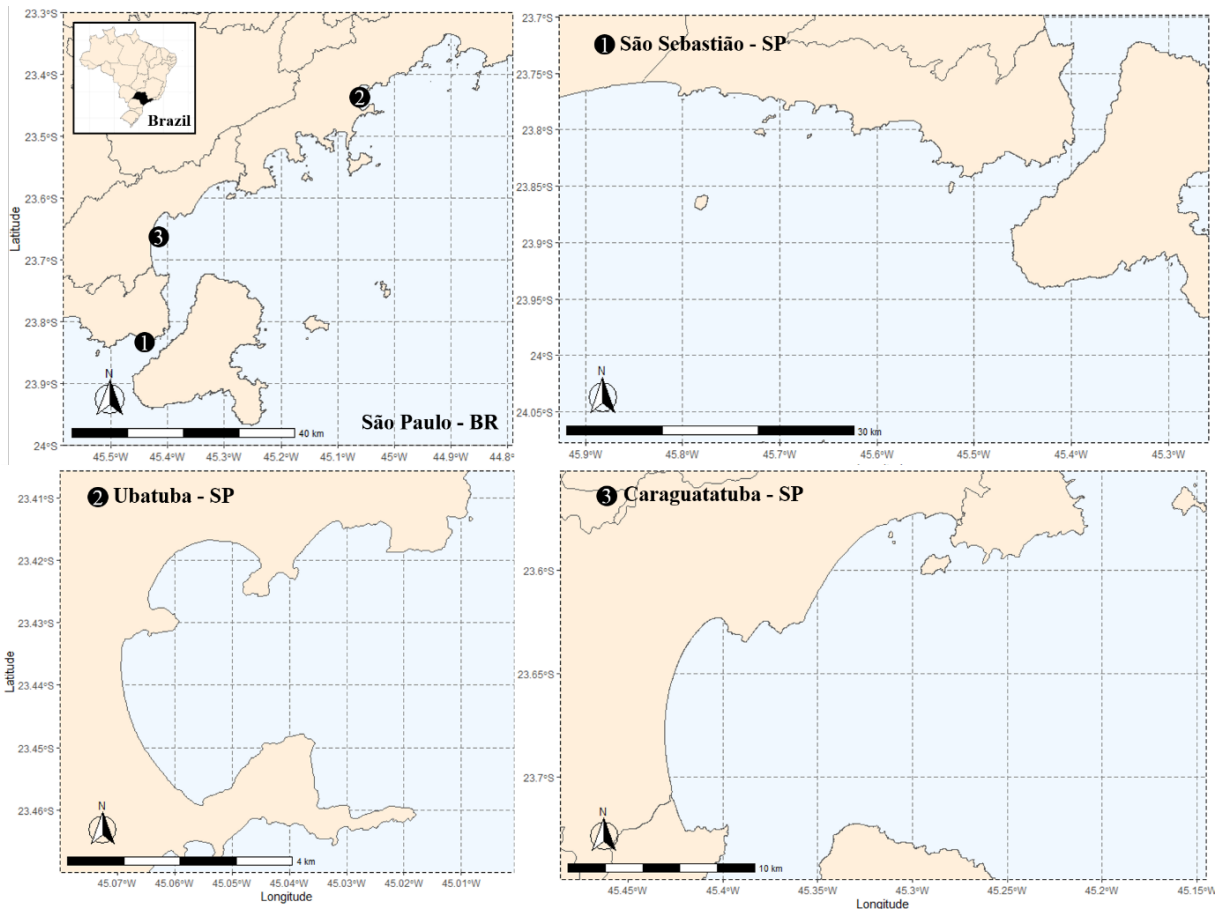

Figure 1: Sampling areas in the coast of São Paulo state, Brazil: 1) São Sebastião; 2) Ubatuba; 3) Caraguatatuba.

The individuals were measured using a digital caliper (0.01mm), with the structures chosen to characterize the growth according to Manning (1969): Total Length (TL), from the end of the rostrum to the final portion of the telson; Carapace Length (CL), from the end of the rostrum to the final portion of the carapace; Rostrum Length (RL); Abdomen Width (AW), third abdominal segment; Telson Width (TeW); Right merus width (MW); right propodus width (PW); right propodus length (PL); right dactyl length (DL), right raptorial claw length (RCL) and left raptorial claw length (LRCL) (Fig. 2a, b).

Figure 2: Measured morphological structures of both species of Stomatopoda ([a] *Gibbesia neglecta*, [b] *G. neglecta* raptorial claw, [c] *Squilla brasiliensis* and [d] *S. brasiliensis* raptorial claw), highlighting of the raptorial claw with the measured structures. TL, total length; AW, abdomen length; TeL, telson length; TW, telson width; MW, meral width; PW, propodus width; DL, dactyl length. Scale = 10 mm.

Allometry

The analysis of relative growth, an estimated major axis regression (MA) was performed, also called "model II regression". Warton *et al.* (2006) study show that the linear regression analysis is appropriate for prediction of points, but when it comes to verifying the slope of lines, the MA model proved to be much more satisfactory for estimating the "line of best fit" for the relationships. As proposed by Hartnoll (1969), the data were log converted to better express linear relations between variables. Allometric relationship (Harvey and Pagel, 1991), expressed by $\log(y) = \log(\gamma) + \beta.\log(x)$, MA regression tests the allometry and verifies the differentiation between the intercept and angulation

between groups (Warton & Weber, 2002), considering a significance interval of 5%, equivalent of analysis of covariance (Sokal & Rohlf 1995). For these analyzes, the species were compared in a non-discriminatory way as regards the sexes, since the low sample number of the species *G. neglecta* made this separation not recommended.

The verification of heterochely (the difference between cheliped sizes) or homochely (no difference between cheliped sizes) was tested with a T-test (α=0.05) between the highest and lowest length of the raptorial claws of each individual, for both species, separately. To improve the reliability of the results, the values obtained through the total length were subjected to an empirical bootstrap analysis (Efron, 1979) to define the 80% confidence interval (bootstrap interactions: 100 000). All analyses were performed by R software (R Development Core Team, 2020 version 3.5.1), using the "stats" (R-Core) and "smatr" (Warton *et al.,* 2012) packages.

Geometric Morphometrics

Individuals were photographed in two dimensions using a NIKON Coolpix P100 camera. For this analysis, 40 individuals of each species were used, 20 males and 20 females, totaling 80 individuals, and the structures photographed were the telson and the raptorial claw. With the confirmation of homochely, only the claw on the right side was used in the analysis.

Using the softwares tpsDig 2.31 and tpsUtil 1.8 (Rohlf 2005a), 18 landmarks were marked on the telson and the raptorial claw, because the articulation of the segments was variable, the points were landmark and semi-landmarks were marked separately for each segment, being in the merus 5 landmarks and 30 semi-landmarks, in propodus 4 landmarks and 30 semi-landmarks and in dactyl 13 landmarks and 13 semi-landmarks (Figure 3). The points marked in the dactyl and propodus were an adaptation of the points used by Anderson (2016).

The coordinates of the points were subjected to an analysis of Procrustes superposition (Dryden & Mardya, 1998) by the MorphoJ 1.07ª software (Klingenberg, 2011). Subsequently, still using the MorphoJ software, an analysis of canonical variables (CVA) and discriminant function analysis (DFA) was performed with 10.000 permutations between the groups: *S. brasiliensis* ♀, *S. brasiliensis* ♂, *G. neglecta* ♀ and *G. neglecta* ♂. This final analysis resulted in the Procrustes distance values and the T-square (equivalent to the Mahalanobis distance test.). The sexes were discriminated in these analyzes since, despite the low sample size, the verification of the geometric morphometry supports such analyses. The graphics with the variations of the forms and the values of the canonical variation were generated by the software MorphoJ 1.07ª and formatted through Adobe Photoshop 22.2.0.

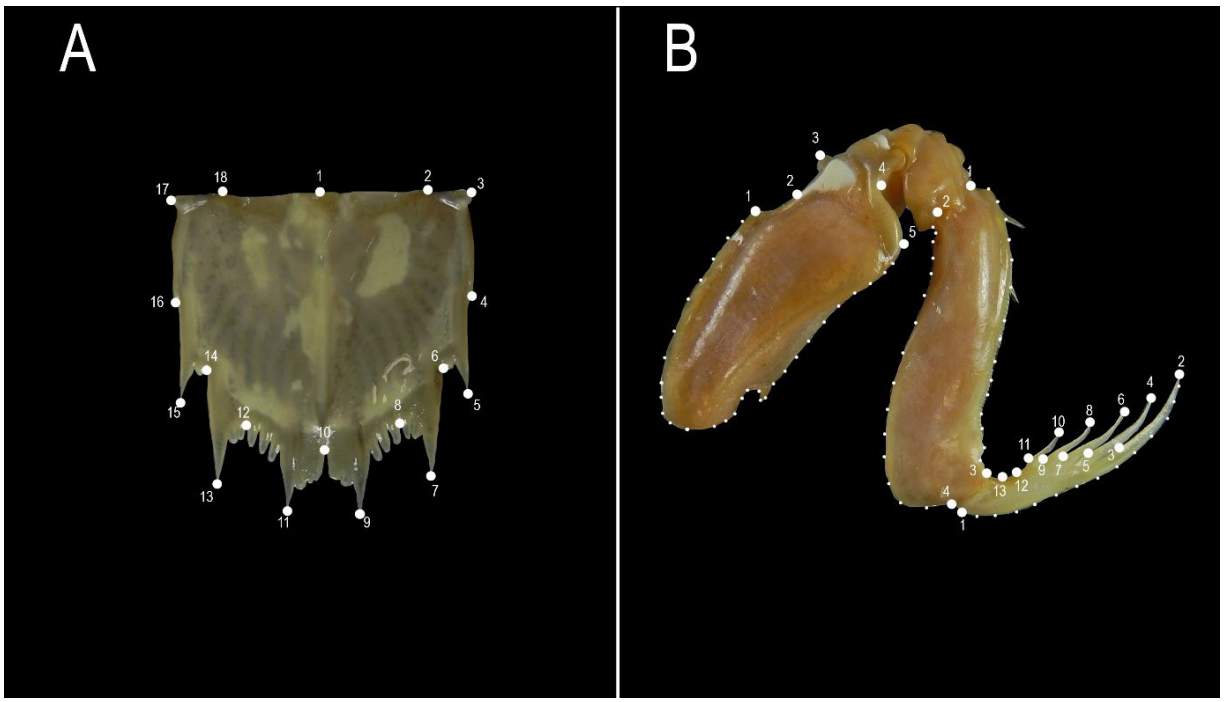

Figure 3: Structures used in geometric analyses with landmark (large dots) and semi-landmark (small dots). (A) Position of the morphological landmarks on the telso; (B) Raptorial claw, being that the three segments of the raptorial claw were analyzed separately.

Results

A total of 123 individuals were collected in the three sites, 75 of *S. brasiliensis* (37 males and 38 females) and 48 of *G. neglecta* (27 males and 21 females). The mean total length for *S. brasiliensis* was 72.23 ± 14.84 mm (minimum of 43.74 and a maximum of 104.3 mm) and for *G. neglecta* the average of the total length was 70.26 ± 10.45 mm (minimum of 53.24 mm and a maximum of 97.45 mm).The empirical analysis of bootstrap verified that the averages of the total length for both species are within the 80% confidence interval showed and for *S. brasiliensis* the range is between 68.65 to 72.91 mm and for *G. neglecta* the mean interval is between 67.68 to 71.42 mm.

Analysis of the raptorial appendages detected homochely between the right and the left for *S. brasiliensis* males (T test, t = 0.203, p = 0.839) and females (T test, t = -0.054, p = 0.956) and for *G. neglecta* males (T test, t = 0.040, p = 0.968) and females (T test, t = 0.093, p = 0.926).

From the MA analyses, satisfactory determination coefficient values were found between the total length and the other structures measured for both species (MA test, $R^2 > 0.68$), thus enabling the analysis of the species without considering the sexes. Besides that, all the structures had a distinct growth (MA test, $P < 0.05$) (Table 1). The measurement of the dimensions of each structure compared between

the species showed that some structures that presented a difference in their growth pattern also obtained a difference in sizes, as shown in Figure 4.

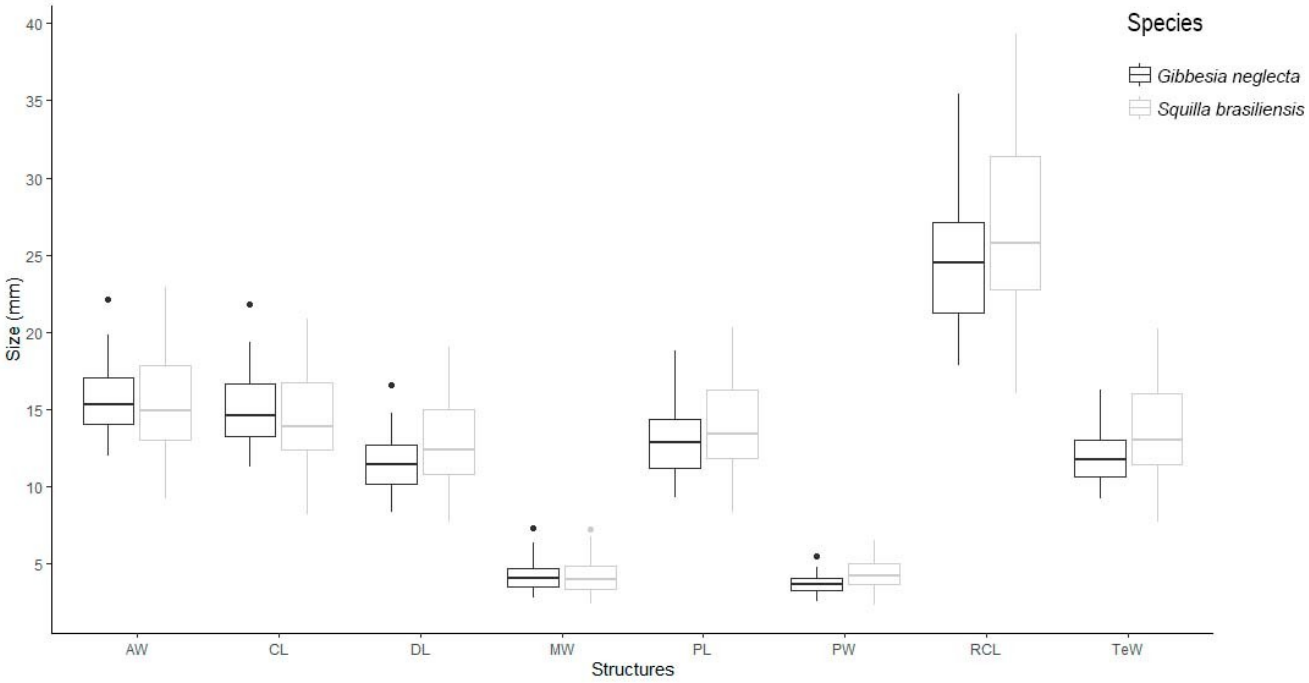

Figure 4: Box plot view of the sizes for each structure between *Squilla brasiliensis* and *Gibbesia neglecta* AW, abdomen length; CL, carapace length; TeW, telson width; MW, meral width; PL, propodus length; PW, propodus width; DL, dactyl length; RCL, raptorial claw length.

Regarding the allometric categorization, a similarity pattern growth occurred for MW (Figure 5), whose allometry was positive, with an allometric coefficient of b = 1.309 for *S. brasiliensis* and b = 1.463 for *G. neglecta*. The species differed allometrically between the other structures, such as the total claw length and its articles (PL, DL and PW), with *S. brasiliensis* showing an isometry and for *G. neglecta* positive allometry for PL, DL and RCL (Figure 6). For PW, positive allometry was observed for *S. brasiliensis* and an isometry for *G. neglecta*. For AW and TeW there was positive allometry for *S. brasiliensis* and for *G. neglecta* were isometric for AW and negative for TeW (Fig. 7). Other structures that did not differentiate allometrically are CL (Fig. 7) and RL, both of which have an isometry for such structures.

Table I. *Squilla brasiliensis* Calman, 1917 and *Gibbesia neglecta* (Gibbes, 1850). Analysis of relative growth for S. brasiliensis and G. neglecta. TL, total length; AW, abdomen width; CC, carapace length; TeW, Telson width; MW, Merus width, PW, Propodus width; PL, propodus length; DL, Dactyl length; RCL, Raptorial claw length; Category, Juvenile and Adults groups; a, linear coefficient; b, angular coefficient; r^2, coefficient of determination; p (slope), differences between slopes ($\alpha \leq 5\%$); Allometry: o, -, +, isometry, negative and positive allometry, respectively Among groups, analyzes of a and b between the sexes; Factor, (a) elevation and (b) slope; p, significant for $\alpha \leq 5\%$; sig, Significant (*).

			Regression: $\log(y)=\log(\gamma)+\beta .\log(x)$,								
Relation	Species	N	*a*	*b*	r^2	p (slope)	Alometry	Interspecific Category	Factor	p	sig
Total Length *vs* Abdomen Width	*S.brasiliensis*	75	-0,782	1,062	0,95	0,020	+	*S* vs *G*	b	0,009	*
	G. neglecta	48	-0,544	0,942	0,93	0,119	0	*S* vs *G*	a	0,00	*
Total Length *vs* Carapace Length	*S.brasiliensis*	75	-0,693	0,998	0,96	0,926	0	*S* vs *G*	b	0,778	
	G. neglecta	48	-0,686	1,008	0,961	0,780	0	*S* vs *G*	a	0,00	*
Total Length *vs* Telson Width	*S.brasiliensis*	75	-0,897	1,096	0,96	0,00	+	*S* vs *G*	b	0.00	*
	G. neglecta	48	-0,653	0,938	0,97	0,01	-	*S* vs *G*	a	0.00	*
Total Length *vs* Meral Width	*S.brasiliensis*	56	-1,831	1,309	0,83	0,00	+	*S* vs *G*	b	0,22	
	G. neglecta	48	-2,086	1,463	0,77	0,00	+	*S* vs *G*	a	0,001	*
Total Length vs Propodus Width	*S.brasiliensis*	75	-1,352	1,074	0,95	0,007	+	*S* vs *G*	b	0,748	
	G. neglecta	48	-1,383	1,057	0,92	0,203	0	*S* vs *G*	a	0.00	*
Total Length vs Propodus Length	*S.brasiliensis*	75	-0,757	1,025	0,97	0,178	0	*S* vs *G*	b	0,026	*
	G. neglecta	48	-0,963	1,122	0,94	0,001	+	*S* vs *G*	a	0.00	*
Total Length vs Dactyl Length	*S.brasiliensis*	75	-0,811	1,036	0,93	0,25	0	*S* vs *G*	b	0,22	
	G. neglecta	48	-0,968	1,098	0,94	0,01	+	*S* vs *G*	a	0.00	*
Total Length vs Raptorial Claw Length	*S.brasiliensis*	75	-0,468	1,023	0,96	0,281	0	*S* vs *G*	b	0,051	*
	G. neglecta	48	-0,652	1,103	0,95	0,002	+	*S* vs *G*	a	0.00	*

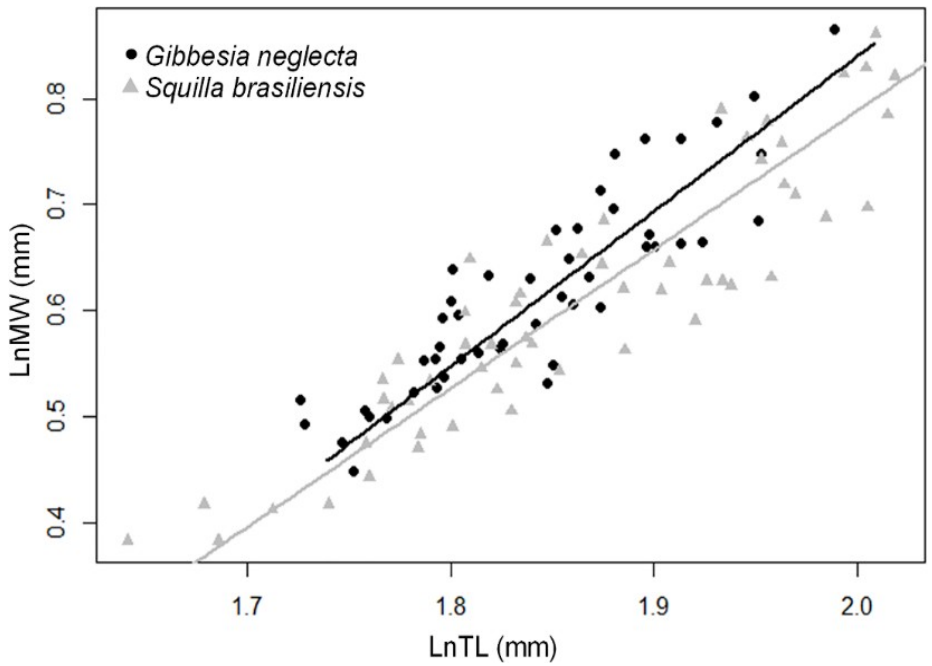

Figure 5: Relationship of Total Length (LnTL in X axis) vs merus width (LnMW in Y axis) between *Squilla brasiliensis* and *Gibbesia neglecta*. Logaritized data.

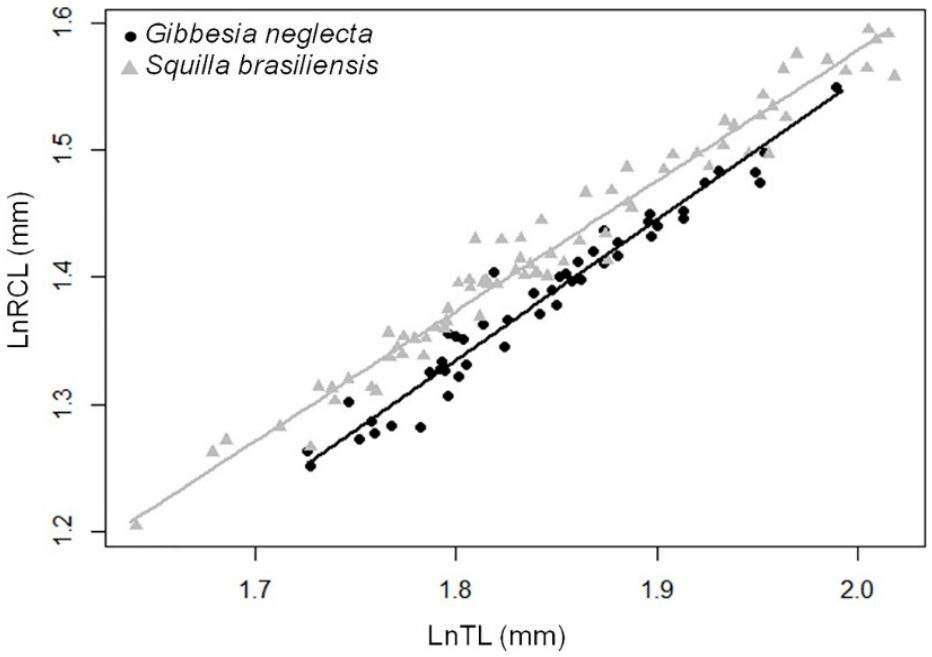

Figure 6: Relationship of the Total Length (LnTL in X axis) vs Raptorial Claw Length (LnRCL in Y axis) between *Squilla brasiliensis* and *Gibbesia neglecta*. Logaritized data.

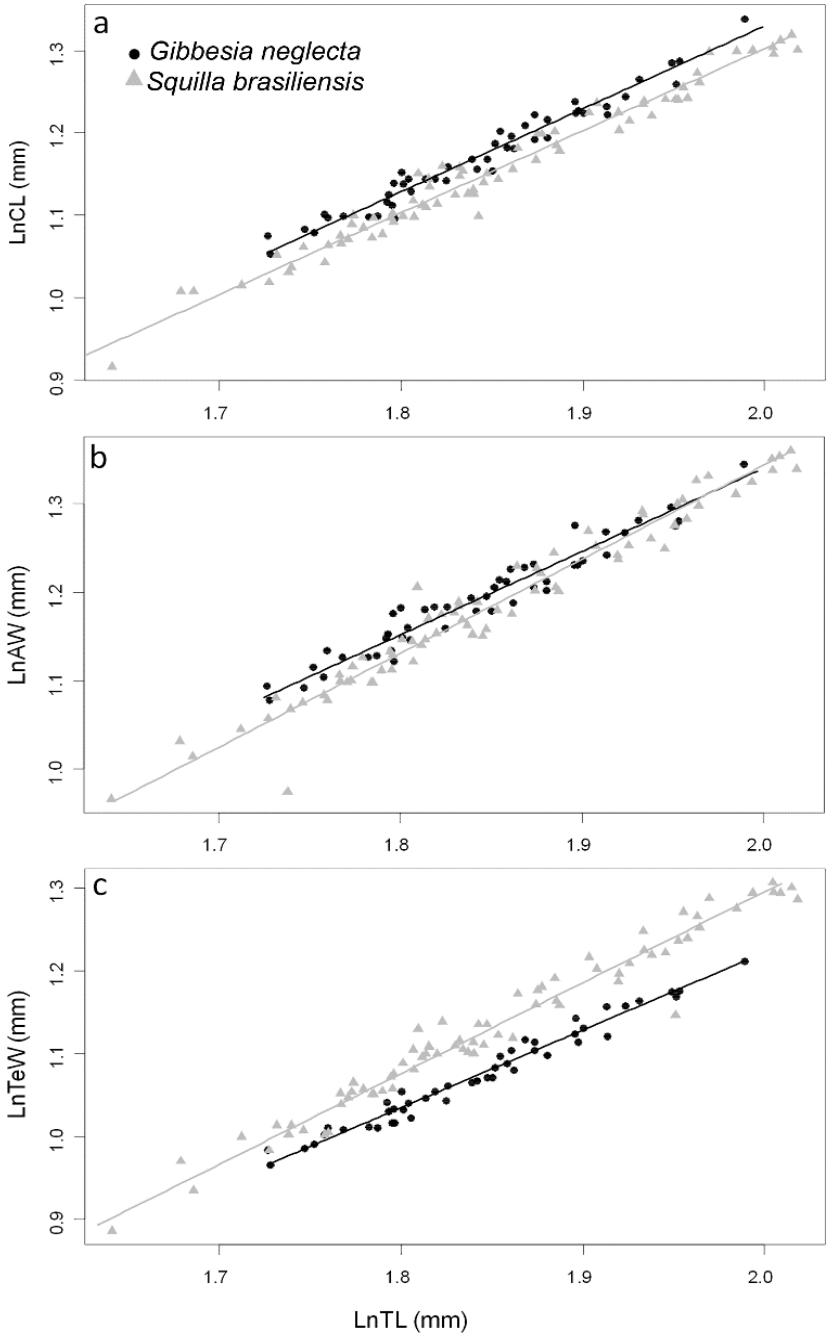

Figure 7: *Squilla brasiliensis* and *Gibbesia neglecta* and their relationship to total length (X axis) vs: (**a**) Carapace length; (**b**) abdomen width; (**c**) telson width, (all Y axis structures).

With the analysis of geometric morphometry, it is possible to verify values of the distance of Procrustes and T-square for the relationships between males of different species, females of different species and between sexes of the same species. It can be seen that some structures showed significant values for such parameters, indicating the significant difference between the forms (Table II). The distributions of landmarks and semi-landmarks in the plans revealed that the shapes of the telson and the claw segments can vary between sex and species, mainly the interspecific relationships comparisons. For telson, both males and females of *S. brasiliensis* are more robust than *G. neglecta*, with the region

between landmarks 3 – 8 and 12 - 17 being wider. However, in the region between landmarks 7 – 13, the telson for the *G. neglecta* is longer than for the *S. brasiliensis*, especially in males (Figure 9).

As for the raptorial claw structures, the merus showed subtle difference in males, with a widening in the region between the landmarks 4-10. Comparing the females of both species, the difference becomes quite evident in regions 4-16 and 23 -35, where *G. neglecta* has a greater robustness than *S. brasiliensis* (Figure 8, 9). For the propodus, for both sexes it is possible to observe that *S. brasiliensis* has greater width between landmark regions 20 - 27 and a shortening of 29 - 34 when compared to *G. neglecta* (Figure 8). As for the dactyl, the comparison between species showed that the species *G. neglecta* has more elongated spines, indicated by landmarks 4, 5, 9 and 10, for both sexes (Figure 9).

Table II. Resultados estatísticos da análise da morfometria geométrica. S.b, *Squilla brasiliensis*; G.n, *Gibbesia neglecta*; T-square, similar test of Mahalanobis distance; p, Procustes distance p value ($p \leq 0.05$).

Structures	Intraspecific Relations	T-square	p	Interspecific Relations	T-square	p
Telson	S.b ♂ *vs.* S.b ♀	0.0205	0.0262	S.b ♂ *vs.* G.n ♂	<.0001	<.0001
	G.n ♂ *vs.* G.n ♀	0.5025	0.8451	S.b ♀ *vs.* G.n ♀	<.0001	<.0001
Merus	S.b ♂ *vs.* S.b ♀	<.0001	<.0001	S.b ♂ *vs.* G.n ♂	<.0001	<.0001
	G.n ♂ *vs.* G.n ♀	0.0003	<.0001	S.b ♀ *vs.* G.n ♀	<.0001	<.0001
Propodus	S.b ♂ *vs.* S.b ♀	<.0001	<.0001	S.b ♂ *vs.* G.n ♂	<.0001	<.0001
	G.n ♂ *vs.* G.n ♀	0.1142	0.0007	S.b ♀ *vs.* G.n ♀	<.0001	<.0001
Dactyl	S.b ♂ *vs.* S.b ♀	0.0167	<.0001	S.b ♂ *vs.* G.n ♂	<.0001	<.0001
	G.n ♂ *vs.* G.n ♀	0.2182	0.0283	S.b ♀ *vs.* G.n ♀	<.0001	<.0001

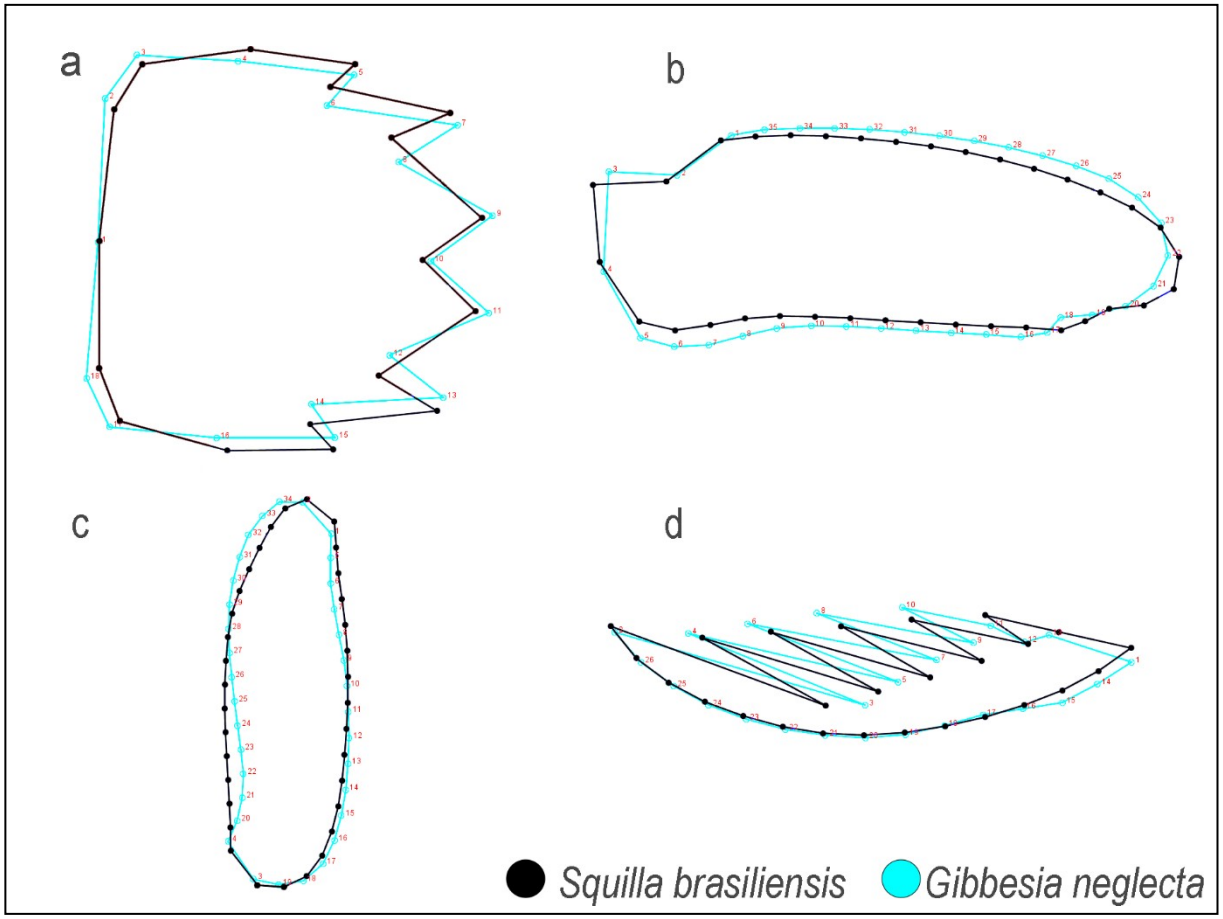

Figure 8: Shapes differences for female structures between *Squilla brasiliensis* and *Gibbesia neglecta*. [a] telso, [b] merus segment, [c] propodus segment and [d] dactyl segment.

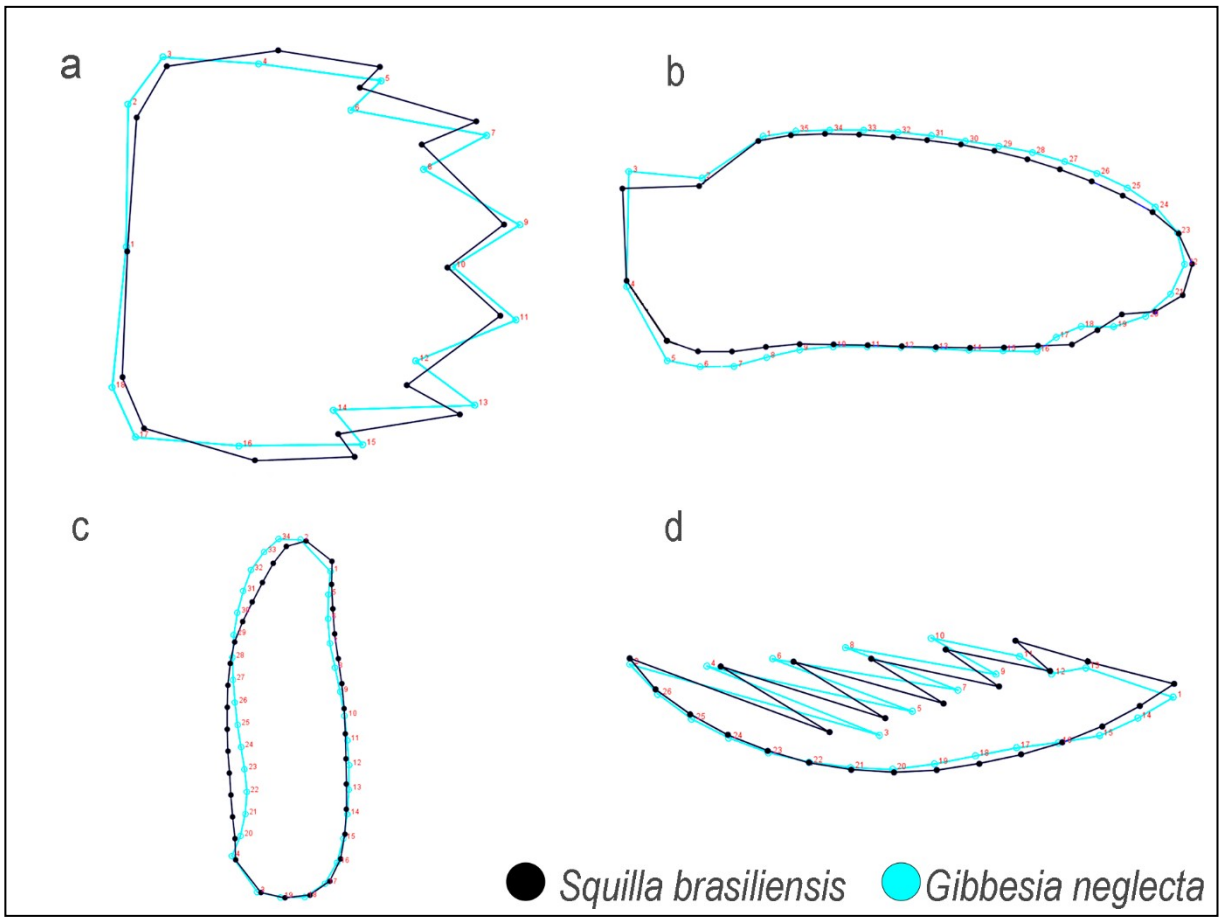

Figure 9: Shapes differences for males structures between *Squilla brasiliensis* and *Gibbesia neglecta*. [a] telso, [b] merus segment, [c] propodus segment and [d] dactyl segment.

Discussion

In this study was noted differences in allometrics patterns in their structures and for the shapes of some structures between the two Stomatopod specimens, *S. brasiliensis* and *G. neglecta*. Interspecific dimorphism was present for the telson, as for *S. brasiliensis*, the relationship between the width of this structure was allometrically positive, reaching greater widths when compared to *G. neglecta*, which has a negative allometry. In addition, the study of geometric morphometry showed a significant difference between species, and for both males and females of *S.brasiliensis* the telson proved to be more robust than the *G.neglecta*. For the group of "spearers", this structure is often used to block their holes, protecting their entry against any type of threat (Caldwell & Dingle, 1975). Stomatopoda females also incubate their embryos inside the tunnels, avoiding predators, injuries and possible dangers (Hamano & Matsuura, 1984), using the telson to block their holes. Considering that the species *S. brasiliensis* reaches lengths greater than *G. neglecta*, it is possible to relate the size of the animal to the size of its burrow. Thus, *S. brasiliensis* has greater protection when it has a higher telson growth rate, capable of blocking entry to your burrows.

Regarding the width of the abdomen, in our study *S. brasiliensis* obtained a positive allometry, whereas for *G. neglecta* it was characterized as isometric. Although *G. neglecta* registers greater

abdominal widths than *S. brasiliensis*, throughout development both have similar abdominal widths between 87mm and 95 mm of TL. The width of the abdomen is of great importance for the reproduction in Stomatopoda, being attributed to the maturation of these individuals (Kodama, 2004). The evidence related to maturation that these results bring is not very concrete, as this characteristic refers primarily to females and in these analyses, the sexes were not discriminated. However, it is possible to relate this area to an unprotected and sensitive region for both sexes, which makes it possible to visualize the relationship between the development of the abdomen and the strength of the telso.

In allometric terms, in this study some structures did not differ between species, such as MW, presenting a positive allometry, with the greatest widths are reached in *G. neglecta*. However, analyzing the merus shape indicated a significant difference between species, making it possible to observe that *G.neglecta* presents a great robustness, mainly in the region associated with the elastic system known as V-meral. The allometric similarity highlights the importance of this structure in Stomatopoda, since the V-meral is responsible for the force of the impact, due to the relaxation of the muscles that are located in this region (Zack, 2009). Allied to that, both species also had a similarity for the length of the carapace, but this structure for *G. neglecta* reaches larger sizes. This is due to the fact that the carapace is totally related to the presence of raptorial claw muscles, where a larger carapace houses stronger muscle (Dingle *et al.* 1973; Caldwell & Dingle 1976). The energy stored in this system has great importance in the claw force-speed trade-off, since the "spearers" use is more robust to generate greater frequency of attacks (Blanco *et al.*, 2014). This is related to the fact that males and females have frequent agonistic relationships, intraspecific and interspecific, where the energetic potential for the group of "spearers" is not completely used in foraging, indicating that the investment in the merus robustness can be related mainly to agonistic relationships (Ahyong & Jarman, 2009; deVries *et al.*, 2012).

The species *S. brasiliensis* also obtained a positive allometric growth for the propodus width, as for *G. neglecta* this structure presented an isometry. However, when analysed the shapes of the propodus using geometric morphometry, it is possible to observe that *S. brasiliensis* excels in the robustness of the propodus only in the portion close to the dactyl, whereas in the area close to the merus, *G. neglecta* has greater robustness. This may be related to the fact that the propodus participates in the energetic transmission released by the V-meral (Patek, et al. 2007).

As for the dactyl, despite the positive allometry of *G.neglecta*, *S. brasiliensis* presented greater lengths of this structure. However, geometric morphometry indicated elongated teeth for *G.neglecta*, when compared to *S.brasiliensis*. This may be related to greater capture efficiency, as dactyl teeth are needed to capture evasive prey (deVries et al., 2012).

The relation between the claw length, including propodus, dactyl and merus, showed a positive allometry for *G. neglecta*, while for *S. brasiliensis* the isometry was indicated, where longer claws were observed in *S. brasiliensis*, despite its allometry. This can indicate different tactics of prey capture, as was discussed in the study by deVries (2012), with two perforating species, *Lysiosquillina maculata* (Fabricius, 1793) and *Alachosquilla vicina* (Nobili, 1904), showing that individuals with greater claw

lengths can reach prey over longer distances, but for this it is necessary a more delicate control of the musculature, allowing greater precision in the capture (Higham, 2007). Individuals with a shorter range also would have to wait for a moment for the prey to be in their range, thus having to guarantee a higher speed, instead of a precision of the charge (deVries, 2012). The punctuated differences between the species in our study, together with what was proposed by deVries, may elucidate the foraging tactics of these species, since *G. neglecta* has a raptorial claw with a shorter reach, but has a more robust merus and an elongated tooth in dactyl, guaranteeing thus a greater speed and lethality in the attack. As for *S. brasiliensis*, the width of the mere is not as robust as in *G. neglecta*, but it has greater precision and greater range for capturing prey, ensuring greater success in predation.

It can be observed that the differences that led to taxonomic differentiation between species are not only found in the area of morphology, but also in the morphometry of some structures, which may indicate a difference between niches of predation. This differentiation may hypothesize that such species feed on different prey, such as fish that swim closer to the substrate for the *G. neglecta* members and fish that swim further away from the substrate for the *S. brasiliensis* members. These findings not only led to an expansion of knowledge about these species, but also reinforce knowledge about the order of Stomatopoda, which may lead to future studies to discover more about the amazing behaviors of these animals.

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Considerações Finais

A partir dos nossos resultados a espécie *S. brasiliensis* foi a mais abundante. Tal espécie apresentou um grau de diferenciação entre os sexos, indicando diferentes estratégias na obtenção de um sucesso reprodutivo. As fêmeas desta espécie apresentaram uma alometria positiva para o desenvolvimento da largura do abdome, o que está atribuído a maturação destes indivíduos. Além disso, este estudo demonstrou que as fêmeas de *S. brasiliensis* possuem garras raptoriais mais compridas e télson mais largos, podendo estar atribuído a maior necessidade de um forrageamento efetivo e a uma maior defesa, respectivamente, provavelmente relacionados a maior captação de alimentos consequentemente energia para a reprodução e cuidados parentais com os embriões. Com este estudo, pôde-se ressaltar a importância da força das garras raptoriais, que é atribuída diretamente a largura do mero, aos embates agonísticos, considerando que os machos de *S. brasiliensis* apresentaram uma alometria positiva estrutura, devido ao combate constante por território e por fêmeas.

Quanto a comparação entre as duas espécies, *S. brasiliensis* e *G. neglecta*, indicam uma diferença entre as proporções das garras. Esta diferença se encontra em duas características: alcance (comprimento da garra raptorial) e potência (largura do mero). Pode-se observar que para *G. neglecta* a garra raptorial possui um maior comprimento quando comparado com a *S. brasiliensis*, sendo que *G. neglecta* possui uma garra mais robusta na parte do mero. Aliado a estas observações, a análise da morfometria geométrica indicou também distinções entre tais espécies na estrutura do mero, principalmente na região atrelada ao V-meral, o qual é pertencente do importante mecanismo responsável pela força da garra raptorial.

Os membros da ordem Stomatopoda são alvo de redes de arrasto na grande maioria do nosso território nacional. Parte destes indivíduos acaba sendo rejeitado, podendo causar um grande impacto nos ambientes costeiros devido ao seu importante papel nos nichos em que participa. Diante dos resultados desse estudo no litoral norte do estado de São Paulo, foi possível trazer informações sobre diferenciações morfológicas das espécies *S. brasiliensis* e *G. neglecta*, as quais estarão disponíveis para melhor entendimento da ecologia e manutenção das espécies. Os conhecimentos adquiridos com este trabalho, podem ser um utilizados em futuros estudos compreendendo a reprodução dos membros da ordem Stomatopoda que habitam o litoral brasileiro. Com isso, poderá se formar uma maior rede de saberes, como período de reprodução, período para alcance da maturidade, e assim a ciência poderá trabalhar aliada a BRDs ("*Bycatch Reduction Devices*"), para que assim se construa um esforço com o conjunto de pescadores, gestores e pesquisadores para adotar medidas relacionadas à dinâmica dos sistemas pesqueiros, afim de adotar medidas que diminuam os impactos aos ecossistemas marinhos.