

Universidade Estadual Paulista “Júlio de Mesquita Filho” - Campus de Botucatu
Instituto de Biociências de Botucatu
Programa de Pós-Graduação em Ciências Biológicas (Zoologia)

TESE DE DOUTORADO

**Variação geográfica dos camarões Dendrobranchiata nas regiões Sudeste e Sul do
Brasil: teste de hipóteses sobre o paradigma do efeito latitudinal**

Raphael Cezar Grabowski
Orientador: Professor Dr. Antonio Leão Castilho

Botucatu, São Paulo
2017

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Tese apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Zoologia) da Universidade Estadual Paulista “Júlio de Mesquita Filho” (UNESP), Instituto de Biociências de Botucatu, como requisito parcial à obtenção do título de Doutor em Ciências Biológicas (Zoologia).

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Palavras-chave: Crescimento; Dendrobranchiata; Distribuição; Recursos pesqueiros; Reprodução.

“Muitas das verdades às quais nos apegamos dependem muito do nosso próprio ponto de vista”.

Obi-Wan Kenobi

“Nada existe de permanente, exceto a mudança”.

Heráclito

“Faça ou não faça. Tentativa não há”.

Yoda

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Considerações Iniciais

Os Dendrobranchiata e a fauna acompanhante

Em uma recente revisão taxonômica, De Grave *et al.* (2009) apontaram que, atualmente, existem aproximadamente 15.000 espécies viventes pertencentes à ordem Decapoda Latreille, 1802. Os decápodes representam cerca de um terço de todos os crustáceos conhecidos, tendo como principal característica diagnóstica a presença de cinco pares de apêndices birremes, ou patas, os quais podem apresentar-se modificados, não sendo necessariamente utilizados apenas na locomoção (Kaestner 1970, Fransozo & Negreiros-Fransozo 2016). Esta ordem subdivide-se em duas subordens: Pleocyemata Burkenroad, 1963 (indivíduos que utilizam filobrânquias ou tricobrânquias para trocas gasosas, e desenvolvimento embrionário pleopodial) e Dendrobranchiata Spence Bate, 1888 (de modo geral, exclusiva a animais que apresentam dendrobrânquias como principal estrutura de trocas gasosas e desenvolvimento embrionário sem encubação pleopodial) (Fransozo & Negreiros-Fransozo 2016). À subordem Pleocyemata pertencem os caranguejos, siris, ermitões, tatuíras, lagostas e lagostins, enquanto que Dendrobranchiata inclui camarões marinhos, em sua maioria, peneídeos (superfamília Penaeoidea Rafinesque, 1815) e sergestídeos (superfamília Sergestoidea Dana, 1852) (Pérez-Farfante & Kensley 1997, Brusca & Brusca 2003, Fransozo & Negreiros-Fransozo 2016).

Dentre os indivíduos inseridos em Dendrobranchiata, muitos apresentam considerável importância econômica na pesca de camarões no mundo inteiro, sendo que a maioria de tais espécies é atualmente explorada em níveis acima da sua sustentabilidade (Brusca & Brusca 2003). Dentre as espécies de camarão comercialmente exploradas, D’Incao *et al.* (2002) destacaram que ao longo da costa Sudeste do Brasil, são explorados principalmente os camarões-rosa *Farfantepenaeus brasiliensis* (Latreille, 1817) e *F. paulensis* (Pérez-Farfante, 1967), sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862), barba-ruça *Artemesia longinaris* Spence Bate, 1888, santana *Pleoticus muelleri* (Spence Bate, 1888) e branco *Litopenaeus schmitti* (Burkenroad, 1936).

Infelizmente, devido à baixa seletividade dos apetrechos de pesca comumente utilizados nesta atividade (Keunecke *et al.* 2007), não apenas as populações das espécies-alvo sofrem as consequências da atividade pesqueira, mas também todos os organismos que partilham do mesmo hábitat. De acordo com a Organização das Nações Unidas para Agricultura e Alimentação (FAO) (2015), a biomassa de organismos coletados acidentalmente e sem interesse comercial durante as pescas de camarão

(*bycatch*, ou fauna acompanhante) pode ser de 3 a 15 vezes maior que a de espécies de interesse comercial. Frente a esta situação, faz-se imprescindível que o subsídio intelectual utilizado na concepção de políticas de proteção dos estoques pesqueiros leve em consideração não apenas as espécies-alvo, mas também a fauna que compõe o *bycatch*. Apenas desta maneira torna-se possível evitar o colapso dos estoques de espécies que não possuem interesse comercial, todavia, representam um importante elo na cadeia trófica local.

A variação latitudinal nos parâmetros populacionais de peneídeos

Diversos autores (Bauer 1992, Clarke 1993, Boschi 1997, Castilho *et al.* 2007, Costa *et al.* 2010, entre outros) afirmam que parâmetros e recursos ambientais são fatores altamente influentes nos padrões observados na dinâmica populacional de uma espécie. Dentre os fatores que regem tais processos, é possível citar como exemplo a variação na temperatura e a consecutiva produtividade planctônica. Tais características, por sua vez, estão variavelmente condicionadas à latitude local, moldando a distribuição e ciclo de vida de tais organismos. Adicionalmente, Lenihan & Micheli (2001) apontam que tais diferenças em cada gradiente latitudinal estão atadas às mudanças adaptativas observadas em comunidades bentônicas, as quais são associadas ao movimento, transporte, isolamento e às inter-relações entre as espécies. Portanto, cada espécie possui uma amplitude geográfica específica, e sua distribuição se encontra mais ou menos limitada por condições ambientais e, assim, cercada por áreas que dificultam o estabelecimento satisfatório de uma população, por prejudicar sua sobrevivência ou reprodução.

Dentro deste contexto, vale lembrar que cada fator ambiental apresenta um gradiente de variação específico, e que as espécies respondem de formas distintas quanto à tolerância apresentada aos mesmos, podendo ser consideradas euritópicas (ecologicamente tolerantes) ou estenotópicas (ecologicamente intolerantes). Independentemente do grau de tolerância apresentado, cada espécie só pode atingir a eficiência plena de suas funções em uma porção mais ou menos limitada de cada gradiente, e em direção a qualquer um dos seus limites, a espécie sofre um crescente estresse fisiológico. Assim, a amplitude e a localização de tais limites, junto da mudança dos padrões de abundância dentro desses limites refletem na dinâmica populacional e na influência dos fatores ambientais na sobrevivência, reprodução e dispersão dos indivíduos (Brown & Lomolino 2006, Cox & Moore 2009).

Considerando-se camarões peneóideos, há muito é sugerida a existência de um paradigma (= padrão) geográfico em parâmetros de sua dinâmica populacional (Bauer 1992, Boschi 1997, Costa & Fransozo 2004, Castilho *et al.* 2007, entre outros). Considerando este paradigma, supõe-se, por exemplo, que indivíduos de uma mesma espécie sejam aptos a atingir tamanho corpóreo maior e viver por mais tempo em latitudes maiores, quando comparados a camarões amostrados em regiões mais próximas ao equador (Bauer 1992). A razão para a ocorrência de tal padrão seria a variação nos fatores ambientais ao longo da distribuição das espécies (especialmente temperatura), somada à variação na disponibilidade de recursos alimentares, especialmente para as fases larvais iniciais. Sendo assim, a tendência à homogeneidade nas condições climáticas observadas em ambientes marinhos tropicais seria responsável pela continuidade na periodicidade reprodutiva nestes locais, enquanto que em regiões de maiores latitudes, a flutuação climática ao longo do ano levaria a uma maior sazonalidade reprodutiva, por exemplo (Orton 1920, Baker 1938, Thorson 1950).

Porém, a região costeira do Brasil apresenta diversas singularidades, as quais apresentam potencial suficiente para influenciar, ou até mesmo alterar o padrão observado nos parâmetros populacionais em peneóideos. Nesta área, localizada em uma região subtropical conhecida como “zona de ressurgência do Atlântico”, a circulação oceânica é dominada pelos fluxos opostos das correntes do Brasil (subtropical) e das Malvinas (subantártica), as quais se encontram na latitude média de 36°S. Dentre as massas de água que influenciam a região, estão a Água Central do Atlântico Sul (ACAS), a Água Costeira e a Água Tropical. A mistura de características de diferentes fontes pode resultar em um aumento na produção primária e, consecutivamente, de produção secundária e, dentre elas, a ACAS é a que surte mais efeitos em áreas rasas, ainda que seja formada em regiões distantes da costa (Acha *et al.* 2004). A ACAS aproxima-se da região costeira durante o fim da primavera, e traz consigo baixa salinidade e temperatura, como resultado da mistura das correntes do Brasil e das Malvinas, emergindo também em uma situação de ressurgência na região de Cabo Frio (Castro-Filho *et al.* 1987, Castro-Filho & Miranda 1998, Acha *et al.* 2004). Como consequência de tais singularidades, é possível observar, em regiões tropicais, temperaturas similares às de regiões temperadas, em uma situação contrária ao esperado onde, teoricamente, regiões com menores latitudes apresentariam médias de temperatura mais elevadas (Brown & Lomolino 2006, Cox & Moore 2009).

Sobre as espécies estudadas

Partindo deste princípio, nesta tese, três espécies de camarões Dendrobranchiata pertencentes a famílias distintas foram analisadas quanto à variação latitudinal nos parâmetros de sua dinâmica populacional.

Popularmente conhecido como “camarão santana”, *P. muelleri* (Penaeoidea: Solenoceridae) (Fig. 1) completa seu ciclo de vida inteiramente no ambiente marinho, sendo encontrado exclusivamente ao longo do Atlântico Ocidental, do estado do Rio de Janeiro (23°S), Brasil, à província de Santa Cruz, na Argentina (50°S) (Boschi 1997, Costa *et al.* 2003).

Sicyonia dorsalis Kingsley, 1878 (Penaeoidea: Sicyoniidae) (Fig. 2), conhecida popularmente como “camarão pedra”, distribui-se do estado de Carolina do Norte (34°N), Estados Unidos, até o estado de Santa Catarina (26°S), no Brasil (Costa *et al.* 2003), habitando a região costeira durante todo seu ciclo de vida (Dall *et al.* 1990).

Popularmente conhecido como “camarão ferrinho”, *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea: Penaeidae) (Fig. 3) distribui-se da província de Nova Escócia (43°N) (Canadá) ao estado de Santa Catarina (26°S) (Brasil), em profundidades de até 127 m, completando seu ciclo de vida inteiramente em ambiente oceânico (Dall *et al.* 1990, Costa *et al.* 2003).

As espécies foram amostradas em quatro regiões distintas ao longo de sua distribuição na costa brasileira, dentro de uma variação latitudinal de aproximadamente cinco graus: Macaé, RJ ($\approx 22^\circ\text{S}$), Ubatuba, SP ($\approx 23^\circ\text{S}$), Cananéia, SP ($\approx 25^\circ\text{S}$) e São Francisco do Sul, SC ($\approx 26^\circ\text{S}$).



Figura 1: *Pleoticus muelleri*, vista lateral. Imagem: Castilho AL, 2010.



Figura 2: *Sicyonia dorsalis*, vista lateral. Imagem: Castilho AL, 2010.



Figura 3: *Rimapenaeus constrictus*, vista lateral. Imagem: Castilho AL, 2010.

Plano de estudo

À sombra do cenário descrito acima, o esforço amostral foi realizado com o intuito de testar as seguintes hipóteses:

- A periodicidade reprodutiva das espécies se altera conforme a posição latitudinal em que se encontram. Em latitudes menores, existe uma tendência de continuidade no período reprodutivo, e conforme há um aumento na latitude, este tende a apresentar uma maior sazonalidade, devido à variação nas condições ambientais que influenciam seu desenvolvimento gonadal e o desenvolvimento inicial da prole;
- A estrutura populacional apresenta diferentes características quando analisada em localidades diferentes, podendo apresentar diferenças no que diz respeito ao tamanho do corpo quando são amostradas em latitudes distintas. Para locais de maior latitude, presume-se que os indivíduos alcancem maiores tamanhos, bem como maturidade sexual tardia, quando comparados àqueles observados em latitudes inferiores;
- Os peneóideos atingem maiores constantes de crescimento quando em latitudes menores, resultando em comprimentos assintóticos e longevidades menores, quando comparados com estimativas realizadas para indivíduos coletados em latitudes maiores, resultado da variação climática ao longo do gradiente latitudinal;
- As características ambientais singulares encontradas ao longo da costa Sudeste e Sul do Brasil apresentam força suficiente para alterar os padrões esperados na dinâmica populacional dos peneóideos, como resultado da história de vida de cada espécie, que pode responder de formas distintas a tal cenário.

Para testar as hipóteses propostas acima, a presente tese conta com três capítulos, redigidos sob a forma de artigo científico. Vale lembrar que, através da oportunidade oferecida pelo Programa Institucional de Bolsas de Doutorado Sanduiche no Exterior (PDSE, processo #99999.006696/2015-05), foi possível analisar os dados aqui apresentados sob a supervisão do professor Dr. Raymond T. Bauer, na Universidade de Luisiana em Lafayette (Lafayette, LA, Estados Unidos). Este pesquisador trouxe valiosas sugestões na análise, redação e discussão dos resultados, motivo pelo qual os capítulos foram redigidos em inglês (facilitando assim o processo

de correção, no qual o professor Raymond teve participação efetiva). Também, a escrita dos capítulos em inglês certamente facilitará e encurtará o processo de publicação, realizadas as correções sugeridas pela banca examinadora da tese.

O primeiro capítulo abordará a variação geográfica nos parâmetros populacionais (estrutura populacional, biologia reprodutiva e crescimento populacional) de *S. dorsalis*. Excepcionalmente neste capítulo, os parâmetros de crescimento populacional foram analisados sob uma óptica temporal, com dados provenientes de amostras obtidas com um intervalo de 10 anos. Esta singularidade foi adicionada ao esforço amostral com o objetivo de testar a influência da criação de uma área de proteção ambiental (APA) em Ubatuba, uma vez que as amostras foram realizadas em um período antes (2001-2003) e outro depois (2013-2014) da criação da APA (no ano de 2008). No segundo capítulo, a espécie *P. muelleri* foi analisada quanto aos parâmetros de sua dinâmica populacional (crescimento e estrutura populacional, e biologia reprodutiva) e, por fim, no terceiro capítulo, foram analisados os parâmetros de biologia reprodutiva e estrutura populacional de *R. constrictus*.

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Capítulo 1

**Local environmental conditions alter latitudinal
patterns in population dynamics of *Sicyonia dorsalis*
Kingsley, 1878 from southeastern Brazil**

**Local environmental conditions alter latitudinal patterns in population dynamics
of *Sicyonia dorsalis* Kingsley, 1878 from southeastern Brazil**

Resumo

O objetivo deste estudo foi testar a hipótese de gradientes latitudinais na influência ambiental sobre parâmetros populacionais de *Sicyonia dorsalis* na costa sudeste do Brasil. Também, comparamos o crescimento da espécie em um período de dez anos na região de Ubatuba, amostrando cinco anos antes e cinco anos depois do estabelecimento de uma área de proteção marinha (APM). Amostras mensais foram realizadas em quatro regiões (Macaé ($\approx 22^\circ\text{S}$), Ubatuba ($\approx 23^\circ\text{S}$), Cananéia ($\approx 25^\circ\text{S}$) e São Francisco do Sul ($\approx 26^\circ\text{S}$)), utilizando barcos de pesca artesanal, em diferentes períodos entre julho de 2010 e junho de 2014. Para determinar a influência do estabelecimento da APM em Ubatuba, os parâmetros de crescimento também foram estimados para dados obtidos de julho de 2001 a junho de 2003. A influência da salinidade e temperatura da água de fundo foi testada utilizando a análise de correlação cruzada ($p \leq 0,05$), e os períodos reprodutivos e de recrutamento foram considerados como os períodos com maior frequência de fêmeas reprodutivas e jovens, respectivamente, para cada região. Os parâmetros de crescimento foram analisados utilizando o modelo de crescimento de Von Bertalanffy, e a longevidade foi calculada a partir do mesmo modelo, invertido, comparando as curvas médias de cada região utilizando o teste F ($p \leq 0,05$). Foram analisados 3.038 indivíduos, e em todas as regiões, as fêmeas atingiram maiores tamanhos, uma provável influência de seu sistema de cópula, o qual desconsidera o tamanho de machos, ou então uma adaptação para aumentar a fecundidade de fêmeas. As fêmeas também foram mais abundantes, uma consequência de diferentes atividades migratórias e taxas de mortalidade entre os sexos. Foi possível observar uma tendência à diminuição do tamanho corpóreo à medida que aumentou a latitude, o oposto à tendência esperada de aumento no tamanho corpóreo com o aumento da latitude, indicando uma conexão migratória entre grupos que podem pertencer a uma mesma população. Adicionalmente, os resultados da análise de crescimento mostraram um efeito positivo do estabelecimento da APM em Ubatuba, com uma tendência de aumento em tamanho assintótico entre 2001-2003 e 2013-2014. A reprodução apresentou uma tendência à sazonalidade em maiores latitudes, possivelmente induzida pela sazonalidade na disponibilidade de alimento larval e na influência de massas de água na costa brasileira.

**Local environmental conditions alter latitudinal patterns in population dynamics
of *Sicyonia dorsalis* Kingsley, 1878 from southeastern Brazil**

Abstract

The aim of this study was to test the hypothesis of latitudinal gradients in environmental influence over growth and reproductive parameters in *Sicyonia dorsalis* along the southeastern Brazilian coast. We also tested the differences in growth of the species over a ten-year period in Ubatuba, where data was collected 5 years before and then 5 after the establishment of a marine protected area (MPA). Monthly samples were carried out in four different regions throughout the Brazilian coastal area (Macaé ($\approx 22^\circ\text{S}$), Ubatuba ($\approx 23^\circ\text{S}$), Cananéia ($\approx 25^\circ\text{S}$) and São Francisco do Sul ($\approx 26^\circ\text{S}$)), using artisanal fishing boats, in different periods from July 2010 through June 2014. To determine the influence of the establishment of the MPA in Ubatuba, we also estimated growth parameters for data sampled from July 2001 through June 2003. We tested the influence of bottom water temperature and salinity over the population dynamics using cross-correlation analyses ($p \leq 0.05$). Reproductive and juvenile recruitment periodicity were considered as the periods with higher frequency of reproductive females and immature individuals, respectively, for each region separately. Growth parameters were analyzed using the Von Bertalanffy's growth model, while longevity was calculated using its inverse formula, comparing the results for each region by the F test ($p \leq 0.05$). We analyzed 3,038 individuals to its reproductive and growth aspects. In all regions, female were bigger than males, a likely evolutionary influence of their mating system, in which there is no selection for larger males, or an adaptation to increase females size and consequent fecundity. Females were also more abundant, a consequence of different migration activities and mortality rates between sexes. There was a decreasing trend in maximum body size and asymptotic length as latitude increased, the opposite of the expected trend of larger body size with increasing latitude, what can be considered as an evidence of the migratory connection between groups that are part of the same population. The estimated growth analyses' results also showed a possible positive effect of the establishment of the MPA in Ubatuba, since we observed an increasing trend in asymptotic lengths estimated for 2001-2003 and 2013-2014. We observed a tendency towards seasonal reproduction in higher latitudes, possibly induced by the seasonality in larval food availability and the influence of water masses along the Brazilian coast.

Introduction

Environmental factors often show gradients with latitude and depth in marine habitats, and different species tend to respond differently to such gradients (Bauer 1992, Eckelbarger & Watling 1995). The location and amplitude of these gradients may cause variable effects on the population dynamics (abundance, mortality, growth, reproduction, etc.) on both ecologically and commercially important species (Brown & Lomolino 2006, Cox & Moore 2009). Generalizations about biological phenomena are useful in summarizing knowledge, serving as models or paradigms which stimulate proposal and testing of hypotheses on factors responsible for observed patterns. Quite often, however, such generalizations are oversimplifications, and do not hold up as further studies are conducted about them, often with the discovery of contradictory or unexpected results (Bauer 1992, Marquet *et al.* 2004, Fernández *et al.* 2009). Trends in growth rates and reproductive periodicity can be observed in marine animals that are correlated with gradients in environmental seasonality. Individuals of tropical populations tend to be smaller in size than those from higher latitudes, and continuous reproduction in the tropics becomes increasingly seasonal with the increase in latitude (Thorson 1950, Bauer 1992, Hartnoll 2001).

According to Hartnoll (2001), the impact of basic environmental factors (e.g., temperature, salinity, nutrient concentrations, food for planktonic larvae) on growth and reproduction have been demonstrated under laboratory conditions and can vary spatially and temporally in the natural environment. In general, an increase in temperature accelerates growth in crustaceans by shortening the intermoult period, increasing moult increment, or both. This has an antagonistic effect on growth rate, because reducing time between moults also reduces the size increment at each moult. Nonetheless, the former effect is proportionately greater, and thus the almost universal outcome is an increase in growth rate. On the other hand, decreases in temperature increase intermoult interval, but it leads to an increased molt increment in size, as well as an increase in lifespan. Thus, at higher latitudes, the net effect on growth is positive, and marine organisms from higher latitudes often attain larger body size than conspecifics or congeners from lower latitudes (e.g., *Pandalus borealis* Krøyer, 1838, Haynes & Wigley 1969; *Sicyonia* spp., Bauer 2004).

Orton (1920) first hypothesized that temperature is responsible for reproductive periodicity of marine invertebrates. According to this author, a constant warm temperature condition in tropical seas is the main cause for their continuous

reproduction. Seasonal variation in water temperature, which is generally associated with subtropical to polar latitudes, is an environmental factor affecting gametogenesis, thus imposing reproductive seasonality in these animals outside of the tropics. On the other hand, Thorson (1950) postulated that the major selective pressure on the timing of reproduction for species with planktotrophic larvae is the seasonal variation in larval food supply (primary and secondary productivity), which is correlated with seasonality of factors affecting productivity. The variation in food supply for planktotrophic larvae of crustaceans, molluscs, and other marine species may be considered the ultimate factor (“evolutionary” cause) selecting for different patterns of reproductive seasonality. Therefore, environmental variables such as temperature, photoperiod, and nutrient concentration can be considered as environmental cues, or “proximate factors”, acting on reproduction and growth, which are highly correlated with the ultimate factor, larval food supply (Baker 1938, Bauer 1992, Marshall *et al.* 2012).

Castilho *et al.* (2007b) pointed out that such a latitudinal pattern is applicable for *Artemesia longinaris* Spence Bate, 1888, a penaeid shrimp. The authors compared populations from Ubatuba, southeastern Brazil (23°S), and Mar del Plata, east-central Argentina (37°S), and found that in the higher latitude location, individuals reached larger body sizes than those at the tropical location. Additionally, there was a delay in the size of sexual maturity, suggesting that environmental factors such as water temperature and primary productivity could be responsible for such a difference. However, such a pattern does not seem to be applicable to all shrimp species occurring along the Brazilian coast. Grabowski *et al.* (2014) estimated growth parameters for *Xiphopenaeus kroyeri* (Heller, 1862) in the adjacent area from Babitonga Bay, southern Brazil, and compared their results to other studies along the Brazilian coast within 10 degrees of latitude range (Santos & Ivo 2000, Campos *et al.* 2011, Heckler *et al.* 2013). No latitudinal patterns were found. Grabowski *et al.* (2014) stated that genetic variation among populations, methodological differences among the studies compared, and effects of fishing pressure might contribute to this lack of latitudinal pattern.

Additionally, Acha *et al.* (2004) pointed out some local variation in currents and water masses in this region which might explain the deviation from an expected latitudinal pattern. They pointed out that the Brazilian coast is strongly influenced by marine fronts, i.e., transitional regions, created by combining features of water masses such as the South Atlantic Central Water (SACW), Coastal Water (CW) and Tropical Water (TW). The SACW is often formed in regions far from the coast; however, it can

get closer in late spring and early summer, in depths of 10-15 m. The SACW brings lower salinity and temperature (temperature: $< 18^{\circ}\text{C}$; salinity: < 36 psu) by mixing water from the warm Brazilian current (temperature: $> 20^{\circ}\text{C}$; salinity: > 36 psu) and the cold Falklands current (temperature: $< 15^{\circ}\text{C}$; salinity: < 34 psu), and emerges in the Cabo Frio region as an important upwelling area (Castro-Filho & Miranda 1998, Acha *et al.* 2004). According to Merino & Monreal-Gómez (2009), upwelling is the physical process that most influences marine organisms in the regions where it occurs. Some studies carried out in upwelling areas have shown dramatic effects on the genetic structure, distribution and reproductive biology of *A. longinaris* (Carvalho-Batista *et al.* 2014, Sancinetti *et al.* 2014, 2015), reproductive biology of *X. kroyeri* (Silva *et al.* 2015) and shrimp species diversity and distribution (Pantaleão *et al.* 2016). The approach of the SACW to the coastal region of Brazil and its upwelling in Cabo Frio region results in a decrease in bottom water temperature, which has a retarding effect on growth and reproduction of tropical species. However, upwelling leads to a transport of nutrients from the lower layers into the euphotic zone, which influences primary productivity and the subsequent larval food supply (Valentin 1984, Odebrecht & Castello 2001, Gaeta & Brandini 2006), so that the SACW is a water mass high in nutrient concentration.

There is a considerable concern and effort to improve fisheries management of penaeoid species in Brazilian waters (Pitcher 2000). The current legislation concerning Brazilian fisheries imposes a closed season on shrimp fishing in southern and southeastern coastal waters from March through May (IBAMA, CEPSUL). In addition, the Brazilian Ministry of the Environment has established MPAs (Marine Protected Areas) in which commercial fishing is not allowed (Almeida *et al.* 2012). Investigation on growth and longevity in shrimp species is needed not only to understand their basic population biology, but as importantly, to provide basic information necessary for their conservation and management (Die 1992, Keunecke *et al.* 2008, Vogt 2012). The penaeoid shrimp *Sicyonia dorsalis* Kingsley, 1878 is not commercially fished, primarily because of its small size. However, this species makes up to 92% of all of the sicyoniid species captured as bycatch in Brazilian waters, and is the seventh most abundant penaeoid species taken. The lack of economic interest does not justify the exclusion of a given species from the current fishing management, and it is necessary to highlight their ecological importance as components in the food web (Severino-Rodriguez *et al.* 2002, 2007, Graça-Lopes *et al.* 2002, Costa *et al.* 2005, Castilho *et al.* 2008c). We consider it

a good penaeoid species model, with which to study effects of MPAs on growth and other population parameters in shrimp fisheries in Brazilian waters.

The aim of this study was to test the hypothesis of latitudinal gradients in growth and reproductive parameters in *S. dorsalis* over a relatively narrow range of latitude along the Brazilian coast. We also measured variation in basic abiotic factors in sample locations to determine if they might be responsible for any deviation from the expected latitudinal pattern. Additionally, we tested the null hypothesis of no differences in growth over a ten-year period at a location in which data was collected for 5 years before and then after the establishment of a marine protected area.

Material and methods

Sampling

Samples were carried out in four different regions throughout the Brazilian coastal area, covering a 5-degrees range of latitude (Fig. 1). For all sampling locations, similar gear and methods were adopted to avoid sampling failures and consequent errors in estimation of parameters. Sampling was carried out using shrimp-fishing boats outfitted with double-rig nets the same size and mesh as used in artisanal fishing (mesh size: $\cong 3$ cm; mesh gap: $\cong 11.5$ m; boat velocity during trawls: $\cong 1.5$ knots; total distance traveled during trawls: $\cong 0.5$ miles), with monthly 30-min trawling at each sampling station for each region.

In the Macaé region (MA) ($\approx 22^\circ\text{S}$), in northern Rio de Janeiro state, six sampling stations were selected, covering 5-15 m depth from July 2010 through June 2011. In the Ubatuba region (UB I) ($\approx 23^\circ\text{S}$), northern São Paulo state, four sampling stations were adopted, covering a 5-15 m depth variation, from July 2013 through June 2014. For long-term comparison of growth parameters in this area, we also analyzed data sampled from July 2001 through June 2003 at Ubatuba (UB II) (sampling in Castilho *et al.* 2008b), comprising six sampling stations under a 5-35 m depth. In the Cananéia region (CA) ($\approx 25^\circ\text{S}$), southern São Paulo state, seven stations (5-15 m depths) were sampled from July 2012 through May 2014. In the São Francisco do Sul region (SFS) ($\approx 26^\circ\text{S}$), five sampling stations were sorted, covering a 5-17 m depth variation (Fig. 1), from July 2010 through June 2011.

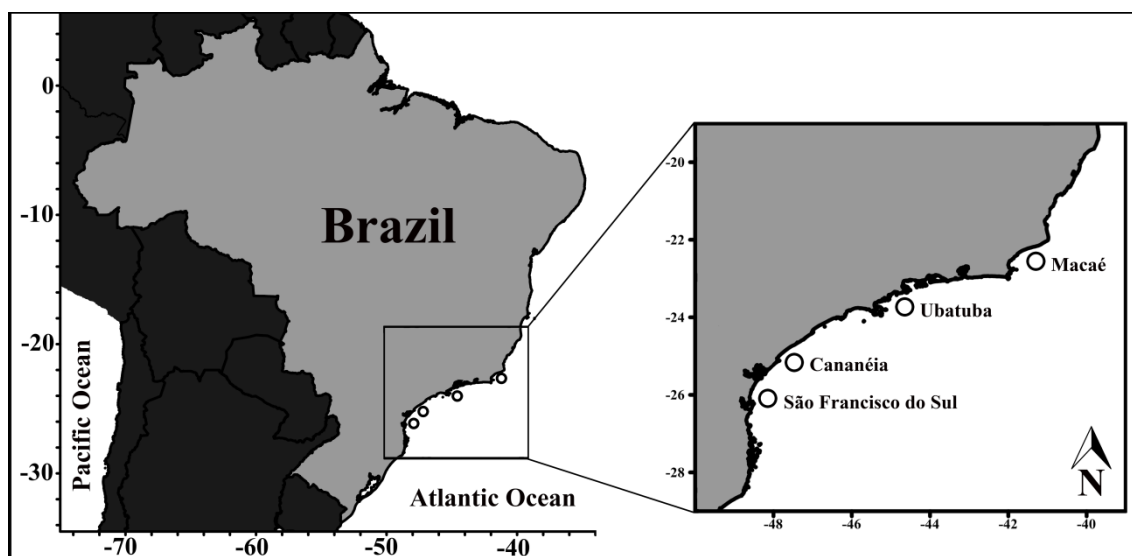


Figure 1: Map of the Brazilian coastal area, highlighting the southeastern littoral and the sampling locations.

Environmental data

Since *S. dorsalis* only inhabits the bottom, only temperature and salinity of bottom were included in analyses. Bottom water samples were taken for each month using a Van Dorn bottle. Temperature was measured with a mercury thermometer, and salinity was determined using an optical refractometer. To assess the influence of environmental factors on the abundances of reproductive females and adult males, and juveniles (new recruits) and their interaction, we performed cross-correlation analyses. In such analyses, two data series are compared as a function of time lag (n), measuring the relationships between values of one data series and another months earlier (negative lag) or months later (positive lags), using the Pearson correlation coefficient. A correlation coefficient value of lag 0 shows no lag (Statsoft 2011). We considered lag coefficient values higher than 0.5 (positive or negative) as biologically significant when the analysis was statistically significant ($p \leq 0.05$).

Sex ratio and population structure

At all sampling locations, individuals were identified to species (Costa *et al.* 2003), carapace length (CL) measured with vernier calipers as the linear distance from the posterior border of the carapace to the orbital angle (to the nearest 0.1 mm) and sexed according to the presence of a thelycum in females, and petasma in males (Pérez-Farfante & Kensley 1997). Sex ratio was calculated as the quotient between the

abundance of males and the total abundance of individuals per month. Deviations from 0.5 (a 1:1 sex ratio) were tested by a binomial test ($p \leq 0.05$) (Wilson & Hardy 2002, Baeza *et al.* 2013). The length frequency distribution was evaluated separately for each sex using 1-mm CL intervals. Both were compared using Kolmogorov-Smirnov two-sample tests ($p \leq 0.05$), for each location separately, in which the null hypothesis adopted was that size distribution among sexes did not differ (Zar 1999, Castilho *et al.* 2008c).

Reproduction and recruitment

The reproductive condition of females was assessed by macroscopic observation of the degree of ovarian development, according to its color and volume occupied in the cephalothorax, which is visible through the transparent exoskeleton (Castilho *et al.* 2007a, 2008a, c). Thus, ovaries were classified as immature (juveniles) (ovaries varying from thin transparent strands to thicker strands); spent (whitish colored ovaries, much larger and thicker than the ones observed for juveniles); and reproductive (thicker ovaries ranging from light to olive green). Reproductive intensity was given as the frequency (percentage) of reproductive females in the adult (spent and reproductive gonadal stages) population, monthly, for each region (Castilho *et al.* 2008a, c). In penaeid shrimps, male sexual maturity is, in general, assessed by observation of the degree of linking of the petasmas lobes. In this study, sexual condition in males was defined as mature when petasma lobes (endopods of first pleopods) were linked and immature (juveniles) when not (Boschi 1989, Bauer & Rivera Vega 1992, Castilho *et al.* 2008a, c). Juvenile recruitment was estimated as the percentage of juveniles in the entire monthly population sample.

Individual growth and longevity

Growth and longevity were analyzed only for females since the abundance of males was not sufficient to distinguish monthly cohorts. Growth analysis was performed based on the Von Bertalanffy growth model (Von Bertalanffy 1938), following the methodology proposed by Simões *et al.* (2013) as follows: modal peaks (CL) were obtained with the software PeakFit (Automatic Peak Fitting Detection and Fitting, Method I-Residual, no Data Smoothing), using 0.5 mm size classes. The modal peaks were plotted on a scatter graph vs. age, in order to assess the cohort growth. The growth parameters (CL_{∞} : asymptotic carapace length; k : growth coefficient (day^{-1}); t_0 :

theoretical age at size zero) were estimated using the Solver supplement in Microsoft Excel (v. 2013) for Windows 7, which applies the Von Bertalanffy growth model: $CL_t = CL_{\infty}[1 - \exp^{-k(t-t_0)}]$ (CL_t : carapace length at age t). The validation of a cohort was evaluated based on its similarity to the maximum body sizes sampled for each area. Growth data were pooled and growth parameters were estimated. The average growth curves obtained for each region were compared to each other using the F test ($p \leq 0.05$), in order to attest if they were different (one region from another) (Cerrato 1990). Longevity was estimated using the inverse Von Bertalanffy growth model, with a modification suggested by D’Incao & Fonseca (1999): $\text{longevity} = 0 - (1/k) \ln[1 - (CL_t/CL_{\infty})]$ (considering $t_0 = 0$, and $CL_t/CL_{\infty} = 0.99$).

Results

Environmental data

Monthly mean values of bottom water salinity varied from 35.7 to 38 psu in MA (average mean: 36.9 psu); from 34.3 to 37 psu in UB I (average mean: 35.5 psu); from 20.6 to 36.1 psu in CA (average mean: 31.5 psu); and from 31.4 to 35.6 psu in SFS (average mean: 33.4 psu) (Fig. 2). Bottom water temperature monthly means varied from 19.5 to 22.9 °C in MA (average mean: 20.8 °C); from 19.9 to 25.5 °C in UB I (average mean: 22.5 °C); from 17.5 to 29.3 °C in CA (average mean: 23.3 °C); and from 18.2 to 26.1 °C in SFS (average mean: 22.3 °C) (Fig. 3).

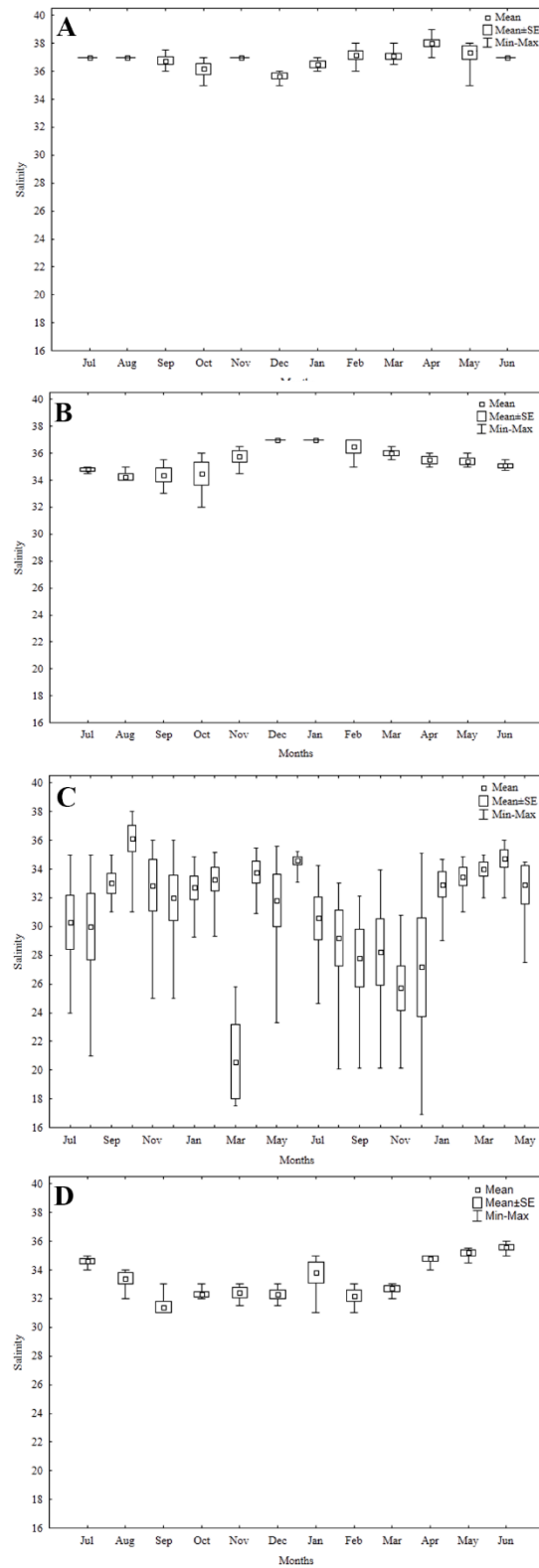


Figure 2: Monthly mean values on bottom water salinity (psu) sampled from: A) July 2010 through June 2011 in the Macaé region; B) July 2013 through June 2014 in the Ubatuba region; C) July 2012 through May 2014 in the Cananéia region; and D) July 2010 through June 2011 in the São Francisco do Sul region. SE: standard error; Min: minimum values; Max: maximum values.

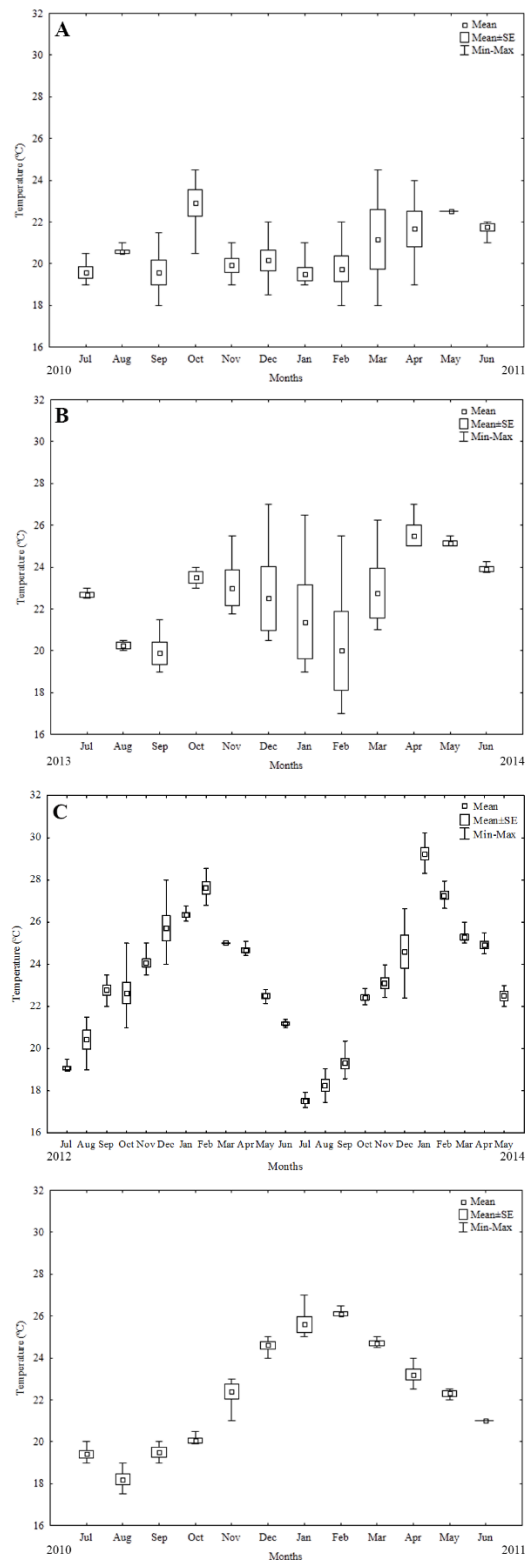


Figure 3: Monthly mean values on bottom water temperature (°C) sampled from: A) July 2010 through June 2011 in the Macaé region; B) July 2013 through June 2014 in the Ubatuba region; C) July 2012 through May 2014 in the Cananéia region; and D) July 2010 through June 2011 in the São Francisco do Sul region. SE: standard error; Min: minimum values; Max: maximum values.

Population structure

During the sampling period, 3,038 individuals were collected and used in analyses of population structure and reproductive parameters: 571 from MA, 1,034 from UB I, 1,131 from CA and 301 from SFS. In all regions, females were more abundant than males, and they predominated in the higher size classes, showing significantly bigger body sizes when compared to males (Kolmogorov-Smirnov, $p < 0.05$). Additionally, we could observe a tendency of decreasing average and maximum body size with increasing latitude (Fig. 4).

In MA, 565 adults and 6 juveniles were sampled, from which the mean size of males CL ($n = 118$) was 7.6 mm (size range: 4.9-11.6 mm), and 9.9 mm for females ($n = 453$) (size range: 4.8-20.5 mm) (Fig. 4). In UB I, 996 adults and 38 juveniles were sampled, from which the mean size recorded for males CL ($n = 104$) was 7.3 mm (size range: 5.0-11.3 mm), and 9.8 mm for females ($n = 930$) (size range: 5.6 to 16.8 mm) (Fig. 4). In CA, 855 adults and 276 juveniles were sampled, from which the mean size of males CL ($n = 85$) was 6.9 mm (size range: 4.4-10.1 mm), and 9.1 mm for females ($n = 1046$) (size range: 4.4 to 14.5 mm) (Fig. 4). In SFS, we sampled 298 adults and 3 juveniles, from which the mean size of males CL ($n = 03$) was 6.0 mm (size range: 5.2-7.3 mm), and 9.9 mm for females ($n = 298$) (size range: 4.5-13.9 mm) (Fig. 4).

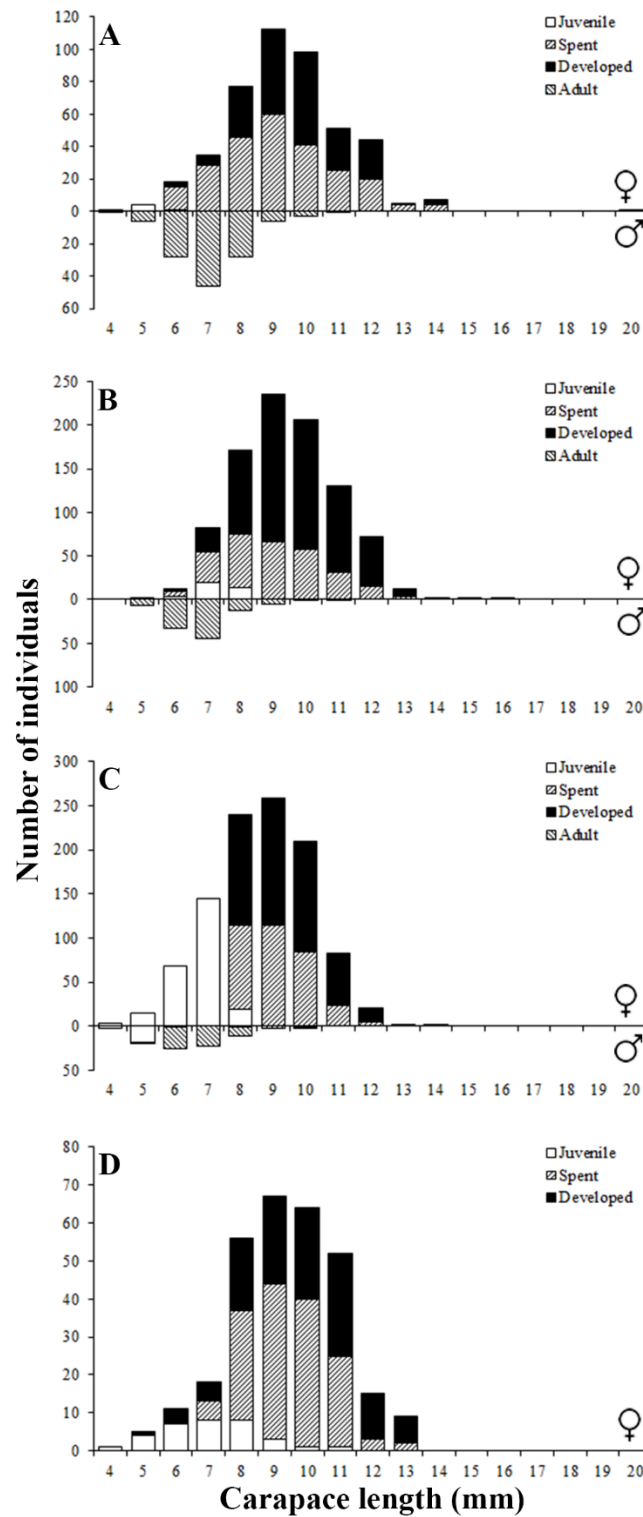


Figure 4: *Sicyonia dorsalis*: number of individuals per demographic group in each size class. Samples taken in southeastern Brazil from: A) July 2010 through June 2011 in the Macaé region; B) from July 2013 through June 2014 in the Ubatuba region; C) from July 2012 through May 2014 in the Cananéia region; and D) from July 2010 through June 2011 in the São Francisco do Sul region.

Sex ratio

During the studied period, we recorded a strongly female-biased sex ratio (Binomial test, $p < 0.05$) for all months and regions.

Individual growth and longevity

Throughout the regions, 3,258 females were analyzed to their estimate of individual growth parameters (MA: 453 individuals; UB I: 930 individuals; UB II: 829 individuals; CA: 1,046 individuals). As in the population structure (above), we observed that growth estimates also showed a decrease in asymptotic length as latitude increases, even though longevity estimates seems not to follow a clear pattern among the regions studied. Due to the low number of individuals in some sampled months, it was not possible to recognize growth cohorts for the SFS region, preventing us from estimating growth parameters in this area.

Based on modal values, we recognized the cohorts from which we constructed overall mean growth curves grouping all of the cohorts with estimates for CL_{∞} , k and longevity for each region sampled. For MA, 7 cohorts were distinguished, with estimates of $CL_{\infty} = 15.69$ mm, $k = 0.010$ and longevity = 458 days (1.26 year) (Fig. 5). For UB I, 6 cohorts were distinguished, with estimates of $CL_{\infty} = 16.32$ mm; $k = 0.010$ and longevity = 441 days (1.21 year) (Fig. 6). In UB II, 6 cohorts were distinguished, with estimates of $CL_{\infty} = 13.75$ mm, $k = 0.009$ and longevity = 485 days (1.33 year) (Fig. 7). Finally, we recognized 5 cohorts for CA, with estimates of $CL_{\infty} = 13.14$ mm, $k = 0.009$ and longevity = 489 days (1.34 year) (Fig. 8).

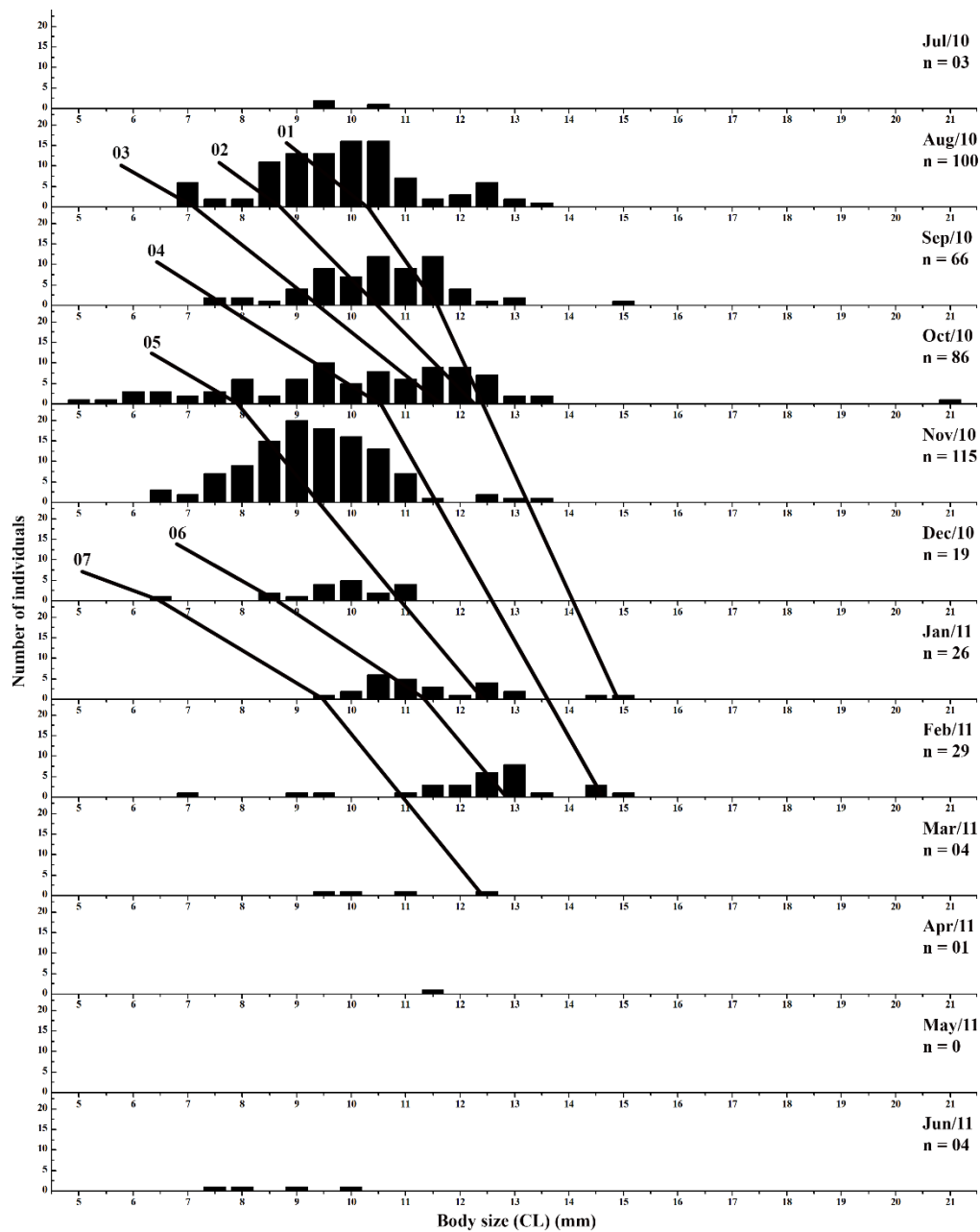


Figure 5: *Sicyonia dorsalis*: growth cohorts observed for females sampled in the Macaé region, from July 2010 through June 2011, based on the Von Bertalanffy growth model.

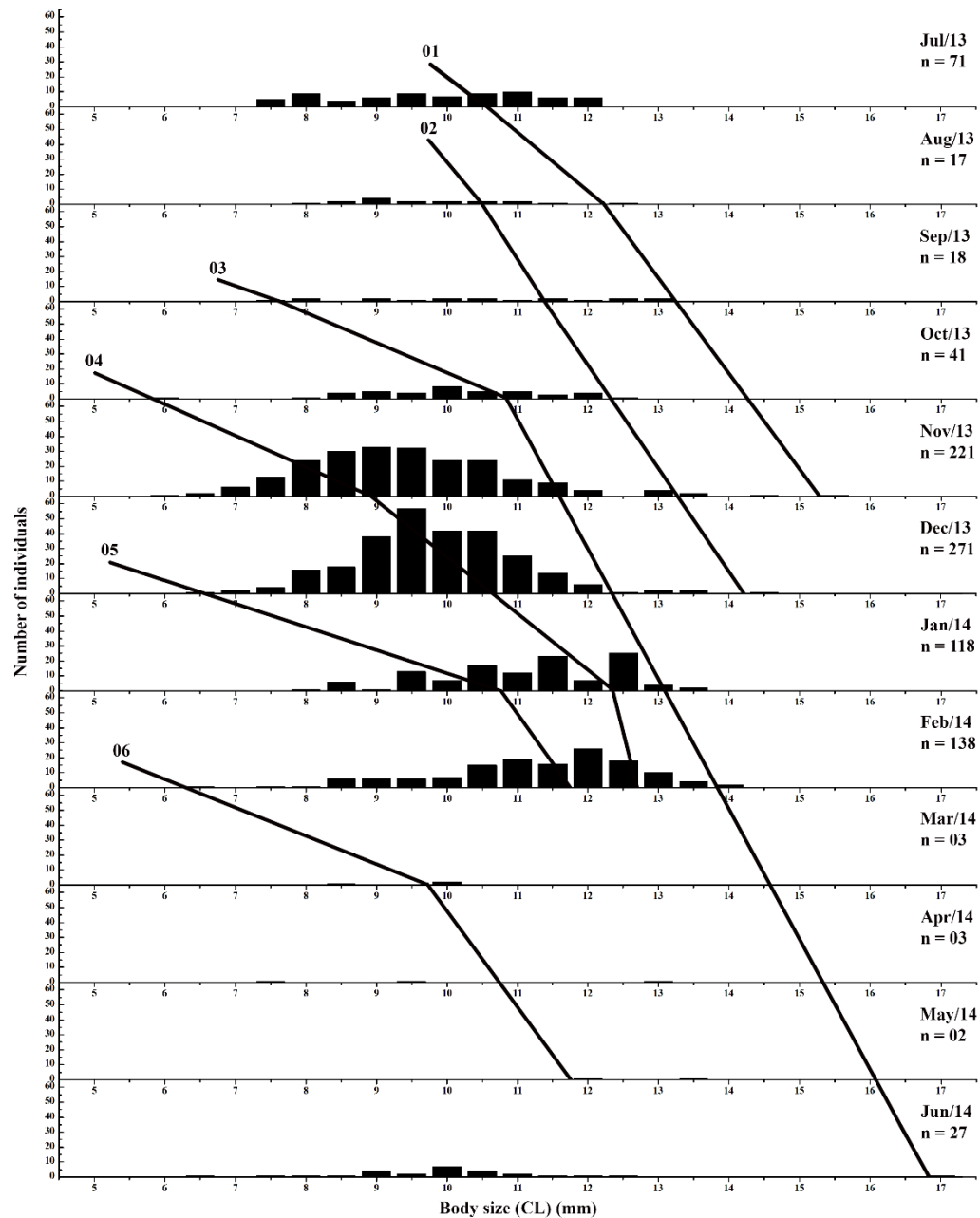


Figure 6: *Sicyonia dorsalis*: growth cohorts observed for females sampled in Ubatuba I region, from July 2013 through June 2014, based on the Von Bertalanffy growth model.

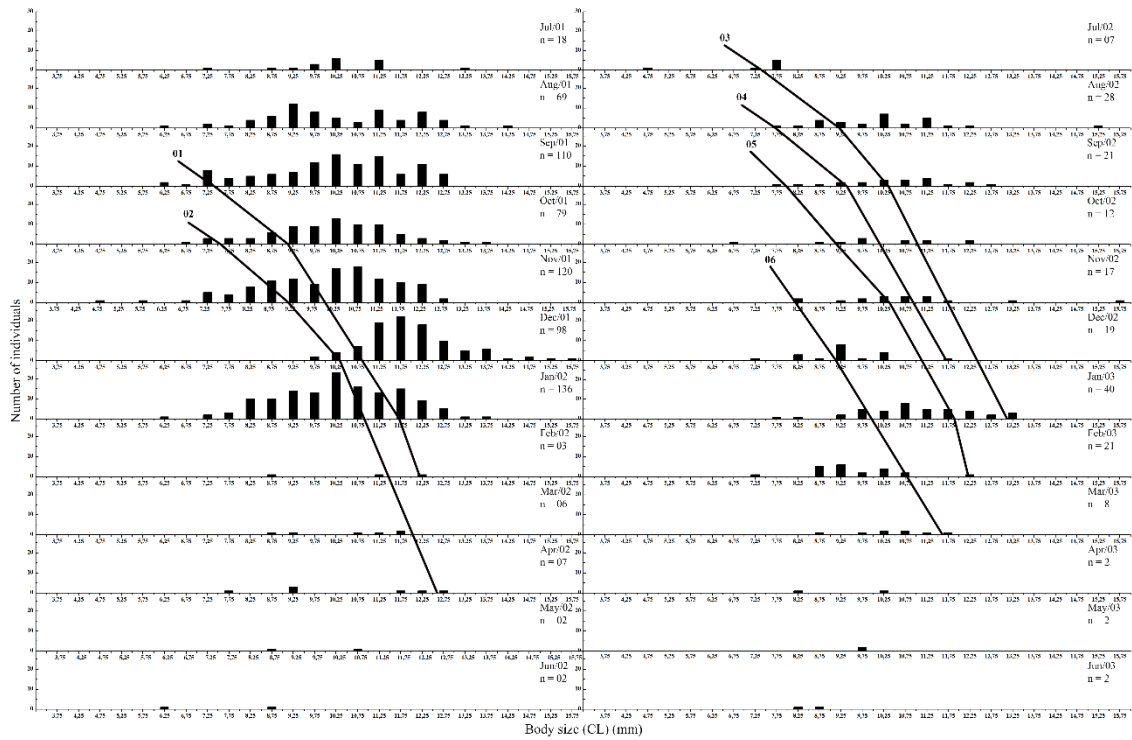


Figure 7: *Sicyonia dorsalis*: growth cohorts observed for females sampled in Ubatuba II region, from July 2001 through June 2003, based on the Von Bertalanffy growth model.

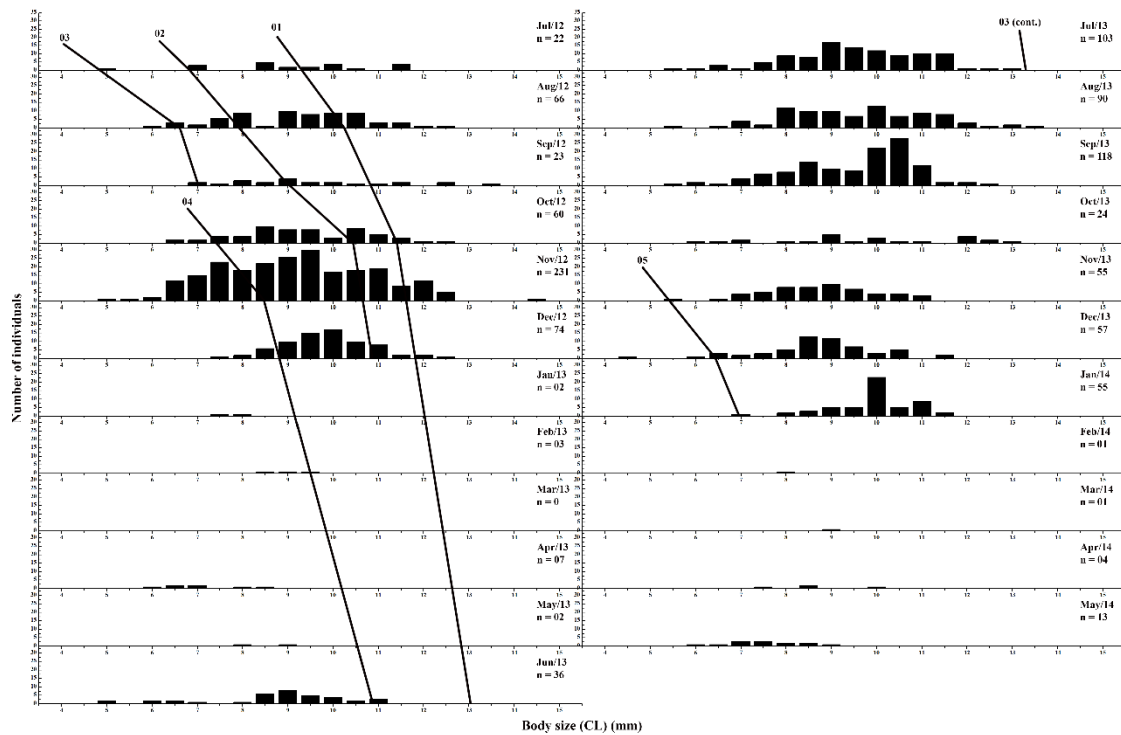


Figure 8: *Sicyonia dorsalis*: growth cohorts observed for females sampled in Cananéia region, from July 2012 through May 2014, based on the Von Bertalanffy growth model.

Growth curves differed significantly among females from all the regions (F test, $p < 0.05$), indicating that one single curve cannot be applied to explain the growth rate for *S. dorsalis* populations sampled in different locations along the southeastern Brazilian coast.

Reproductive periodicity and juvenile recruitment

For all of the regions, we observed that reproductive period was discontinuous throughout the year (seasonal). Even though the percentage of reproductive females was high all year in MA and UB I, during some periods the overall abundance of adult females was very low, so it should not be considered as an effective reproductive period. Using these criteria, we observed a slight decrease in the number of months composing the reproductive period as latitude increased (7-8 months in MA, UB I and CA; 6 months in SFS).

In MA, the reproductive period lasted for 7 months (from August 2010 through February 2011), comprising the winter-summer seasons (Fig. 9). In this area, salinity means negatively influenced the abundance of reproductive females with a +1 month lag (Crosscorrelation= -0.62; $p < 0.05$) and adult males with a +2 months lag (Crosscorrelation= -0.62; $p < 0.05$). The abundance of adult males showed positive correlation with the abundance of reproductive and spent females (Crosscorrelation= 0.96 and 0.82, respectively; $p < 0.05$), with no time lag; and the abundance of juveniles (= recruits) showed a positive association with the number of reproductive females (Crosscorrelation= 0.68; $p < 0.05$) and adult males (Crosscorrelation= 0.65; $p < 0.05$), both in a -2 months lag. However, due to the low number of juvenile individuals throughout the year, it was not possible to determine any recruitment periodicity for this region.

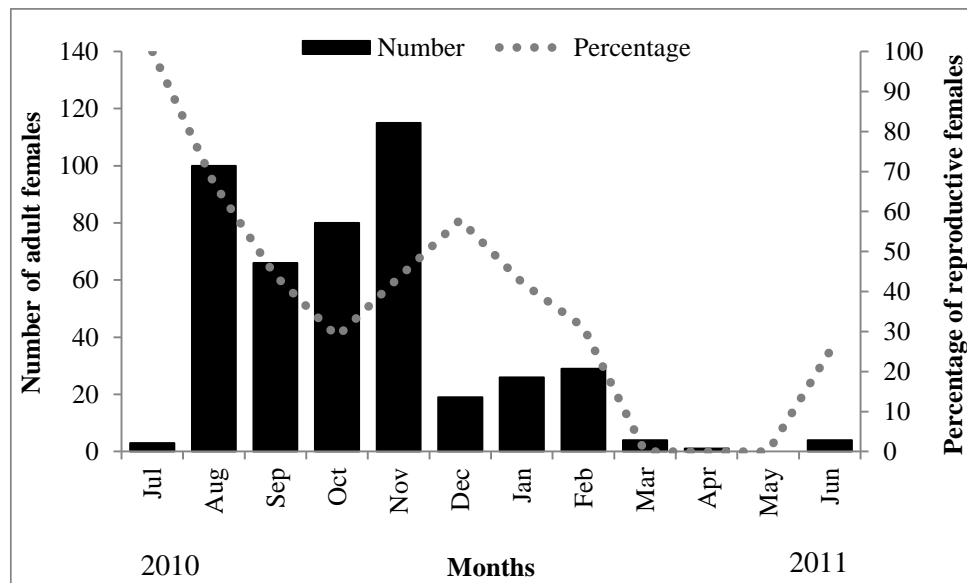


Figure 9: *Sicyonia dorsalis*: reproductive periodicity for individuals sampled from July 2010 through June 2011 in the coastal area from Macaé Region, Rio de Janeiro State, Brazil.

In UB I, the reproductive period lasted for 8 months (from July 2013 through February 2014), comprising the winter-summer season, although the abundances observed in March and April 2014 were not high enough to represent a reliable population sample (Fig. 10). In this area, the abundance of juveniles showed a positive association with that of reproductive females (Crosscorrelation= 0.86; $p < 0.05$) and adult males (Crosscorrelation= 0.73; $p < 0.05$), with a +1 month lag. The abundance of adult males showed positive association with that for reproductive females, with no time lag (Crosscorrelation= 0.85; $p < 0.05$) and with spent females with a 0 and -1 month time lag (Crosscorrelation= 0.63 and 0.69, respectively; $p < 0.05$). The abundance of adult males showed a negative association with temperature means, with a +2 months lag (Crosscorrelation= -0.63; $p < 0.05$), and a negative association with the salinity mean values, with a -3 month lag (Crosscorrelation= -0.75; $p < 0.05$). On the other hand, reproductive females showed a positive association with the salinity mean values, with a 0 and +1 month lag (Crosscorrelation= 0.71 and 0.69, respectively; $p < 0.05$). Recruitment seems to be highly seasonal, once we only obtained juveniles in November and an additional single individual in January.

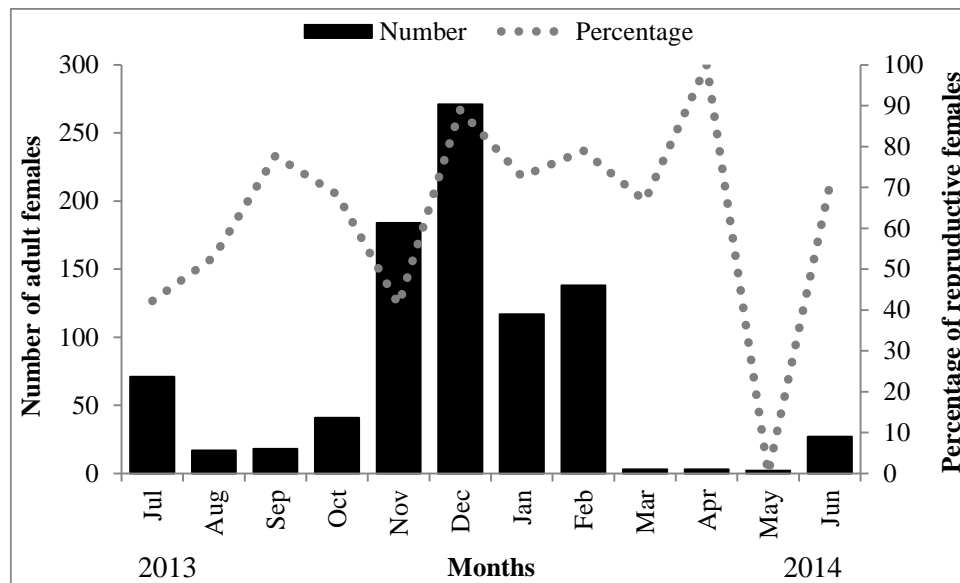


Figure 10: *Sicyonia dorsalis*: reproductive periodicity of individuals sampled from July 2013 through June 2014 in the coastal area from Ubatuba I region, São Paulo State, Brazil.

In CA, the reproductive period lasted for 8 months (from June 2013 through January 2014), comprising the winter-spring season (Fig. 11). We observed a positive association between the abundances of adult males and reproductive females, with no time lag (Crosscorrelation= 0.75; $p < 0.05$), as well as with the abundance of spent females (Crosscorrelation= 0.60; $p < 0.05$). The abundance of juveniles showed a positive association with reproductive females (Crosscorrelation= 0.83; $p < 0.05$) and adult males (Crosscorrelation= 0.82; $p < 0.05$). The abundance of juvenile individuals showed a negative association to the monthly values of temperature (Crosscorrelation= -0.43; $p < 0.05$). The recruitment period showed some similarity to the periods of higher abundance on the percentage of reproductive females (from June 2013 through January 2014), with a peak in November (excluding months in which the abundance of individuals was not satisfactory).

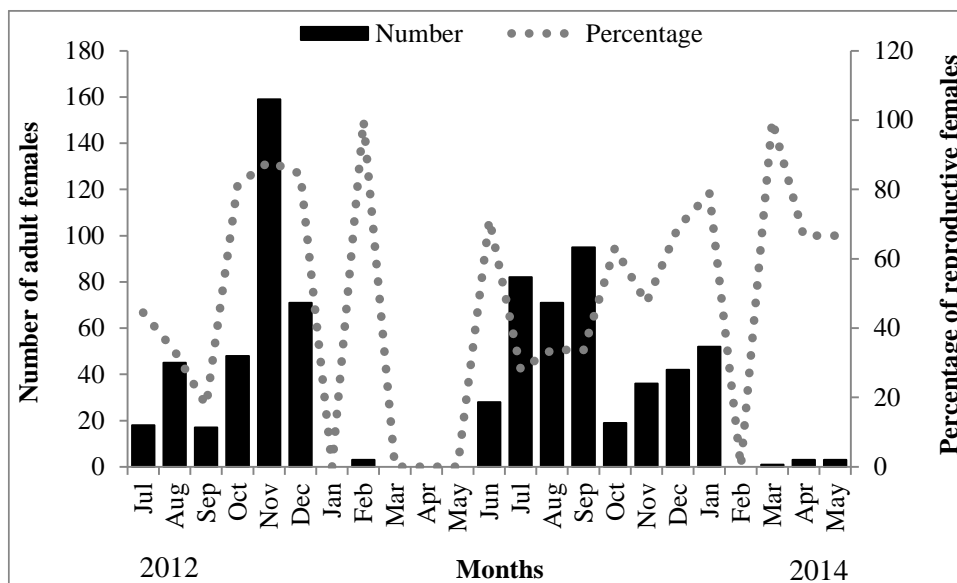


Figure 11: *Sicyonia dorsalis*: reproductive periodicity of individuals sampled from July 2012 through May 2014 in the coastal area from Cananéia region, São Paulo state, Brazil.

In SFS, the reproductive period lasted for 6 months (July-December), comprising winter and spring seasons (Fig. 12). We observed a positive association between the abundance of juveniles and the one observed for reproductive females (Crosscorrelation= 0.77; $p < 0.05$), and a negative association between juveniles and temperature means in a -1 month lag (Crosscorrelation= -0.68; $p < 0.05$). The abundance of reproductive females showed a negative association to the temperature means in a 0 and -1 month lag (Crosscorrelation= -0.77 and -0.80, respectively; $p < 0.05$). Unfortunately, the low abundance of juveniles ($n= 3$) was not satisfactory so that we could define a recruitment period in this area.

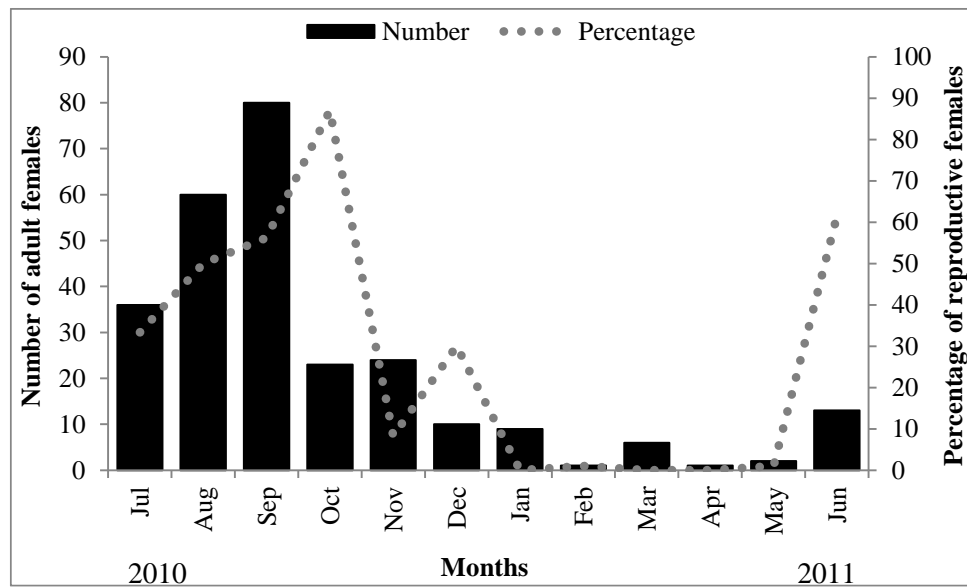


Figure 12: *Sicyonia dorsalis*: reproductive periodicity of individuals sampled from July 2010 through June 2011 in the coastal area from São Francisco do Sul region, Santa Catarina state, Brazil.

Discussion

In this study, we show how local environmental conditions affect growth and reproduction of the shrimp *S. dorsalis* from different locations, even in a narrow range of latitudes. Further, our results suggest that *S. dorsalis* completes its lifecycle in the inshore area in all of the locations studied, given that we sampled both reproductive adults and juvenile recruits (even though the last in a low abundance). Additionally, we could detect a possible effect of an area protected from fishing off Ubatuba, Brazil, over a ten-year period, since larger individuals were sampled in this region after the establishment of this area. Our results complement the current knowledge about shrimp populations, allowing and understanding how the population biology of this and other species have evolved in light of environmental variation in different geographic areas.

In decapod crustaceans, males of some species can show bigger body sizes when compared to females of the same species, what can be considered as a selective pressure associated with their reproductive behavior. In such species, males displaying more robust bodies show a higher success defending females and their mating territory, as well as in agonistic encounters with other males for other resources. However, the mating system of *S. dorsalis* is promiscuous (“pure search”), in which males do not defend or fight over females or mating territories (Bauer 1996). In such penaeoid

species, as in caridean shrimps with similar mating systems, there is no selection for large male size or enhanced weaponry (Bauer 2004).

Females of *S. dorsalis* from all studied regions showed larger sizes when compared to males, showing a strong sexual dimorphism in size in penaeoids from southern Brazil, as already noted also by Castilho *et al.* (2008c) in the UB region for this species. Sexual dimorphism in body size (female > male) is considered the rule in the biology of penaeid shrimps, since female shrimp fecundity increases with size (Boschi 1969, Gab-Alla *et al.* 1990, Castilho *et al.* 2008a, c, 2015b). The same pattern on sexual dimorphism was also observed in other penaeid species in the Brazilian coast, such as *X. kroyeri* (Grabowski *et al.* 2014, 2016, Castilho *et al.* 2015a), *Rimapenaeus constrictus* (Stimpson, 1874) (Costa & Fransozo 2004, Garcia *et al.* 2016, Lopes *et al. in press*) and *A. longinaris* (Castilho *et al.* 2007a, 2015b), among others.

In this study, differences in size were observed in females from different locations by comparing maximum body sizes and estimates of growth parameters. There was a decrease in maximum female body size as latitude increased. The biggest female sizes were observed in MA (most northern investigated region), and the smallest, from samples taken in SFS (most southern studied region). Estimates of asymptotic size were higher in females from UB I and MA, followed by those from CA. Interestingly, this result is just the opposite of the expected trend in larger body size with increasing latitude in decapod shrimps (Bauer 1992). In that paradigm, the lower temperatures of higher latitudes lead to slower growth but increased longevity, allowing individuals to attain larger body sizes in their lifetime. Higher temperatures generally found in lower latitudes may induce an increase to growth coefficient through higher metabolism, with more frequent molting but with smaller size increases at each molt, leading to small lifetime body size in a species with a shorter lifespan (Bauer 1992, Castilho *et al.* 2015a).

This was shown for *A. longinaris* on the eastern South American coast, in which larger female sizes (CL) were observed with increasing latitude, when comparing individuals from the Brazilian and the Argentinean populations (Castilho *et al.* 2007b).

However, Grabowski *et al.* (2014) did not find the same pattern of latitudinal variation for asymptotic body size for *X. kroyeri* along the Brazilian coast. In this study, the authors compared data on the growth of this tropical species and found that the highest asymptotic length estimates were found by Santos & Ivo (2000) in the northeastern region, while the lowest ones were estimated by Heckler *et al.* (2013) in a

southeastern area. Such results were associated with the disagreement in sampling and growth estimating methods along the coast (Fonseca 1998, Freire 2005), the species' overfishing along the analyzed area (D'Incao *et al.* 2002, Vasconcellos *et al.* 2007) or the existence of two *Xiphopenaeus* cryptic species (Gusmão *et al.* 2006).

In this study, however, growth coefficients seemed not to follow a clear pattern with latitude. This could be held as an evidence of a migratory connection between groups that are part of a same population (Castilho *et al.* 2015b). Carvalho-Batista *et al.* (2014) inferred population connectivity for *A. longinaris* along its distributional range, and found no genetic variability for this species at an intraspecific level. According to the authors, the high efficiency on larval dispersal is an important factor that may be responsible for the homogeneity in its distribution over a wide geographical range (Gopurenko & Hughes 2002, Carvalho-Batista *et al.* 2014). For *P. muelleri*, a colder water species, it was observed that larvae can travel along 120 to 300 nautical miles, transported by the coastal currents (Boschi 1989). Adult stage of *Melicertus plebejus* (Hess, 1865) was also observed to migrate, in distances up to 930 km (Ruello 1975) along the Australian coast. Castilho *et al.* (2008b) found that *S. dorsalis* could migrate, following movement of preferred environmental conditions, from southern regions toward northern ones during the spring. They associated this activity to the presence of the SACW. Additionally, Almeida *et al.* (2012) pointed out that similarities in reproductive biology among populations located thousands of kilometers apart could be considered evidences for the existence open metapopulations with extensive connectivity.

Growth analyses' results also showed a possible effect of the establishment of a marine protected area (MPA) in the UB region, in October 2008. Comparing maximum body sizes and asymptotic lengths from 2001-2003 to the ones sampled in 2013-2014, we observed an increased body size (13.75 mm CL and 16.3 mm, respectively), but on the other hand, a decrease in estimated longevity (485 days in 2001-2003, to 441 days in 2013-2014). Almeida *et al.* (2012) investigated the reproductive biology of *X. kroyeri* in Fortaleza Bay, which is also located inside this MPA. The authors highlighted the existence of a nursery ground for the species within the region, and stated the importance of long-term studies to investigate the effects of such protection to the recovery of stocks in areas which are heavily exploited. Even though *S. dorsalis* is not a commercially important species along the Brazilian coast due to its small size and carapace hardness, it comprises a great portion of the bycatch fauna, as pointed out in

the introductive session of this research (for additional information, see Costa *et al.* 2005, Castilho *et al.* 2008b). Therefore, information on its biological requirements are of great value to the preservation of the species and to the effects of a marine protected for other ecologically and commercially important penaeoid shrimps.

Dall *et al.* (1990) pointed out that penaeid shrimps have short life spans, from 1-2 years. However, life span and other population parameters can vary intragenerically when populations from different geographical areas and latitudes are compared. Bauer (1992) suggested different environmental features that might be responsible for such variation in the genus *Sicyonia* Edwards, 1830. The author compared body size and longevity in species from different biogeographical areas: *S. parri* (Burkenroad, 1934) and *S. laevigata* Stimpson, 1871 (Western Atlantic tropical species) showed a size range of 3-9 cm CL and longevity of 6-8 months; *S. brevirostris* (Stimpson, 1874) (Western Atlantic subtropical species), 17-35 cm CL and 20-22 months; and *S. ingentis* (Burkenroad, 1938) (Eastern Pacific temperate species), 24-45 cm CL and ≥ 22 months.

Higher latitude species showed a tendency towards to seasonal reproductive periodicity when compared to tropical species, possibly induced by a concomitant seasonality in larval food availability. Females live longer in higher latitudes, which gives them time enough to select a favorable period to reproduce, while the tropical females (which lives less than a year, at least in many caridean species; Bauer 2004) must establish and grow to the sexual maturity in any time of the year. There are many examples of increasing life span in higher latitudes, but it is important to remember that such feature is not a simple effect of lower temperatures or lower growth coefficient, but an adaptation of a whole life history in different environments (Vogt 2012). In this study, the estimated longevity did not show a clear pattern among the sampled regions, as the highest one was observed in CA, followed by MA and UB. The longevity estimates found in this study agree with those given for penaeid shrimps (1-2 years) (Dall *et al.* 1990). As pointed out by Grabowski *et al.* (2014), migratory activities and larval dispersion could increase gene flow among populations from the limited range of latitudes sampled in this study, perhaps making a latitudinal pattern impossible.

The studied region is strongly influenced by three water masses, from which the most important is the SACW, which brings low temperature and salinity to the areas where it is recognized (Castro-Filho *et al.* 1987, Carvalho *et al.* 1998, Pedrosa *et al.* 2006). The SACW brings with it a high concentration of nutrients, which leads to an increase in primary productivity in waters that it intrudes into (Pires 1992, Silveira *et al.*

2000, Odebrecht & Castello 2001, Castilho *et al.* 2008b, c). Considering that lower temperatures can exert a negative influence on growth, which in turn increases overall body size, it seems reasonable to identify higher carapace length values in UB and MA. Even though CA showed the marked decreases in temperature means (mainly in winter months), in MA and UB, it was lower in spring, but tended to be more homogeneous throughout the year. The connection between temperature, salinity (most altered environmental parameters with the presence of the SACW) and the abundance of individuals could be noted by their negative effect on growth coefficients and asymptotic body size.

Temperature and salinity also influenced reproductive and recruitment periods. Reproduction occurred seasonally, with most of the reproductive females sampled in winter-spring months, and critical decreases in their abundance observed on summer-autumn. Even though the reproductive period was approximately the same for the regions, it was possible to note a slight increase in the number of months in which the higher percentage of reproductive females was observed in each region as latitude decreases (from 6 months in higher latitudes to 7-8 months in lower latitudes). The same pattern (increase in number of reproductive months associated with more favorable temperature levels (in this case, with higher temperatures)) was also found by Aragón-Noriega (2007). In that study, carried out in the Gulf of California, the reproduction occurred during periods of warmer water temperature, varying from 7 months in lower latitudes (higher mean temperatures) to 4 months in higher ones (lower temperatures).

Vega-Pérez (1993) states that, due to the presence of SACW in the UB region, phytoplankton production is increased as shown by higher values on chlorophyll in the water column. Such an increase in primary production possibly stimulates increases in herbivorous zooplankton, as the highest density of planktonic organisms was observed in summer, and the lowest one, in winter. Other studies also pointed out the importance of SACW seasonal dynamics as an enrichment factor for marine communities off the southern Brazilian coast (Pires 1992, De Léo & Pires-Vanin 2006, Rocha *et al.* 2007, Castilho *et al.* 2008d). It is evident that high primary productivity is essential as a resource for larval shrimps, suggested by the match-mismatch hypothesis (Cushing 1975), which suggests that highest reproductive investment of marine planktotrophic species should coincide with seasonal highest abundance on phytoplankton.

Molting frequency is shorter during reproductive months, as energy for growth is funneled into reproductive effort (Anderson *et al.* 1985, Bauer & Rivera Vega 1992). For certain penaeid species, mating and female molting are correlated processes (Bauer 1996). In *Sicyonia* spp., females can store sperm for long periods in seminal receptacles after a reproductive molt and mating (Bauer 1991, 1996). In the present study, we could observe a correlation in the abundances of adult males and spent females, as the latter may molt and mate after using up their sperm supply after various spawns. The same relation between males and spent females was also observed in the Brazilian coast for the seabob shrimp *X. kroyeri* in Southern (Grabowski *et al.* 2016) and Southeastern Brazil (Heckler *et al.* 2013). On the other hand, the low abundance of adult females during certain periods of the year could be an evidence of a migration of females toward greater depths for spawning. Dall *et al.* (1990) stated that after mating, females tend to migrate to greater depths where spawning would occur. Additionally, Juneau (1977) suggested that mating and spawning might occur in deeper waters along the Gulf of Mexico, although it might be possible that they disappeared from study areas by migrating to other areas of similar depth not sampled.

Even though *S. dorsalis* is not exploited commercially along the Brazilian coast as a food source, it may play a critical role in marine food webs where it occurs by converting bacterial biomass from detritus into biomass, which will thus be available to the higher trophic levels (Castilho *et al.* 2008c). Studies on geographical variation of its basic population biology parameters are important in revealing possible inconsistencies in the current paradigms about latitudinal variation in life history parameters. Even though general models on geographical range can be useful in summarizing knowledge, narrow ranges in latitude can show unexpected and interesting results which contributes to knowledge about the population biology of penaeoid shrimps as well as optimize ways of conserving them.

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Capítulo 2

**Environmental singularities affect the population
dynamics of the temperate-region shrimp species
Pleoticus muelleri (Spence Bate, 1888) in the Atlantic
upwelling zone, southeastern Brazil**

Environmental singularities affect the population dynamics of the temperate-region shrimp species *Pleoticus muelleri* (Spence Bate, 1888) in the Atlantic upwelling zone, southeastern Brazil

Resumo

Este estudo teve como objetivo descrever como os fatores ambientais alteram os padrões na dinâmica populacional de *Pleoticus muelleri* ao longo da costa sudeste do Brasil. Amostras mensais foram realizadas em quatro regiões (Macaé ($\approx 22^\circ\text{S}$), Ubatuba ($\approx 23^\circ\text{S}$), Cananéia ($\approx 25^\circ\text{S}$) e São Francisco do Sul ($\approx 26^\circ\text{S}$)), com barcos de pesca de arrasto artesanal em profundidades de 5 a 17 metros, em diferentes períodos de julho de 2010 a junho de 2014. A influência ambiental sobre a dinâmica populacional foi avaliada por meio da análise de redundância para cada região separadamente, considerando significantes apenas as variáveis com valores de *score* maiores que 0,4 e menores que -0,4. Os parâmetros de crescimento foram estimados utilizando a equação de Von Bertalanffy, e a longevidade, utilizando a mesma formula, invertida, comparando os resultados entre as regiões utilizando o teste F ($p \leq 0,05$). Os períodos reprodutivos e de recrutamento foram tidos como os períodos com maior frequência de fêmeas reprodutivas e jovens, respectivamente, para cada região, e diferenças na razão sexual foram analisadas por meio do teste binomial ($p \leq 0,05$). Ao todo, 3.318 indivíduos foram analisados, sendo as fêmeas mais abundantes em todas as regiões, provavelmente devido a diferentes necessidades migratórias ou taxas diferenciais de mortalidade entre os sexos. Fêmeas também alcançaram maiores tamanhos corpóreos, uma possível adaptação evolutiva para aumentar sua fecundidade. Foi possível observar uma tendência de diminuição no tamanho assintótico e tamanho máximo atingido com o aumento da latitude, provavelmente devido às particularidades observadas na costa brasileira. Dentre elas, a influência de massas de água, as quais trazem águas frias de regiões profundas até áreas mais rasas, fazendo com que as regiões ao norte da área estudada apresentem características próximas às observadas em regiões temperadas. A periodicidade reprodutiva apresentou uma tendência à continuidade nas áreas ao norte (mais frias) e à sazonalidade nas áreas ao sul (mais quentes), podendo também estar relacionada à influência de correntes marinhas em Macaé e Ubatuba.

Environmental singularities affect the population dynamics of the temperate-region shrimp species *Pleoticus muelleri* (Spence Bate, 1888) in the Atlantic upwelling zone, southeastern Brazil

Abstract

This study aimed to describe how environmental conditions could alter the expected patterns for population dynamics of *Pleoticus muelleri* along the Brazilian coast. Monthly samples were carried out in four different regions throughout the southeastern Brazilian coastal area (Macaé ($\approx 22^\circ\text{S}$), Ubatuba ($\approx 23^\circ\text{S}$), Cananéia ($\approx 25^\circ\text{S}$) and São Francisco do Sul ($\approx 26^\circ\text{S}$)), using artisanal fishing boats to cover a 5-17 m depth variation, in different periods from July 2010 through June 2014. The influence of environmental factors over the population dynamics was assessed by performing a redundancy analysis (RDA) for each region, separately, considering meaningful only the variables with score values higher than 0.4 and lower than -0.4. Growth parameters were analyzed using the Von Bertalanffy's growth model, while longevity was calculated using its inverse formula, comparing the results for each region using the F test ($p \leq 0.05$). Reproductive and recruitment periodicity were considered as the periods with higher frequency of reproductive females and juveniles, respectively, for each region, and differences in sex ratio were tested by the binomial test ($p \leq 0.05$). We analyzed 3,318 individuals to its population structure and reproductive biology, from which females were more abundant in all regions, a likely response to different migration needs or mortality rates. Females also attained bigger body sizes, an evolutionary adaptation in order to produce a higher number of eggs, increasing their fecundity. We observed a decreasing trend for asymptotic length estimates and maximum attained body sizes as latitude increases, (the opposite from what was expected), probably caused by the geographical singularities observed along the Brazilian coast. Among them, the influence of water masses (mainly the South Atlantic Central Water), which brings deeper cold waters to the shallower areas and makes the northern studied regions to present cool-temperate water features. The reproductive periodicity was similar to the periods with higher abundance of individuals, showing a tendency to continuity at northern (colder) regions, and to seasonality at southern (warmer) ones, what may also be related to the influence of water masses in Macaé and Ubatuba.

Introduction

For decades, decapod crustaceans have been exploited as food resource for human consumption, becoming an income source for uncountable fishermen around the globe. (Lizarraga-Cubedo *et al.* 2008). Despite its socioeconomic importance for several fishing communities along the Brazilian coast, trawling fisheries have been held responsible for many degradation issues related to coastal resources (Mantelatto *et al.* 2016).

Two aspects can be highlighted from the known consequences of trawling on soft bottoms. The first of them is related to damages on the physical aspects of the seafloor and consequent losses in terms of the inhabiting communities. The second one concerns the low selectivity of the adopted fishing gear, and the consequent amount of species which are discarded back to the sea (moribund, or even dead) due to their: a) small size; or b) lack of direct economic interest (Broadhurst & Kennelly 1996, Hall 1999, Kaiser *et al.* 2002, Mantelatto *et al.* 2016). Such amount of discarded animals is known as bycatch fauna, quite diversely composed by fishes, crustaceans, mollusks and other groups. It is always considerably more abundant than the target species, and its biomass can become 3 to 15 times larger than the amount of captured target species (Coelho *et al.* 1986, Branco 2005, FAO 2015).

In the Brazilian southeastern coast, it was possible to observe an increase in the number of shrimp landings over the past few years. Only in the São Paulo state, this number almost tripled, from 6,151 trawling boats in 1998 to 16,594 in 2010 (Castilho *et al.* 2012, Instituto de Pesca, São Paulo <<http://www.pesca.sp.gov.br>>). Most of the fisheries in southern and southeastern Brazil aim to capture *Farfantepenaeus brasiliensis* (Latreille, 1987) and *F. paulensis* (Pérez-Farfante, 1967), *Xiphopenaeus kroyeri* (Heller, 1862), *Artemesia longinaris* Spence Bate, 1888, *Litopenaeus schmitti* (Burkenroad, 1936) and *Pleoticus muelleri* (Spence Bate, 1888). The intense fishery may lead to a natural decrease in abundance of the most profitable species, what consequently increases the economic interest to species such as *P. muelleri* (D’Incao *et al.* 2002, Costa *et al.* 2004, Castilho *et al.* 2012).

In order to achieve the rational exploitation of this resource and avoid the stocks collapse, it is important to create effective fisheries management plans, considering knowledge about its growth and reproductive biology. Such aspects play a crucial role in their population dynamics, and thus, strongly influence their life history strategies (Petriella & Boschi 1997, Lizarraga-Cubedo *et al.* 2008). Consequently, it can be

helpful in monitoring, designing and implementing management policies, which would allow us to reach a balance between exploitation and regeneration of the exploited stocks (Castilho *et al.* 2012).

In the study of geographic variation of marine invertebrates, one of the most well established concepts states that individuals tend to show latitudinal differences in the growth and reproductive biology traits along their geographical distribution (Thorson 1950, Bauer 1992). Among the environmental factors that have been held responsible for such phenomenon since then, it is possible to cite temperature variation (Thorson 1950), availability of larval food resources (Clarke 1988) and the type of habitat (Belk *et al.* 1990), among others. In this sense, latitudinal variation in reproductive aspects of crustaceans is a popular hypothesis, which has been tested for several species (Bauer 1992, Bauer & Lin 1994, Castilho *et al.* 2007b, Costa *et al.* 2010, Grabowski *et al.* 2014). One of the main goals of the research concerning reproductive ecology of benthic invertebrates is to describe and compare latitudinal variation in their population structure and reproductive seasonality, which may reveal the factors that are responsible for such patterns (Bauer 1992, Castilho *et al.* 2007a, b).

Therefore, comparing reproductive strategies among populations from different regions turns possible for us to understand in a better way such variations in latitudinal patterns. Such comprehension can be very useful in order to generate and test hypotheses about causal factors that could act on reproduction. The reproductive traits can differ according to distinct environmental conditions among different latitudes because the behavior of penaeids is strongly affected by their physiological processes, which, in turn, are related to environmental factors (Dall *et al.* 1990, Bauer 1992, Castilho *et al.* 2007b). For several marine invertebrate populations found near the equator, it is possible to observe a continuous reproduction, probably due to the constant temperature conditions found in such tropical seas, which provide high temperatures throughout the year. The seasonal variations in water temperature have historically been considered an environmental stimulus (proximate factor) to gametogenesis, defining the breeding season of uncountable animal species and being strongly tied to latitude (Orton 1920, Bauer 1992). Among the aspects that can be useful in such studies, the breeding period, fecundity and size at the onset of maturity are considered key factors in their life history (Stearns 1976).

Another fundamental aspect of the study on population dynamics of exploited animals is their growth. Particularly for crustaceans, growth is a discontinuous process

that occurs in “jumps”, once their hard exoskeleton does not allow increases in size and weight to be expressed in a continuous way. Therefore, their growth is shown almost as an immediate substantial increase in size, weight and shape that occurs when a molt is produced, implying in the discard of the old exoskeleton and in the synthesis of new tissues, being the whole process regulated by a complex endocrine system (Petriella & Boschi 1997). Therefore, the lack of studies evolving growth in crustaceans is related to the absence of fixed structures that could provide information about aging, what turns difficult to choose the methodology to be adopted. This is the reason why knowledge about growth and longevity of penaeid shrimps is still limited, although these are important aspects on the study of population traits of species which are vulnerable to the human exploitation (Petriella & Boschi 1997, Branco 2005, Vogt 2012). Considering such difficulties in studying the growth of these animals, many estimating methods have been suggested. Among them, the Von Bertalanffy (1938)’s growth model stands out among the other mathematical expressions used to describe growth in marine organisms, due to its efficiency in adjusting itself to crustaceans’ biological processes (Petriella & Boschi 1997).

Concerning the biological aspects that can effectively describe and improve the understanding about the life cycle of a given species, some studies have already been addressed about *P. muelleri* in the southeastern Brazilian coastal area. Among them, Costa *et al.* (2004) and Batista *et al.* (2011) studied its ecological distribution; Castilho *et al.* (2008d) described the relation between several species abundance and environmental factors; Lopes *et al.* (2014) assessed its diel variation in abundance and size; Castilho *et al.* (2008a) addressed its reproductive aspects; and Castilho *et al.* (2012) discussed its growth and reproductive dynamics. Despite their undeniable importance to the scientific knowledge of the species, the studies carried out up to this moment focused on the description of regional *P. muelleri*’s biological aspects. Up to now, the only study available concerning the geographical variation of this species in this region was published by Castilho *et al.* (2012), addressing the Ubatuba and Caraguatatuba regions.

Based on this scenario, this study aimed to describe how local environmental conditions could alter the expected patterns for population dynamics of *P. muelleri* along the Brazilian coast, comparing data from four different locations within a 5-degree latitudinal variation. The specific goals were established in order to test the hypothesis that the water masses occurring along the Brazilian littoral area may lead to

exceptions in the expected variation in their reproductive, growth and ecological aspects.

Material and methods

Sampling

Sampling were conducted along the southeastern Brazilian coast, including four different locations within a 5-degree latitudinal variation (Macaé, Rio de Janeiro state, $\approx 22^{\circ}\text{S}$ - MA; Ubatuba, São Paulo state, $\approx 23^{\circ}\text{S}$ - UB; Cananéia, São Paulo state, $\approx 25^{\circ}\text{S}$ - CA; and São Francisco do Sul, Santa Catarina state, $\approx 26^{\circ}\text{S}$ - SFS). In all of the sampling sites, 30-min monthly trawls were conducted for each station in each region, using similar shrimp-fishing boats, in order to avoid differences in the adopted methodology for each region. In average, boats were equipped with double-rig nets (mesh size: $\cong 3$ cm; mesh gap: $\cong 11.5$ m; boat velocity during trawls: $\cong 1.5$ knots), the same as used in artisanal shrimp fisheries along the Brazilian coast.

In the MA region, four sampling stations were studied, covering a 5-15 m depth variation, from July 2013 through May 2014. In the UB region, four sampling stations were adopted, covering a 5-15 m depth variation, from July 2013 through June 2014. In the CA region, we selected seven sampling stations (5-15 m depths), from July 2012 through May 2014. In the SFS region, five sampling stations were determined, covering a 5-17 m depth range, from July 2010 through June 2011 (Fig. 1). It is noteworthy that due to adverse weather conditions, it was not possible to conduct any samples in March 2013 in the CA region.

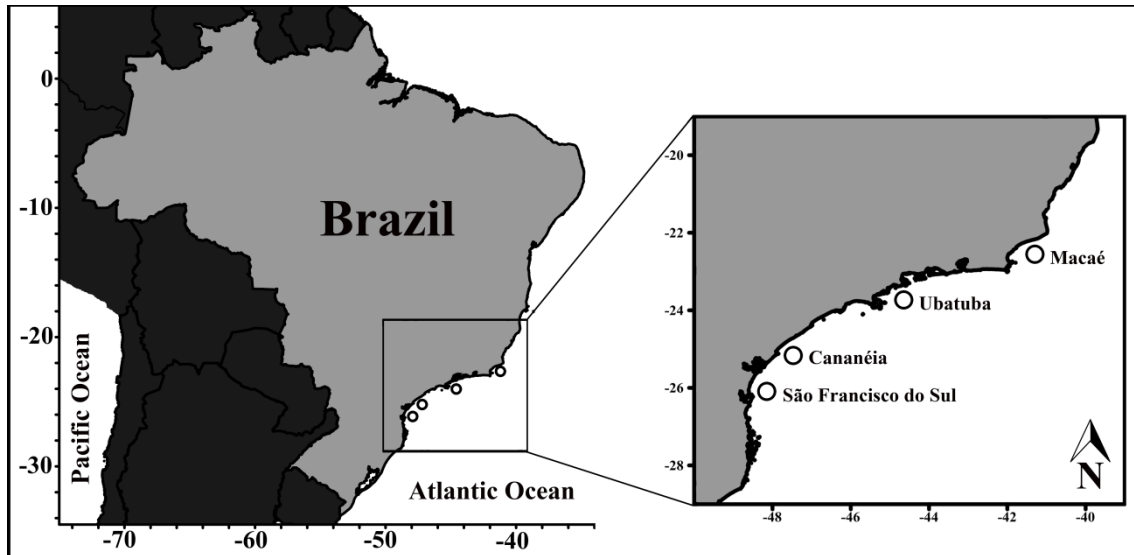


Figure 1: Map of the Brazilian coastal area, highlighting the southeastern littoral and the sampling locations.

Environmental data

A Van Dorn bottle was used to obtain bottom water samples for each month, while a Petersen grab was used to take sediment samples, for each season of the year.

Salinity was measured using an optical refractometer, while temperature was assessed using a mercury thermometer. Sediment samples were obtained in each sampling station for each season of the year (summer: January through March, and so on), and then frozen individually, in order to avoid possible changes in organic matter content (O.M.). In laboratory, samples were oven-dried (70 °C for 72h) and then weighed, from which we took a 10-g subsample to determine the O.M. (ash-weighted), and a 100-g subsample to determine the granulometry, adopting the methodology used by Mantelatto & Fransozo (1999) and Castilho *et al.* (2015), as it follows. Grain size classification followed the American standard, and fractions were expressed on the phi scale (ϕ), using the formula: $\phi = \log_2 d$, where: d = grain diameter (mm) (Tucker 1988) (e.g.: $-1 = \phi < 0$ (very coarse sand); $0 = \phi < 1$ (coarse sand); $1 = \phi < 2$ (intermediate sand); $2 = \phi < 3$ (fine sand); $3 = \phi < 4$ (very fine sand); and $\phi \geq 4$ (silt + clay). Finally, ϕ was calculated by cumulative particle-size curves plotted using the ϕ scale. We used the values corresponding to the 16th, 50th and 84th percentiles to determine the mean sediment diameter, using the formula $Md = (\phi_{16} + \phi_{50} + \phi_{84})/3$ (Castilho *et al.* 2008d).

Population structure, growth and reproductive biology

Individuals were identified to species (Costa *et al.* 2003), measured to its carapace length (linear distance from the orbital angle to the carapace's posterior margin - CL) using vernier calipers, and identified to sex, according to the presence of petasma (males) or thelycum (females) (Pérez-Farfante & Kensley 1997). The length frequency distribution was described separately for each sex using 2-mm CL classes, and then compared to identify differences in its distribution.

Growth and longevity estimates were based on the Von Bertalanffy (1938)'s growth model for males and females separately (Boschi 1969), using the methodology adopted by Simões *et al.* (2013) and Grabowski *et al.* (2014). Modal values were determined for each CL frequency using the software PeakFit (Automatic Peak Fitting Detection and Fitting, Method I-Residual, no Data Smoothing), from 1-mm size classes (Fonseca & D'Incao 2003). Models were plotted on a scatter graph vs. age, aiming to analyze the growth rate of the cohorts. Growth parameters (CL_{∞} : asymptotic carapace length; k : growth coefficient (day^{-1}); t_0 : theoretical age at size zero) were estimated using the Solver supplement (Microsoft Excel v. 2013), applying the Von Bertalanffy (1938) growth model: $CL_t = CL_{\infty}[1 - \exp^{-k(t-t_0)}]$ (CL_t : carapace length at age t). The cohorts growth rhythm were evaluated based on its similarity to previously observed values for this species (Castilho *et al.* 2012), as well as to the maximum sizes obtained in field sampling. The estimated growth curves for both sexes were compared to each other by an F test ($p \leq 0.05$) (Cerrato 1990). Longevity was estimated based on the inverse Von Bertalanffy growth model, with a modification suggested by D'Incao & Fonseca (1999): $\text{longevity} = 0 - (1/k) \ln[1 - CL_t/CL_{\infty}]$, considering $t_0 = 0$ and $CL_t/CL_{\infty} = 0.99$.

The stage on gonadal development in females was assessed by the macroscopic examination of the gonads, which are visible through the transparent exoskeleton. Therefore, according to the color and volume occupied inside the cephalothorax, the degree of ovarian development was classified in three stages. Immature (juveniles) individuals showed ovaries varying from thin to thicker transparent strands; spent showed whitish colored ovaries, larger and thicker than the juveniles' ones; and reproductive, much thicker ovaries, ranging from light to olive green (Costa & Fransozo 2004, Castilho *et al.* 2007a). On the other hand, males' maturity (= adult) condition was determined by examining the shape of the petasma, which presents separated petasmal lobes when juveniles, while linked ones when adults (Pérez-Farfante 1969, Boschi & Scelzo 1977). Concerning adult males, we considered spermatophore-bearing

(reproductive) males the ones in which spermatophores were visible and occupied any portion of (or the entire) terminal ampoules, as well as spent males, the ones with no macroscopically visible spermatophore (Castilho *et al.* 2015, Garcia *et al.* 2016). Thus, the population breeding intensity was measured based on the percentage of reproductive females in each month, as well as juvenile recruitment periods were defined as the months with higher percentage of juveniles in relation to the total number of individuals (Castilho *et al.* 2007a).

Data analysis

Sex ratio was considered as the quotient between the number of males and the total number of individuals in each month. Deviations from a 0.5 (1:1 sex ratio) were tested using the binomial test ($p \leq 0.05$) (Wilson & Hardy 2002, Baeza *et al.* 2013). The length frequency distribution for males and females were compared using Kolmogorov-Smirnov two-sample tests ($p \leq 0.05$) for each region, adopting as null hypothesis the absence of difference in size distribution among sexes (Zar 1999, Castilho *et al.* 2008a, c).

To assess the correlation of the demographic groups with environmental factors, we performed a redundancy analysis (RDA) for each region, separately, first transforming the data matrix of environmental variables to mean 0 and variance 1 ('standardized') (Silva *et al. in press*). To perform the redundancy analyses, we used a matrix of environmental variables and a matrix of the abundance of each demographic class (juveniles, spent females, reproductive females, spent males, reproductive males) (Oksanen *et al.* 2013). Only environmental variables with score values higher than 0.4 and lower than -0.4 were considered as biologically meaningful for RDA axis (Rakocinski *et al.* 1996).

Results

Population structure and growth

Throughout the sampling period, 3,318 individuals were analyzed to its population growth and structure. In all regions, the overall sexual proportion was female-biased, as follows: 137 juveniles and 1,243 adults were sampled in the MA region (412 males and 968 females). In UB, 24 juveniles and 574 adults were sampled (177 males and 421 females). In the CA region, (49 juveniles and 594 adults were sampled (230 males and 413 females). Finally, 158 juveniles and 539 adults were

sampled in the SFS region (250 males and 447 females). Additionally, females were also more abundant in the higher size classes, for all the studied regions (Fig. 2).

In MA, we recorded mean sizes (CL) of 14.4 mm (size range: 8-27.6 mm) and 18.1 mm (size range: 3.9-35.6 mm) for males and females, respectively. The largest immature female in this region had 14.1 mm CL, while the smallest adult female, 8.9 mm, indicating the likely size in which females become sexually mature; the largest immature male had 15.6-mm CL, while the smallest sexually mature one, 8-mm CL (Fig. 2). In UB, we observed a mean size of 12.7 mm (ranging from 8.5 to 16.9 mm) for males, and 17 mm (ranging from 8.5 to 27.7) for females, respectively. In this area, the largest immature female had 15.2-mm CL, while the smallest adult one, 8.5-mm CL, indicating the size in which they become adults. On the other hand, the largest immature male in this area had 13.4-mm CL, while the smallest adult one, 9.1-mm CL (Fig. 2). In CA, the mean size of individuals was 13.2 mm (size range: 6.9-18.9 mm) for males, and 15.7 mm (size range: 6.1-25 mm) for females. In this area, the biggest immature female was 13-mm CL, while the smallest adult one had a 9.2-mm CL, evidencing the size in which they attain sexual maturity. On the other hand, the largest immature male had a 13.1-mm CL, while the smallest adult one, 9.2-mm CL (Fig. 2). In SFS, the mean size of males was 12.4 mm (ranging from 6.4 to 16.9 mm), whereas the mean size of females was 14.7 mm (ranging from 6.4 to 22 mm). In this region, the largest immature female had a 15.7-mm CL, while the smallest adult female, a 10.6-mm CL, the approximate size in which they attain the adult stage. On the other hand, the biggest immature male had a 13.9-mm CL, while the smallest adult one, 9.2-mm CL (Fig. 2). For all regions, we observed statistically significant differences concerning male and female body sizes (Kolmogorov-Smirnov, $p < 0.05$).

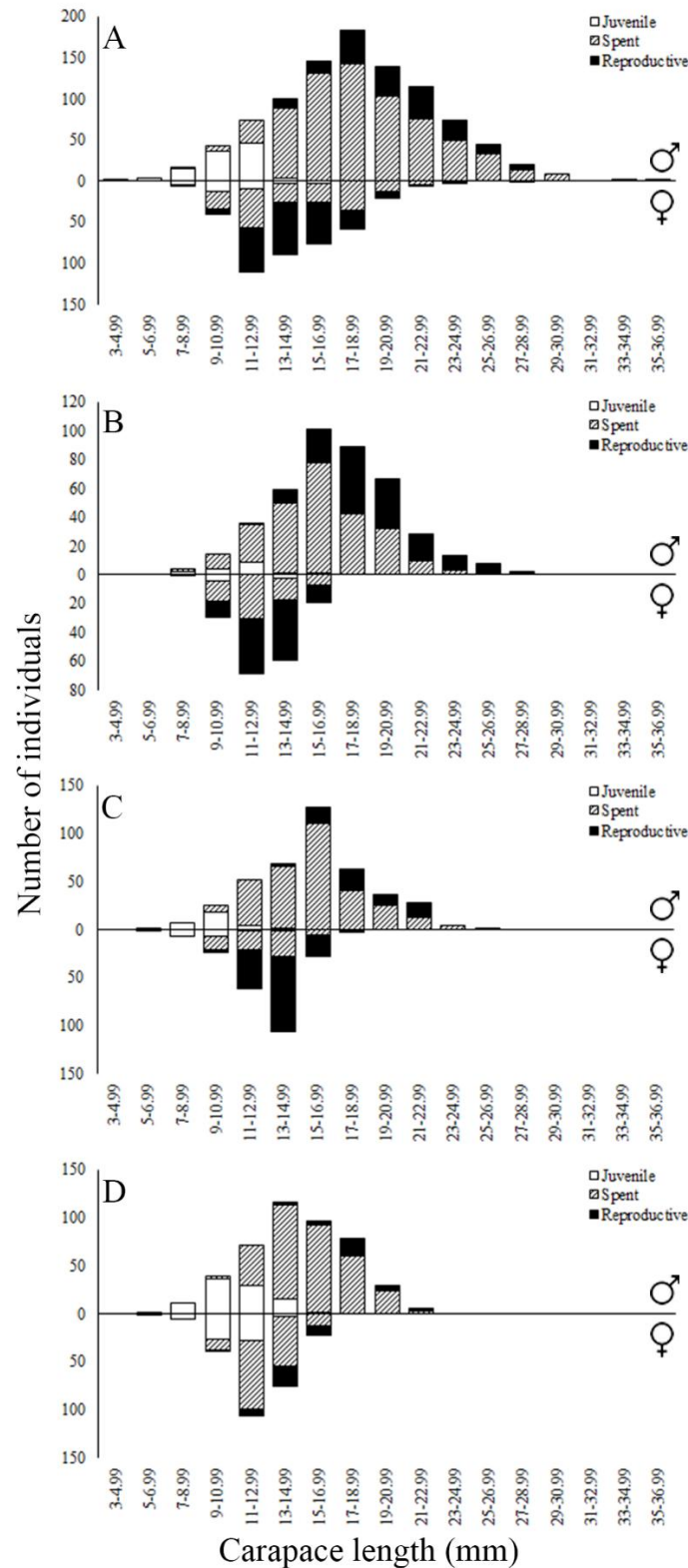


Figure 2: *Pleoticus muelleri*: number of individuals per demographic group in each size class. Samples taken: A) from July 2013 through May 2014 in the Macaé region; B) from July 2013 through June 2014 in the Ubatuba region; C) from July 2012 through May 2014 in the Cananéia region; and D) from July 2010 through June 2011 in the São Francisco do Sul region.

We analyzed 1,967 individuals to its population growth: 1,385 from MA (973 females and 412 males) and 582 from UB (405 females and 177 males). It was not possible to estimate growth parameters in CA and SFS due to the seasonality in the abundance of this species in such regions. Even though, we could observe a decreasing tendency in asymptotic length as latitude increases, as seen below. In MA, we selected 15 growth cohorts for females and 5 for males, resulting in estimates of CL_{∞} = 45.4 mm, k = 0.005 and longevity= 990 days (2.7 years) for females and CL_{∞} = 31.5 mm, k = 0.006 and longevity= 750 days (2.1 years) for males (Figs. 3 and 4). In UB, we selected 10 growth cohorts for females and 3 for males, resulting in estimates of CL_{∞} = 30.2 mm, k = 0.006 and longevity= 737 days (2 years) for females and CL_{∞} = 17.9 mm, k = 0.01 and longevity= 344 days (0.94 year) for males (Figs. 5 and 6). Based on the results obtained with the F test ($p < 0.05$), it was possible to note that a single growth curve does not explain the growth for males and females of the same region, neither explains the growth for sexes comparing different regions.

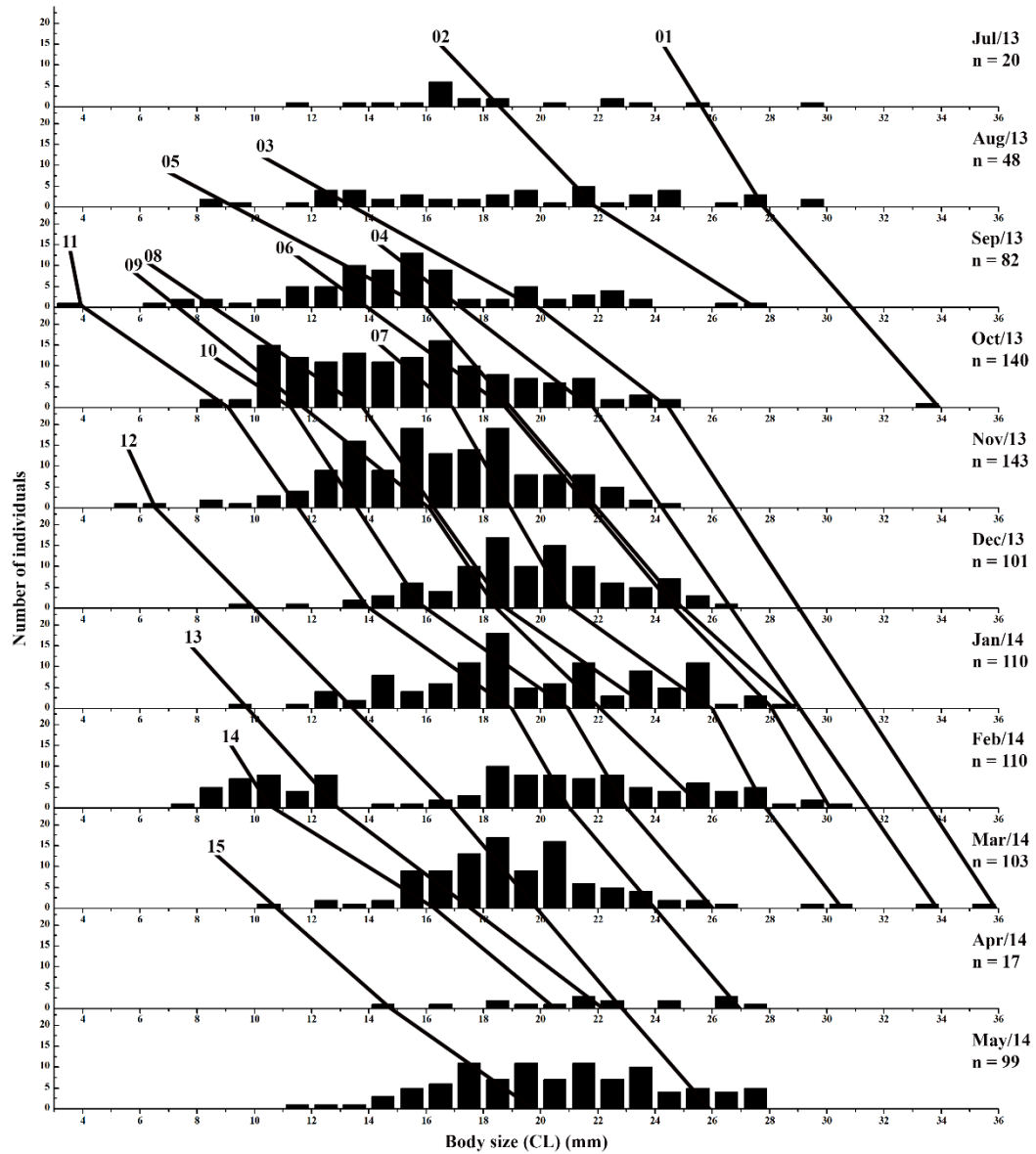


Figure 3: *Pleoticus muelleri*: growth cohorts observed for females sampled in the Macaé region, from July 2013 through May 2014, based on the Von Bertalanffy growth model.

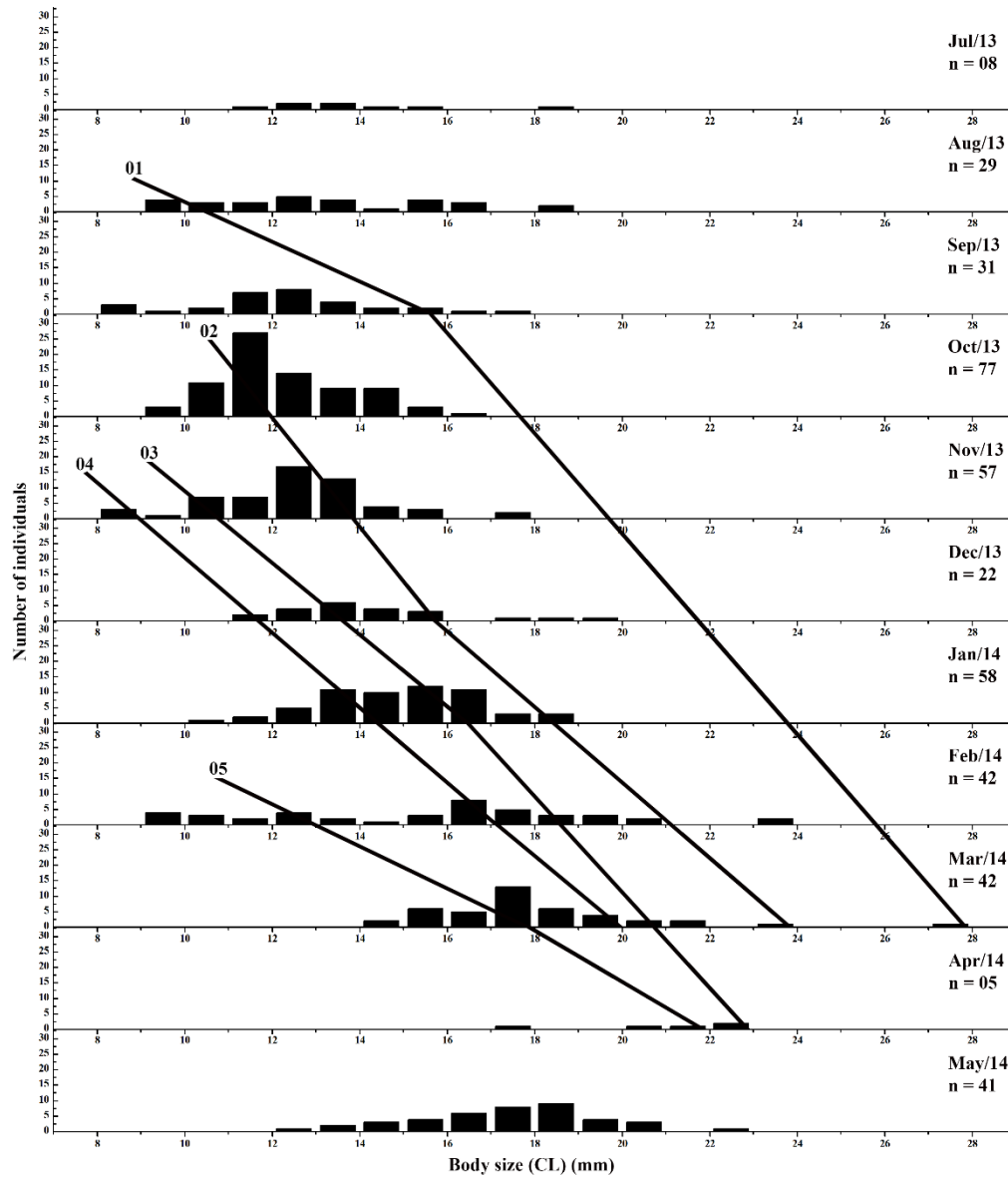


Figure 4: *Pleoticus muelleri*: growth cohorts observed for males sampled in the Macaé region, from July 2013 through May 2014, based on the Von Bertalanffy growth model.

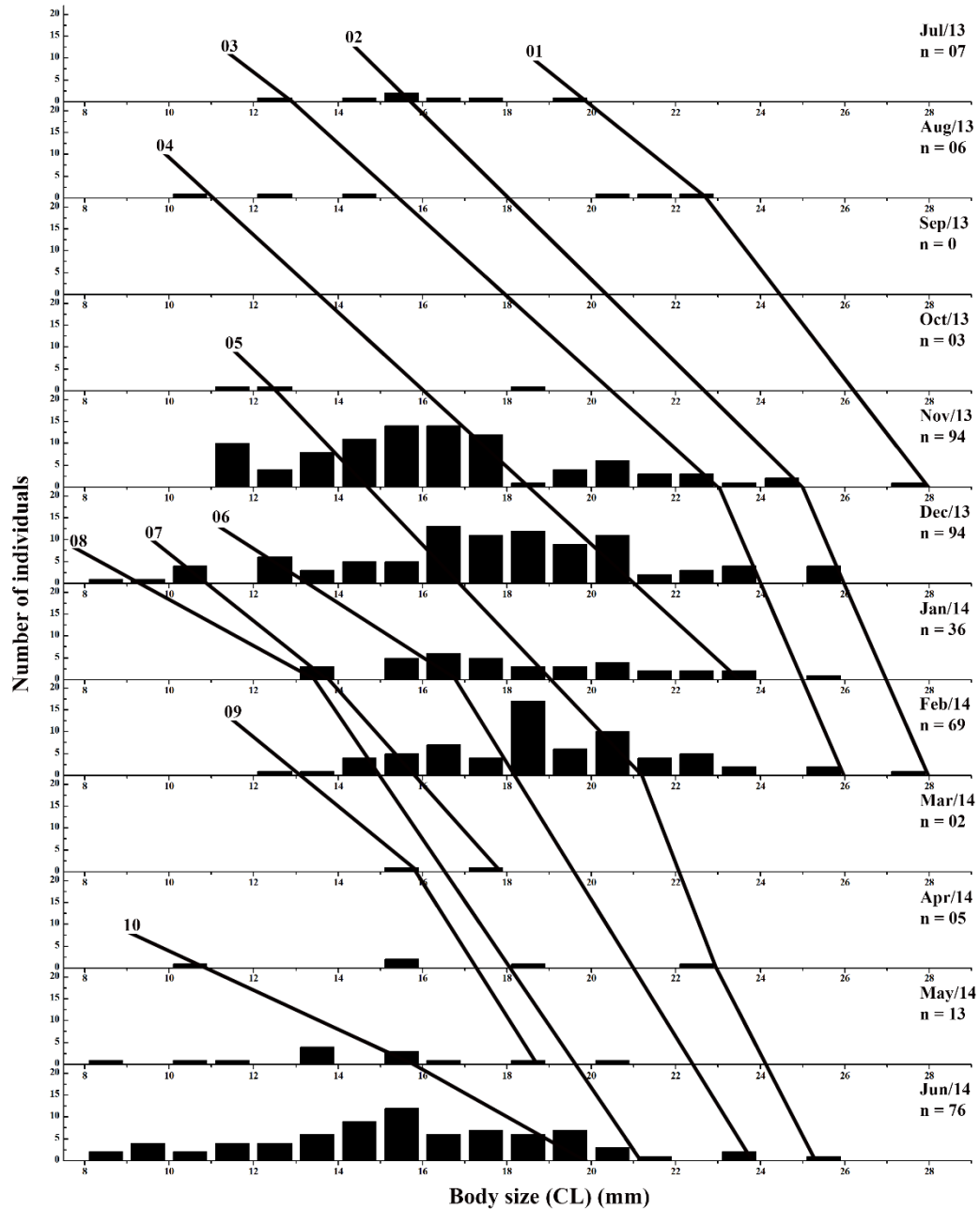


Figure 5: *Pleoticus muelleri*: growth cohorts observed for females sampled in the Ubatuba region, from July 2013 through June 2014, based on the Von Bertalanffy growth model.

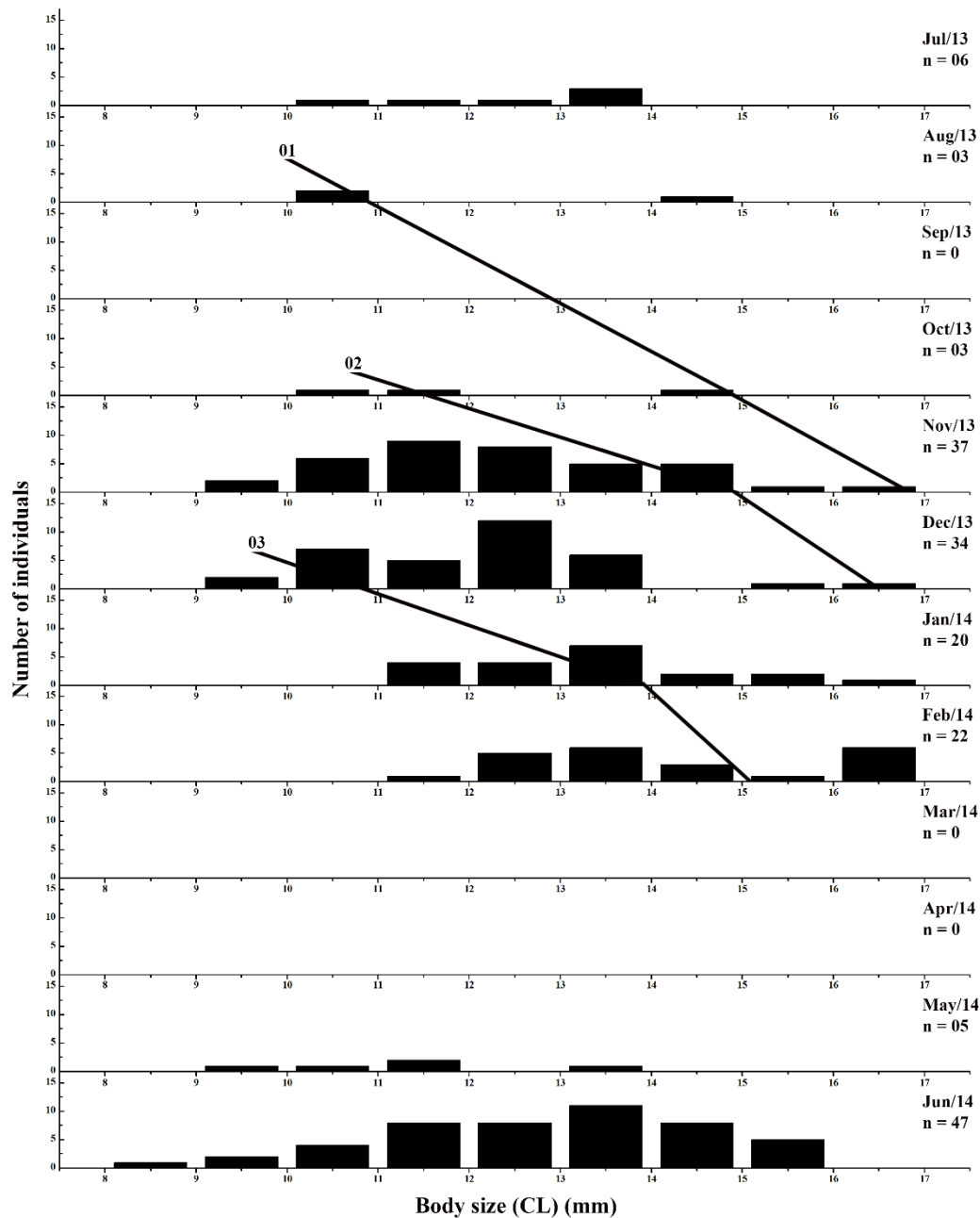


Figure 6: *Pleoticus muelleri*: growth cohorts observed for males sampled in the Ubatuba region, from July 2013 through June 2014, based on the Von Bertalanffy growth model.

Environmental factors

Annual salinity means tended to show a decreasing trend as latitude increases. Monthly means of bottom water salinity varied from 34.8 to 38 psu in MA (average mean: 36.9 psu); from 34.3 to 37 psu in UB (average mean: 35.5 psu); from 27.2 to 37.4 psu in CA (average mean: 34.2 psu); and from 31.4 to 35.6 psu in SFS (average mean: 33.4 psu). Annual bottom temperature means showed an increasing trend as latitude increases. Bottom water temperature monthly means varied from 18.5 to 22.8 °C in MA

(average mean: 20.6 °C); from 19.9 to 25.5 °C in UB (average mean: 22.5 °C); from 17.3 to 28.7 °C in CA (average mean: 22.9 °C); and from 18.2 to 26.1 °C in SFS (average mean: 22.2 °C). Annual means of O.M. showed a decreasing trend as latitude increases. Monthly means of O.M. varied from 10.7 to 14.4% in MA (average mean: 12.7%); from 5.2 to 7.1% in UB (average mean: 6.1%); from 2.6 to 7.6% in CA (average mean: 4.3%); and from 1.4 to 8.0 in SFS (average mean: 3.3%). Finally, annual means of Phi showed a decreasing trend as latitude increases. Phi monthly means varied from 4.7 to 6.0 in MA (average mean: 5.4); from 4.1 to 4.5 in UB (average mean: 4.4); from 3.0 to 4.6 in CA (average mean: 3.9); and from 3.7 to 4.5 in SFS (average mean: 4.0) (Tabs. I-IV).

Table I: *Pleoticus muelleri*: monthly variation in total abundance, sex ratio, percentage of reproductive females, percentage of juvenile individuals, phi, organic matter content (O.M.) and mean bottom water salinity and temperature. Samples taken in the Macaé region, monthly from July 2013 through May 2014.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|-------------|----------|-----|------|
| Jul/13 | 28 | 0.3* | 3.6 | 0 | 21.8 | 38 | 4.7 | 12.5 |
| Aug/13 | 76 | 0.4* | 13.2 | 11.6 | 21.5 | 37.5 | 4.7 | 12.5 |
| Sep/13 | 111 | 0.3* | 19.8 | 23.8 | 21 | 38 | 5.7 | 12.5 |
| Oct/13 | 344 | 0.4* | 16.0 | 29.1 | 21.5 | 37.5 | 5.7 | 12.5 |
| Nov/13 | 636 | 0.3* | 7.5 | 25.1 | 19 | 36.8 | 5.7 | 12.5 |
| Dec/13 | 847 | 0.2* | 3.3 | 38.6 | 18.5 | 34.8 | 4.7 | 10.7 |
| Jan/14 | 1,282 | 0.3* | 6.3 | 39.7 | 19 | 34.9 | 4.7 | 10.7 |
| Feb/14 | 647 | 0.3* | 28.1 | 19.9 | 19.9 | 35.6 | 4.7 | 10.7 |
| Mar/14 | 764 | 0.3* | 2.0 | 4.4 | 21.5 | 36.6 | 6.0 | 14.4 |
| Apr/14 | 22 | 0.2* | 0 | 11.8 | 22.8 | 37.5 | 6.0 | 14.4 |
| May/14 | 281 | 0.3* | 3.6 | 1.0 | 20.9 | 37.7 | 6.0 | 14.4 |

*: sex ratio statistically different from 0.5 (Binomial test)

Table II: *Pleoticus muelleri*: monthly variation in total abundance, sex ratio, percentage of reproductive females, percentage of juvenile individuals, phi, organic matter content (O.M.) and mean bottom water salinity and temperature. Samples taken in the Ubatuba region, monthly from July 2013 through June 2014.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|-------------|----------|-----|------|
| Jul/13 | 13 | 0.4* | 23.1 | 0 | 22.7 | 34.8 | 4.5 | 6.9 |
| Aug/13 | 9 | 0.3* | 0 | 16.7 | 20.3 | 34.3 | 4.5 | 6.9 |
| Sep/13 | 0 | 0 | 0 | 0 | 19.9 | 34.4 | 4.5 | 6.9 |
| Oct/13 | 6 | 0.5 | 16.7 | 33.3 | 23.5 | 34.5 | 4.1 | 5.2 |
| Nov/13 | 185 | 0.3* | 0 | 33.6 | 23.0 | 35.8 | 4.1 | 5.2 |
| Dec/13 | 210 | 0.2* | 0 | 58.0 | 22.5 | 37.0 | 4.1 | 5.2 |
| Jan/14 | 56 | 0.4* | 1.8 | 41.7 | 21.4 | 37.0 | 4.4 | 7.1 |
| Feb/14 | 91 | 0.2* | 0 | 49.3 | 20.0 | 36.5 | 4.4 | 7.1 |
| Mar/14 | 2 | 0 | 0 | 50.0 | 22.8 | 36.0 | 4.4 | 7.1 |
| Apr/14 | 5 | 0 | 0 | 60.0 | 25.5 | 35.5 | 4.5 | 5.3 |
| May/14 | 18 | 0.3* | 0 | 23.1 | 25.1 | 35.4 | 4.5 | 5.3 |
| Jun/14 | 123 | 0.4* | 15.4 | 9.8 | 23.9 | 35.1 | 4.5 | 5.3 |

*: sex ratio statistically different from 0.5 (Binomial test)

Table III: *Pleoticus muelleri*: monthly variation in total abundance, sex ratio, percentage of reproductive females, percentage of juvenile individuals, phi, organic matter content (O.M.) and mean bottom water salinity and temperature. Samples taken in the Cananéia region, monthly from July 2012 through May 2014.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|-------------|----------|-----|------|
| Jul/12 | 0 | 0 | 0 | 0 | 19.1 | 34.3 | 3.0 | 2.6 |
| Aug/12 | 64 | 0.4 | 31.3 | 0 | 19.6 | 34.8 | 3.0 | 2.6 |
| Sep/12 | 17 | 0.4 | 0 | 10 | 22.4 | 34.5 | 3.0 | 2.6 |
| Oct/12 | 6 | 0.5 | 0 | 0 | 21.8 | 37.4 | 4.6 | 7.6 |
| Nov/12 | 1 | 0 | 0 | 0 | 23.8 | 35.8 | 4.6 | 7.6 |
| Dec/12 | 0 | 0 | 0 | 0 | 24.5 | 35.0 | 4.6 | 7.6 |
| Jan/13 | 0 | 0 | 0 | 0 | 26.1 | 34.3 | 3.3 | 4.9 |
| Feb/13 | 0 | 0 | 0 | 0 | 27.0 | 34.7 | 3.3 | 4.9 |
| Mar/13 | - | - | - | - | - | - | - | - |
| Apr/13 | 0 | 0 | 0 | 0 | 24.4 | 35.3 | 4.3 | 4.2 |
| May/13 | 0 | 0 | 0 | 0 | 22.8 | 35.4 | 4.2 | 5.0 |
| Jun/13 | 0 | 0 | 0 | 0 | 21.1 | 35.0 | 4.2 | 5.0 |
| Jul/13 | 5 | 0.4 | 80.0 | 0 | 17.3 | 33.5 | 4.2 | 3.4 |
| Aug/13 | 13 | 0.6 | 69.2 | 0 | 17.7 | 33.0 | 4.2 | 3.4 |
| Sep/13 | 111 | 0.4* | 1.8 | 11.4 | 19.7 | 31.1 | 4.1 | 3.0 |
| Oct/13 | 44 | 0.5 | 29.5 | 0 | 22.2 | 31.6 | 3.9 | 3.0 |
| Nov/13 | 438 | 0.3* | 0.2 | 20.9 | 22.6 | 27.2 | 3.9 | 3.0 |
| Dec/13 | 54 | 0.4 | 0 | 46.9 | 23.1 | 34.4 | 3.9 | 3.0 |
| Jan/14 | 0 | 0 | 0 | 0 | 28.7 | 34.6 | 3.9 | 4.9 |
| Feb/14 | 0 | 0 | 0 | 0 | 26.9 | 34.8 | 3.9 | 4.9 |
| Mar/14 | 0 | 0 | 0 | 0 | 25.1 | 35.0 | 3.9 | 4.9 |
| Apr/14 | 1 | 0 | 0 | 0 | 24.6 | 35.8 | 3.6 | 2.7 |
| May/14 | 3 | 0 | 0 | 0 | 22.4 | 34.3 | 3.6 | 2.7 |

*: sex ratio statistically different from 0.5 (Binomial test)

Table IV: *Pleoticus muelleri*: monthly variation in total abundance, sex ratio, percentage of reproductive females, percentage of juvenile individuals, phi, organic matter content (O.M.) and mean bottom water salinity and temperature. Samples taken in the São Francisco do Sul region, monthly from July 2010 through June 2011.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|-------------|----------|-----|------|
| Jul/10 | 86 | 0.4 | 69.8 | 5.3 | 19.4 | 34.6 | 3.8 | 1.4 |
| Aug/10 | 381 | 0.4* | 22.8 | 5.5 | 18.2 | 33.4 | 3.8 | 1.6 |
| Sep/10 | 194 | 0.3* | 10.3 | 10.1 | 19.5 | 31.4 | 4.4 | 6.8 |
| Oct/10 | 87 | 0.4* | 0 | 21.4 | 20.1 | 32.3 | 4.5 | 8.0 |
| Nov/10 | 11 | 0.1* | 18.2 | 0 | 22.4 | 32.4 | 4.2 | 4.6 |
| Dec/10 | 0 | 0 | 0 | 0 | 24.6 | 32.3 | 4.2 | 5.0 |
| Jan/11 | 0 | 0 | 0 | 0 | 25.6 | 33.8 | 3.7 | 2.4 |
| Feb/11 | 0 | 0 | 0 | 0 | 26.1 | 32.2 | 3.7 | 1.8 |
| Mar/11 | 1 | 0 | 0 | 0 | 24.7 | 32.7 | 3.8 | 2.0 |
| Apr/11 | 1 | 0 | 0 | 0 | 23.2 | 34.8 | 3.8 | 2.0 |
| May/11 | 1 | 0 | 0 | 0 | 22.3 | 35.2 | 4.3 | 2.4 |
| Jun/11 | 85 | 0.5 | 25.9 | 3.2 | 21 | 35.6 | 4.3 | 2.2 |

*: sex ratio statistically different from 0.5 (Binomial test)

Sex ratio and reproductive biology

We observed a strongly female-biased sex ratio for most of the studied months, especially for months in which reproduction took place. In MA, females were more abundant in all of the months (Tab. I); in UB, exceptions to such a pattern were recorded only in October 2013 and March-April 2014 (Tab. II). On the other hand, in CA, differences from a 1:1 sex ratio were statistically (binomial test, $p < 0.05$) biased toward females only in September and November 2013 (Tab. III); while in SFS, females showed significantly higher abundances only from August through November 2010 (Tab. IV).

In general, the abundance of reproductive females seemed to follow the same pattern observed for general abundance patterns in each region (i.e., they were observed in most of the months when abundance was significant). In MA, we observed reproductive females throughout the entire year, with a peak in abundance recorded in December-January, when approximately 40% of the sampled adult females showed developed gonads (smallest reproductive female: 13 mm CC) (Tab. I). In UB, reproductive females were also sampled throughout most of the year (except for July and September 2013), with higher abundances recorded from November 2013 through February 2014, when the percentage of reproductive females varied from 33.6% (November) to 58% (December) (smallest reproductive female: 12.3 mm). In this region, the reproductive females' percentages from October 2013 and March-May 2014 were not taken under consideration, due to the low abundance of sampled individuals

(Tab. II). In CA, reproduction seems to be episodic, since the abundance of reproductive females was observed only in 4 out of 23 sampled months. In this region, their higher abundances were observed in November and December 2013 (when 20.9% and 46.9% of all adult females showed developed gonads, respectively) (smallest reproductive female: 14.3 mm) (Tab. III). In SFS, higher percentages of reproductive females were recorded in September-October 2010, when 10.1% and 21.4% of the adult females showed developed gonads, respectively (smallest reproductive female: 13.5 mm). The reproductive abundance recorded for June 2011 was not taken under consideration due to the low abundance of individuals ($n=1$) (Tab. IV).

The juveniles' abundance tended to be similar to the general abundance of individuals (i.e., once individuals were abundant, juveniles were as well). In MA, it was possible to observe a continuous recruitment pattern, since juveniles were sampled throughout the entire studied period, with peaks in late winter (September 2013) and summer (February 2014). In UB, recruitment seemed to be episodic (discontinuous), since juveniles were sampled only in 4 out of 12 studied months (July and October 2013 and January and June 2014). In CA, juveniles were sampled in 6 out of 23 sampled months (August 2012 and July-October 2013), characterizing an episodic recruitment pattern (Tab. III). While in SFS, juveniles were sampled in July-November 2010 and June 2011, with peaks in July-September 2010 and June 2011 (Tab. IV).

The environmental influence over population dynamics

In MA, the first RDA axis represented approximately 95% of the variation in abundance of demographical classes. In this region, temperature and salinity were the most influential environmental factors over the distribution of demographic classes (with a negative correlation), while Phi and O.M. influenced them positively, however, with lower score values (Tab. V). In UBA, the first RDA axis represented 87% of the entire variation in the abundance of demographical classes. In this area, bottom water salinity positively influenced the abundance of individuals (except for juveniles, which were negatively influenced), while sediment features influenced them negatively (except for juveniles, who were positively influenced by the sediment features) (Tab. VI). In CA, the first RDA axis represented approximately 99% of the variation in the abundance of demographical classes. In this region, only bottom water salinity exerted a statistically significant influence over the distribution of individuals (with a positive correlation with juveniles, and negative with other demographic classes) (Tab. VII). In

SFS, the first RDA axis explained approximately 90% of the variation in the abundance of demographic classes. In this region, the abundance of demographic classes showed a negative association with temperature and salinity (Tab. VIII).

Table V: *Pleoticus muelleri*: summary of results of the Redundancy Analysis (RDA) for the abundance of demographical classes (juveniles, spent males, reproductive males, spent females and reproductive females) and environmental factors. Samples taken monthly from July 2013 through May 2014 in the Macaé region, southeastern Brazil.

| | RDA 1 | RDA 2 |
|---|--------------|-------|
| Eigenvalue | 7192.1 | 276.5 |
| % of variance | 95.20% | 3.70% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | 0.86 | -0.47 |
| Bottom water salinity | 0.78 | -0.04 |
| Organic matter content | -0.52 | -0.37 |
| Phi | -0.45 | -0.28 |
| <i>Abundance of individuals</i> | | |
| Juveniles | -3.65 | -1.68 |
| Spent males | -2.34 | -1.48 |
| Reproductive males | -5.64 | 0.62 |
| Spent females | -13.16 | -0.78 |
| Reproductive females | -7.49 | 2.18 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Table VI: *Pleoticus muelleri*: summary of results of the Redundancy Analysis (RDA) for the abundance of demographical classes (juveniles, spent males, reproductive males, spent females and reproductive females) and environmental factors. Samples taken monthly from July 2013 through June 2014 in the Ubatuba region, southeastern Brazil.

| | RDA 1 | RDA 2 |
|---|--------------|--------|
| Eigenvalue | 89.66 | 13.18 |
| % of variance | 86.58% | 12.73% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | -0.36 | 0.57 |
| Bottom water salinity | 0.70 | -0.56 |
| Organic matter content | -0.74 | -0.67 |
| Phi | -0.73 | 0.14 |
| <i>Abundance of individuals</i> | | |
| Juveniles | -0.09 | 0.47 |
| Spent males | 0.93 | 0.27 |
| Reproductive males | 0.98 | 0.52 |
| Spent females | 2.95 | 0.94 |
| Reproductive females | 2.95 | -1.18 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Table VII: *Pleoticus muelleri*: summary of results of the Redundancy Analysis (RDA) for the abundance of demographical classes (juveniles, spent males, reproductive males, spent females and reproductive females) and environmental factors. Samples taken monthly from July 2012 through May 2014 in the Cananéia region, southeastern Brazil.

| | RDA 1 | RDA 2 |
|---|-------------|-------|
| Eigenvalue | 368.00 | 3.42 |
| % of variance | 98.68% | 0.92% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | -0.28 | -0.74 |
| Bottom water salinity | 0.92 | -0.35 |
| Organic matter content | 0.10 | -0.36 |
| Phi | -0.18 | -0.49 |
| <i>Abundance of individuals</i> | | |
| Juveniles | 0.32 | 0.63 |
| Spent males | -0.03 | 0.23 |
| Reproductive males | -3.48 | -0.06 |
| Spent females | -6.64 | 0.14 |
| Reproductive females | -1.78 | -0.28 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Table VIII: *Pleoticus muelleri*: summary of results of the Redundancy Analysis (RDA) for the abundance of demographical classes (juveniles, spent males, reproductive males, spent females and reproductive females) and environmental factors. Samples taken monthly from July 2010 through June 2011 in the São Francisco do Sul region, southern Brazil.

| | RDA 1 | RDA 2 |
|---|-------------|-------|
| Eigenvalue | 204.29 | 21.89 |
| % of variance | 90.12% | 9.66% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | 0.93 | 0.25 |
| Bottom water salinity | 0.43 | -0.70 |
| Organic matter content | -0.21 | 0.81 |
| Phi | -0.05 | 0.76 |
| <i>Abundance of individuals</i> | | |
| Juveniles | -2.16 | -1.69 |
| Spent males | -2.19 | -0.18 |
| Reproductive males | -0.45 | 0.17 |
| Spent females | -4.99 | 0.75 |
| Reproductive females | -0.43 | 0.50 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Discussion

Throughout the sampling period, we could evidence the responses shown by *P. muelleri* to local variation in environmental factors. It was possible to infer that the analyzed populations are well-established throughout the southeastern Brazilian coast, since we sampled individuals of all demographic groups, from juveniles to adults of both sexes. It confirms the assertion made by Castilho *et al.* (2008a) that this species completes its life cycle along the southeastern Brazilian coast. In our study, we could also evidence the sexual dimorphism related to body size and the limiting factors that can shape the geographical variation of the species.

Environmental effects

Several authors have stated that penaeoid tend to show variations in population traits that can be associated with environmental factors, which in turn, undergo changes related to latitudinal variation (Bauer 1992, Costa *et al.* 2004, Castilho *et al.* 2007b, 2012). On the other hand, the success of a given species depends on several aspects (environmental aspects and ecological relationships, among others), which can act

isolated or together (Meireles *et al.* 2006, Furlan *et al.* 2013). As a rule, in tropical regions, temperature is expected to be homogeneous throughout the year, while in locations far from the equator, seasonal variations in temperature tend to be more evident, with lower water temperatures in winter and higher ones during summer (Brown & Lomolino 2006).

However, most of the studied area is located in a subtropical area referred as the Atlantic upwelling zone (which comprehends the marine area located between 23 and 29°S). Such region is strongly influenced by marine fronts (transitional areas that combine features of two or more waters, such as the South Atlantic Central Water (SACW), Coastal Water (CW) and Tropical Water (TW)), which result in an increased primary and consequent secondary production (Acha *et al.* 2004). The SACW is formed far from the coast; however, it can get closer to the shallower areas near the coast during late spring and/or early summer. This water mass is characterized by bringing lower salinity and temperature levels (temperature <18 °C and salinity <36 psu), mixing water from the warm Brazilian current (temperature >20 °C and salinity >36 psu) and the Falklands current (temperature <15 and salinity <34 psu), emerging at Cabo Frio region as an upwelling event (Castro-Filho & Miranda 1998, Acha *et al.* 2004). In the UB region, for instance, the occurrence of SACW can be noted during spring and/or summer, and in such periods, it is possible to observe a decrease in temperature to levels between 15 and 21 °C (Costa *et al.* 2005), which could be observed in our study as well, analyzing the minimum temperature records mainly in the northern areas.

Several authors (among them, Dall *et al.* 1990 and Costa *et al.* 2004) pointed out that the grain size of the seafloor plays an important role in modeling the penaeoid distributional patterns, since they burrow themselves in the sediment. When burrowed, they have a lower energetic cost, besides being protected against predators (Simões *et al.* 2010). Burrowing in areas where the sediment is composed mainly by finer grains can make the burrowing habit easier, since smaller grains are lighter in weight and so, easier to move (Ruello 1973, Dall *et al.* 1990). This influence was already stated for other penaeoids such as *Sicyonia dorsalis* Kingsley, 1878 and *A. longinaris*, for instance (Castilho *et al.* 2008b and Costa *et al.* 2005, respectively). However, this relation is strongly tied to the capability of the shrimps to circulate water through their branchial chambers when they are burrowed. Penn (1984) stated that several *Penaeus* species did not seek to burrow themselves in highly-soft composed sediments due to the fact that

they were unable to reverse the water flow that runs through their branchial chamber, and thus, were unable to prevent its clogging.

In this study, such relation between finer grains and the abundance of demographical classes was observed in MA, while the opposite was registered in UB, i.e., as phi values increase (grains become smaller), the abundance of individuals decreases. It runs against the results available in the literature (Costa *et al.* 2004, Batista *et al.* 2011), which attests the association between *P. muelleri* and the sediment composed mainly by finer grains for the littoral from São Paulo state. According to Williams (1958), the shrimp-burrowing habits may consider other requirements besides the protection or the ability to move heavier grains. In this sense, substrates composed by coarser grains would allow a faster pumping in the respiratory processes when compared to the ones composed by finer grains and mud. It may be considered as an evidence that the species adjust their burrowing habits to the respiratory requirements besides the ease to burrow.

In our study, the environmental peculiarities displayed in the Brazilian coast resulted in different influences that environment can exert over the populations. *Pleoticus muelleri* is considered an indicator species of the presence of cold waters along its distributional pattern in the Brazilian coast (Costa *et al.* 2005, Castilho *et al.* 2008a, d), and in this study, such influence could be evidenced by the negative association found between the abundance of individuals and the temperature levels. However, such influence was not statistically significant for any of the demographic groups, neither in UB nor in CA. It may have been happened because of the bathymetric distribution pattern of *P. muelleri* in UB, which may include depths up to 40m (Costa *et al.* 2003, Castilho *et al.* 2012). Thus, even though we sampled individuals from all demographical groups in all studied areas, it is possible that the temperature range we considered in UB was not sufficient to predict a statistical association between the environmental and the biological data. A similar situation may occur in CA; despite the absence of statistical significance, the only periods in which we sampled *P. muelleri* were the ones which showed decreases in water temperature. Furthermore, in both regions, it is possible that other non-considered environmental factors influenced the population with a higher intensity, as noted by Grabowski *et al.* (2014) for *X. kroyeri* in southern Brazil.

Growth and reproductive aspects

Throughout the studied period, females showed larger body sizes when compared to males for all the sampled regions, what was also observed for other shrimp species by several authors, being considered a rule for penaeoid (Boschi 1989, Costa & Fransozo 2004, Castilho *et al.* 2008a, c, 2012, Grabowski *et al.* 2014, 2016). Gab-Alla *et al.* (1990) and Yamada *et al.* (2007) purpose that such a difference may be related to reproductive processes, since female fecundity increases exponentially with body size (i.e., larger female body sizes may be an adaptation in order to produce a greater number of eggs).

Furthermore, such a pattern was similar comparing the estimated asymptotic lengths in MA and UB, in which the attained size decreases as latitude increase. However, this is the opposite from what is expected taking under consideration the latitudinal effect paradigm, which states that growth in penaeoid shrimp undergo a strong influence exerted by environmental conditions which, in turn, are tied to the local latitude. If so, higher temperature levels in tropical areas could lead to a substantial increase in growth coefficient through a higher metabolism rate, however, resulting in a decreased body sizes (Bauer 1992). However, some particularities displayed by the Brazilian coast can dramatically change this scenario. Off southeastern Brazil, the SACW current may be held responsible for decreases in water temperature during summer (Castro-Filho *et al.* 1987).

The SACW is a part of the subtropical convergence and is among the factors responsible for the Cabo Frio upwelling, one of the two upwelling regions comprehended in the region between the latitudes of 23°S and 29°S, known as the Atlantic upwelling zone (Castro-Filho *et al.* 1987, Acha *et al.* 2004). This is why even though MA is located in a tropical region, the environmental conditions observed there are very similar to the ones observed in cool-temperate regions, a likely result of the influence of the Cabo Frio upwelling (Sancinetti *et al.* 2015). Considering this information, it becomes reasonable to note that species sampled in this region not only show a disagreement to the pattern they were supposed to display, but also break the purposed pattern. Similarly, Sancinetti *et al.* (2015) also observed such situation studying *A. longinaris* (a cold-temperate penaeoid species, as well as *P. muelleri*) in MA. In their study, they found out that the maximum body sizes sampled in MA were higher than all the other ones sampled in other Brazilian regions, becoming even higher

than the maximum body size observed by Boschi & Mistakidis (1966), at the latitude of 43°S (Chubut Province, Argentina) (for more details, see Sancinetti *et al.* 2015).

Besides showing bigger body sizes, females were also more abundant when compared to males during all the studied period in MA, and in most of the months when abundance was considerably high for the other regions. Throughout the southeastern Brazilian coast, similar results were observed for *Rimapenaeus constrictus* (Stimpson, 1874) (Costa & Fransozo 2004, Lopes *et al. in press*), *X. kroyeri* (Grabowski *et al.* 2014, 2016), *A. longinarius* (Castilho *et al.* 2007a) and *P. muelleri* (Castilho *et al.* 2008a, 2012), for instance. Such a skewed sex ratio can be associated to the differential distribution patterns shown by males and females year-round (Signoret 1974, Branco 2005), or higher mortality rates of males (Cha *et al.* 2002). Additionally, Kevrekidis & Thessalou-Legaki (2006) stated that during the gonadal maturation period of *Melicertus kerathurus* (Forskål, 1775), the metabolic demand of females grows considerably higher, leading them to feed for longer periods. During foraging, animals become more vulnerable to sampling gears, thus biasing the general sex ratio towards females.

The reproductive periods for all the regions seemed to be related to the periods with higher general abundance of individuals. In the northern areas (MA and UB), reproductive females were sampled year-round, displaying a continuous trend, even though with peaks recorded mainly when the general abundance was higher as well (late spring-early summer). On the other hand, in the southern regions (CA and SFS), reproduction took place only in a few months during the sampling periods, mainly in periods characterized by lower water temperature levels. In both areas, reproductive periods seemed to be closely related to winter months rather than spring or summer, as observed for the northern areas. In all the areas, recruitment seemed to be episodic, since we could not observe a clear recruitment pattern, neither associations between the abundance of reproductive females and juveniles. Similarly to the reproductive periodicity, the abundance of juveniles followed the trend in general abundance, i.e., when general abundance increased, the abundance of juveniles increased as well.

As pointed out by Acha *et al.* (2004) and Olson & Backus (1985), the result of the increased mixing of waters that compose a front often is an increase in primary and secondary productivity, which lead these areas to be marked by a high phytoplankton biomass, and many times, consequent enhanced activity in higher trophic levels. The effect observed to be a result of the Cabo Frio upwelling is seasonal, and grows stronger during summer, induced mainly by the Northeastern winds, and contributing to the

penetration of SACW (Silveira *et al.* 2000, Sancinetti *et al.* 2015). The intrusion of the SACW represents an important mechanism that provides nutrients increase (chlorophyll levels, for instance) to the shallower waters, and consequently, increases the phytoplankton biomass and the subsequent production of herbivorous zooplankton as well (Vega-Pérez 1993, Silveira *et al.* 2000, De Léo & Pires-Vanin 2006). The period in which higher abundances of individuals were sampled in the northern areas coincide with the ones in which such changes are supposed to occur in the water features (spring-summer). Based on this, one may suggest that the food availability for larval protozoa (phytoplankton production) could play a selective role shaping the breeding period of this species (Castilho *et al.* 2007b) in UB and MA. The same pattern was observed by Castilho *et al.* (2007a, b) and Sancinetti *et al.* (2015) for *A. longinarius* in UB and MA, respectively; by Costa & Fransozo (2004) for *R. constrictus* in UB; and by Castilho *et al.* (2008a, 2012) and Boschi (1989) for *P. muelleri* in UB and in the Argentinean Patagonian littoral, respectively.

However, the same pattern was not observed for the individuals sampled in the southern areas (CA and SFS), where the periods in which most of the abundance of individuals was found were during winter-spring. As well as *P. muelleri*, *A. longinarius* also presents an evolutionary history associated to sub-Antarctic regions (Boschi 2000). Based on this information, Sancinetti *et al.* (2015) pointed out that it is possible to infer that *A. longinarius* may have migrated to the Brazilian coast through evolutionary time by migration processes evolving larval drift. The authors also hypothesized that using the same migratory processes, the species takes advantage of the SACW currents to travel through long distances, and to successfully establish populations in regions where environmental conditions are more favorable (the Cabo Frio region and adjacent areas, such as MA and UB, for instance). Based on this idea, one may infer that the absence (or low abundance) of individuals from early spring through late autumn in the southern regions is probably due to the increased temperature in these periods, when individuals might migrate to deeper areas searching for more suitable temperature levels. When temperature decreases in the lower depths (late autumn to early spring), individuals are able to inhabit such areas, and so their abundance increases again. Such idea grows even stronger when analyzing the number of months in which we did not sample reproductive females for each region (1-2 months in MA and UB; several months in CA and SFS). It may also be a reflex of the limiting force that temperature exerts over the

reproduction of the species in areas in which the SACW does not display a strong influence, and consequently, temperature is slightly higher throughout the year.

Pleoticus muelleri finds suitable conditions to complete its life cycle throughout the Brazilian coast and is influenced by the singular geographical conditions displayed by this area. The differences in growth, population structure and reproductive dynamics seem to be related to the temporal fluctuations in sediment features (grain size and O.M.) and bottom water salinity and temperature, which are strongly modulated by water masses along the Brazilian coast. This study evidences how, even within a narrow range variation in latitude, it is possible to observe exceptions to well-established patterns in the study of penaeoid population dynamics, such as the latitudinal effect paradigm. Therefore, it provides valuable information about the population dynamics of the species and how these traits vary through the Brazilian coast. Together with the oncoming ones, this research must be taken under consideration in order to design more appropriated fishing management policies, avoiding the overexploitation of the species before its collapse.

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Capítulo 3

**Ecological evidences for the behavioral plasticity of
Rimapenaeus constrictus (Stimpson, 1874): the
responses of a tropical shrimp species to local
environmental singularities in southeastern Brazil**

Ecological evidences for the behavioral plasticity of *Rimapenaeus constrictus* (Stimpson, 1874): the responses of a tropical shrimp species to local environmental singularities in southeastern Brazil

Resumo

O objetivo deste estudo foi testar a aplicabilidade da tendência do “efeito latitudinal” à dinâmica populacional de *Rimapenaeus constrictus* ao longo da costa sudeste do Brasil. Amostras mensais foram realizadas em quatro áreas desta região (Macaé ($\approx 22^\circ\text{S}$), Ubatuba ($\approx 23^\circ\text{S}$), Cananéia ($\approx 25^\circ\text{S}$) e São Francisco do Sul ($\approx 26^\circ\text{S}$)), utilizando barcos de pesca artesanal para amostrar em profundidades de 5 a 17 m, em diferentes períodos de julho de 2010 a junho de 2014. A influência ambiental sobre a dinâmica populacional foi testada com uma análise de redundância (RDA) para cada região, separadamente, considerando biologicamente coerentes apenas as variáveis com *scores* maiores que 0,4 e menores que -0,4. Os períodos reprodutivos e de recrutamento foram considerados como os de maior frequência de fêmeas reprodutivas e de juvenis, respectivamente, para cada região, enquanto diferenças na razão sexual foram testadas usando o teste binomial ($p \leq 0,05$). Ao todo, 3.481 camarões foram analisados (9 em Macaé, 1.584 em Ubatuba, 1.694 em Cananéia e 194 em São Francisco do Sul), para os quais a razão sexual foi desviada a favor das fêmeas, em todos os meses, devido a diferenças em padrões migratórios, taxas de mortalidade ou consequências da alta taxa metabólica em machos, diminuindo sua longevidade. Foi possível observar uma tendência à reprodução contínua à medida que a latitude diminui, possivelmente devido ao influxo de nutrientes provenientes da ação de massas de água nestas áreas. Por outro lado, o recrutamento episódico pode ser uma consequência da maior mortalidade nos estágios iniciais do desenvolvimento, devido às adversidades ambientais durante a fase planctônica. A ausência de aplicabilidade dos parâmetros populacionais ao “paradigma do efeito latitudinal” é possivelmente uma resposta às particularidades geográficas da costa brasileira, como a influência de frentes marinhas. Tal proposta ganha força considerando-se que a espécie (conhecida por sua plasticidade fenotípica) foi amostrada continuamente ao longo das regiões, exceto por Macaé, onde baixas temperaturas foram observadas no verão.

Ecological evidences for the behavioral plasticity of *Rimapenaeus constrictus* (Stimpson, 1874): the responses of a tropical shrimp species to local environmental singularities in southeastern Brazil

Abstract

The aim of this study was to test if the population dynamics of *Rimapenaeus constrictus* follows the “latitudinal effect” trend along the southeastern Brazilian coast. Monthly samples were performed in four regions throughout this area (Macaé ($\approx 22^\circ\text{S}$), Ubatuba ($\approx 23^\circ\text{S}$), Cananéia ($\approx 25^\circ\text{S}$) and São Francisco do Sul ($\approx 26^\circ\text{S}$)), using artisanal fishing boats to cover a 5-17 m depth variation, in different periods from July 2010 through June 2014. The environmental influence over the population dynamics was tested with a redundancy analysis (RDA) for each region, separately, considering meaningful only variables with score values higher than 0.4 and lower than -0.4. Reproductive and recruitment periodicity were considered as the periods with higher frequency of reproductive females and juveniles, respectively, for each region, while differences in sex ratio were tested using the binomial test ($p \leq 0.05$). We analyzed 3,481 specimens of *R. constrictus* (9 from Macaé, 1,584 from Ubatuba, 1,694 from Cananéia and 194 from São Francisco do Sul), from which sex ratio was female-biased in all regions, maybe due to differences in migratory needs, mortality rates or consequences of the males’ higher metabolic rates, leading to decreased longevity. We observed a continuous trend in reproductive periodicity as latitude decreases, possibly related to the nutrients influx coming along with the water masses in these regions. There was an episodic trend for the juvenile recruitment, possibly related to the early stages’ mortality, mainly during the planktonic period. The lack of applicability of the population parameters to the “latitudinal effect paradigm” (in which species tend to grow bigger and live longer in higher latitudes) may be a response to geographical features of the Brazilian coast, such as the influence of marine fronts. Our hypothesis grows stronger considering that this species (known for having a high phenotypic plasticity) was sampled year-round in all regions, except for Macaé, where cold temperatures were observed during the summer season.

Introduction

In southern and southeastern Brazil, the artisanal shrimp-fishing activities are developed mainly over the stocks of the pink shrimp, *Farfantepenaeus brasiliensis* (Latreille, 1817) and *F. paulensis* (Pérez-Farfante, 1967), and of the seabob shrimp, *Xiphopenaeus kroyeri* (Heller, 1862). On the other hand, the industrial shrimp fisheries aims to capture *Artemesia longinaris* Spence Bate, 1888, *Pleoticus muelleri* (Spence Bate, 1888) and *Litopenaeus schmitti* (Burkenroad, 1936) (D’Incao *et al.* 2002). However, Castilho *et al.* (2008b) pointed out that the continuous exploitation of the commercially important crustaceans overload not only the target species’ stocks, but also stocks of all the species that share the same habitat as shrimp. Due to the closing of net meshes when trawling, there is a low selectivity of the fishing gear, and consequently, a great diversity of organisms is accidentally caught along with the target species. Such individuals are generically known as the bycatch fauna, and their biomass can become 3 to 15 times higher than the target species’ one (Keunecke *et al.* 2007, Branco *et al.* 2015, FAO 2015).

The on-board discarding of a considerable part of the accidental capture is one of the biggest (if not the one) challenges faced by the fishing professionals (Vianna & Almeida 2005). The species we addressed in this study, *Rimapenaeus constrictus* (Stimpson, 1874), presents a wide geographical distribution, occurring from Canada to southern Brazil (Santa Catarina state), in depths up to 127 m (in the southeastern Brazilian littoral, the species was sampled up to 40 m) (Costa *et al.* 2003). Such a wide distribution range reflects in their flexibility in environmental needs, however, makes them susceptible to the capture as bycatch for several target species fisheries along the Western Atlantic. Dias Neto (2011) claims that only a minority of the bycatch fauna is landed and locally commercialized (most of the times at very low prices), while most of the bycatch organisms is discarded back to the sea, dying or already dead, due to their negligible commercial interest. Among the species composing the seabob shrimp bycatch, *R. constrictus* occupies the fourth place in captured biomass in the Paraná state (Robert *et al.* 2007), and among the pink shrimp bycatch, it is in the second place in total biomass in northern São Paulo state (Keunecke *et al.* 2007).

Several authors (Bauer 1992, Castilho *et al.* 2007b and Grabowski *et al.* 2014, among others) discuss the existence of a latitudinal effect paradigm in the population dynamics of penaeid species. Orton (1920) first hypothesized that the more constant temperature levels in regions close to the equator, with warm temperatures year-round,

could be the cause of the continuous reproductive periodicity observed for several tropical marine invertebrate species. According to the author, the temperature variation, which is strongly tied to latitude, has always been considered an environmental stimulus defining the breeding season of marine invertebrates through triggering and maintaining gametogenesis. In addition, Thorson (1950) suggested that the temporal variation in larval food supply for marine invertebrates with planktotrophic larvae (primary and secondary productivity) might be the selective pressure acting on timing of their reproduction. Therefore, while temperature (and/or other environmental issues) may act as a “proximate factor” on their physiological system, fluctuations in the availability of food supply is supposed to be the “real” reason, or “ultimate factor” to the seasonality in reproduction (Sastry 1983, Bauer 1992).

In his study, Bauer (1992) states that although theoretical reviews and summaries on reproduction of marine invertebrates indicate a tendency for extended reproductive periodicity in lower latitudes and restricted breeding seasons at higher ones, many exceptions are known in crustaceans. Along the Brazilian coast, the lack of applicability to such paradigms could be already observed for *X. kroyeri* (Grabowski *et al.* 2014), for instance. In order to predict such patterns and monitor the population dynamics of a given species, an accurate description of the reproductive processes is indispensable to improve the understanding of the recruitment and spawning stocks development in penaeid shrimp. Only by acquiring such knowledge is it possible to establish effectively sustainable fishery techniques, especially because reproductive traits can differ according to the environmental singularities found in each latitude (Castilho *et al.* 2007b, 2008a).

Despite being an important species composing the bycatch fauna (Keunecke *et al.* 2007, Robert *et al.* 2007), and also playing an important ecological role as part of the trophic web within its distribution range (Costa & Fransozo 2004a), only a few studies concerning *R. constrictus* were carried out along the Brazilian coast up to the date. Costa & Fransozo (2004a, b) described its reproductive biology and ecological distribution, respectively, in Ubatuba, SP; Hiroki *et al.* (2011) addressed its bathymetric distribution, also in Ubatuba; Garcia *et al.* (2016) studied their growth and population structure in Cananéia, SP; and Lopes *et al.* (*in press*) addressed its long-term growth analysis in Ubatuba, SP. Up to now, no studies concerning the geographical variation in the environmental influence over such population traits were carried out along the Brazilian coast.

Facing the scenario described above, the aim of this study was to test the hypothesis that the population dynamics of *R. constrictus* follows such a geographical trend (i.e., the latitudinal effect paradigm) along its distribution in southeastern Brazilian coast. To achieve this goal, we analyzed its population structure, reproductive periodicity and recruitment patterns, as well as the environment influence over such traits.

Material and methods

Biological sampling

Sampling were performed at four areas throughout the Brazilian coast, in different periods from July 2010 through June 2014, covering a 5-degree latitudinal range in depths up to 17 meters. In all the regions, we used similar shrimp-fishing boats to avoid sampling failures, which could lead to consequent errors when analyzing the data. The boats were equipped with double-rig nets the same size as used in artisanal fishing (mesh size: $\cong 3$ cm; mesh gap: $\cong 11.5$ m; boat velocity during trawls: $\cong 1.5$ knots; total distance traveled during trawls: $\cong 0.5$ miles), used to perform monthly 30-min trawls in each sampling station, for each region.

In the Macaé region (MA) ($\approx 22^\circ\text{S}$), northern Rio de Janeiro state, four sampling stations were sorted, comprehending a 5-15 m depth variation, from July 2013 through May 2014. In the Ubatuba region (UB) ($\approx 23^\circ\text{S}$), four sampling stations were studied, covering a 5-15 m depth variation, from July 2013 through June 2014. In the Cananéia region (CA) ($\approx 25^\circ\text{S}$), seven sampling stations were sampled, covering a 5-15 m depth variation, from July 2012 through May 2014. Finally, in the São Francisco do Sul region (SFS) ($\approx 26^\circ\text{S}$), five stations were determined, covering a 5-17 m depth range, from July 2010 through June 2011 (Fig. 1).

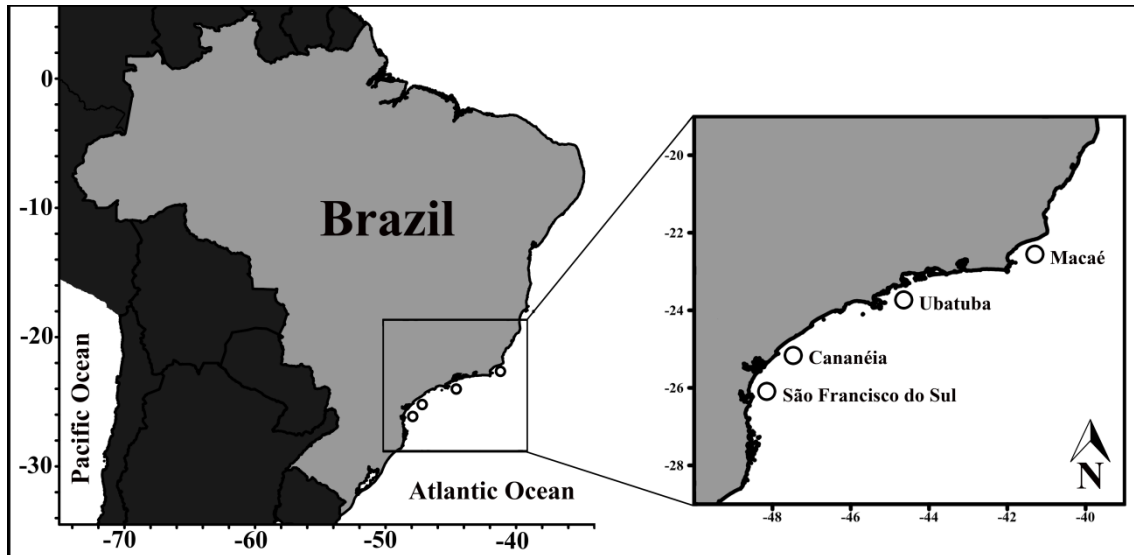


Figure 1. Map of the Brazilian coastal area, highlighting the southeastern littoral and the sampling locations.

Environmental data

Sediment features were sampled for each season of the year, while water characteristics were sampled monthly, for each region, in each sampling station. Since *R. constrictus* inhabits the bottom, we only analyzed features of the bottom water.

Bottom water samples were taken using a Van Dorn bottle. From such samples, salinity was assessed using an optical refractometer, and temperature was measured with a mercury thermometer. Sediment samples were obtained using a Petersen grab and frozen until the moment of laboratory analysis, in order to minimize the organic matter content (O.M.) loss during their transport. In the laboratory, samples were dried (70 °C for 72h) and ash-weighed (10-g subsample) to determine the O.M. Afterward, we took a 100-g subsample from each sample to determine the grain size of the sediment, adopting the same methodology as used by Mantelatto & Fransozo (1999) and Castilho *et al.* (2015b), as it follows. Grain size classification followed the American standard, and fractions were expressed on the phi scale (ϕ), using the formula: $\phi = \log_2 d$, where: d = grain diameter (mm) (Tucker 1988) (e.g.: $-1 = \phi < 0$ (very coarse sand); $0 = \phi < 1$ (coarse sand); $1 = \phi < 2$ (intermediate sand); $2 = \phi < 3$ (fine sand); $3 = \phi < 4$ (very fine sand); and $\phi \geq 4$ (silt + clay)). Finally, ϕ was calculated by cumulative particle-size curves plotted using the ϕ scale. We used the values corresponding to the 16th, 50th and 84th percentiles to determine the mean sediment diameter, using the formula $Md = (\phi_{16} + \phi_{50} + \phi_{84}) / 3$ (Castilho *et al.* 2008b).

Population structure

Individuals were identified to the species based on the morphological features pointed out by Costa *et al.* (2003), and sorted to sex according to the presence of petasma in males and thelycum in females (Pérez-Farfante & Kensley 1997). We considered the carapace length (CL), which consists in the linear distance between the orbital angle and the posterior margin of the carapace (measured using vernier calipers), as the body size measurement, from which we analyzed the size classes' distribution. The size distribution was analyzed using 1-mm CL classes for males and females separately, for posterior comparison of the population structure between sexes.

Reproductive biology

The reproductive condition of females was assessed by the macroscopic observation of the ovarian development, i.e., by the color and volume occupied by the gonads throughout their transparent exoskeleton (Costa & Fransozo 2004a). Therefore, we recognized three ovarian development stages: juvenile (sexually immature, ovaries ranging from thin to thicker transparent strands); spent (adult individuals with undeveloped ovaries, thicker than the juvenile ones, yellow to light orange colored); and reproductive (adult individuals with developing - light green colored - or developed - olive green colored - gonads, much thicker and larger than the other stages). Additionally, we thoroughly observed all the females to the presence or absence of sperm masses inside the seminal receptacles (inseminated females), according to the methodology purposed by Bauer & Lin (1994). Therefore, we considered the breeding (= reproductive) periods to be the ones in which we observed higher percentages of reproductive females. Since penaeid species with closed thelycum mate just after ecdysis (when the females are in their spent gonadal stage) (Dall *et al.* 1990), we considered the mating periods as the ones with higher percentages of inseminated spent females.

Male reproductive status was assessed by the shape of petasma, in which juveniles were considered the ones with separated petasmal lobes, as well as adults were considered the ones in which petasmal lobes were linked by the cincinnuli (minute interlocking processes projecting from the margins of the petasmal endopods) (Boschi 1989, Pérez-Farfante & Kensley 1997). Considering adult males, when spermatophores were visible and occupied a portion of (or all) terminal ampoules, individuals were classified as spermatophore-bearing (reproductive), as well as adult males without

visible spermatophore were considered spent (Castilho *et al.* 2015, Garcia *et al.* 2016). For convenience, we considered “mature” (i.e., reproductively active) those individuals with spent and developed gonads (females), or linked petasma (males).

Data analysis

Sex ratio was considered as the quotient between the abundance of males and the total abundance, for each month, in which sex ratios lower than 0.5 corresponds to a female biased sex ratio. Differences from an equal sex ratio were tested using the binomial test ($p \leq 0.05$) (Wilson & Hardy 2002, Grabowski *et al.* 2014). The length frequency distribution for both sexes was compared using Kolmogorov-Smirnov two-sample tests ($p \leq 0.05$), for each location separately, in which the null hypothesis adopted was that size distribution among sexes did not differ (Zar 1999, Castilho *et al.* 2008a)

In order to assess the influence of environmental factors over the demographic groups, we performed a redundancy analysis (RDA) for each region separately, transforming the environmental factors data matrix to mean 0 and variance 1 (‘standardized’) (Silva *et al. in press*). To perform the RDA, we used two matrixes (one composed by environmental variables and the other by demographic groups (juveniles, spent females, reproductive females, inseminated females, spent males and reproductive males)) (Oksanen *et al.* 2013). Only environmental variables with score values higher than 0.4 and lower than -0.4 were considered biologically meaningful for the RDA axis (Rakocinski *et al.* 1996).

Results

Population structure

Throughout the studied period, we analyzed 3,481 specimens of *R. constrictus* to their population structure. In all the regions, females were more abundant than males, as follows: in the MA region, 7 females and 2 males were sampled (all of them adults). In the UB region, 1,051 females and 533 males were collected (12 juveniles and 1,572 adults). In the CA region, 1,268 females and 426 male were sampled (84 juveniles and 1,610 adults). Finally, we sampled 143 females and 51 males in the SFS region (12 juveniles and 182 adults).

In MA, we observed mean sizes of 9.0 mm (size range: 8.7-9.2 mm) and 10.7 mm (size range: 8.8-12.8 mm) for males and females, respectively. All females were

spent until the 11-mm size class, where we observed the smallest reproductive female (11.8 mm CL), which is approximately the body size in which females attain the reproductive maturity in this region (Fig. 2 A). In UB, we recorded mean sizes of 9.5 mm (size range: 5.7-16.7 mm) and 11.9 mm (size range: 4.8-19.0 mm) for males and females, respectively. In this area, the smallest adult male showed 5.9 mm CL, while the smallest reproductive female, 7.5 mm (Fig. 2 B). The smallest inseminated female presented 8.4 mm CL, possibly the approximate size in which females attain their reproductive maturity. In CA, we observed mean sizes of 8.7 mm (size range: 4.8-13.6 mm) and 10.8 mm (size range: 4.6-17.2 mm) for males and females, respectively. In this region, the smallest adult male showed 5.6 mm CL, while the smallest reproductive female, 6.8 mm (Fig. 2 C). The smallest inseminated female presented 8.1 mm CL, possibly indicating the approximate size in which females become mature. In SFS, individuals showed mean sizes of 9.6 mm (size range: 6.9-12.6 mm) and 11.5 mm (size range: 6.9-18.9 mm) for males and females, respectively. In this area, the smallest mature male showed 6.4 mm CL, while the smallest reproductive female showed 11.4 mm (Fig. 2 D). The smallest inseminated female showed 11.7 mm CL, approximately the size in which females become mature. Except for MA, we observed statistically significant differences concerning body size between sexes in all the studied regions (Kolmogorov-Smirnov, $p < 0.05$).

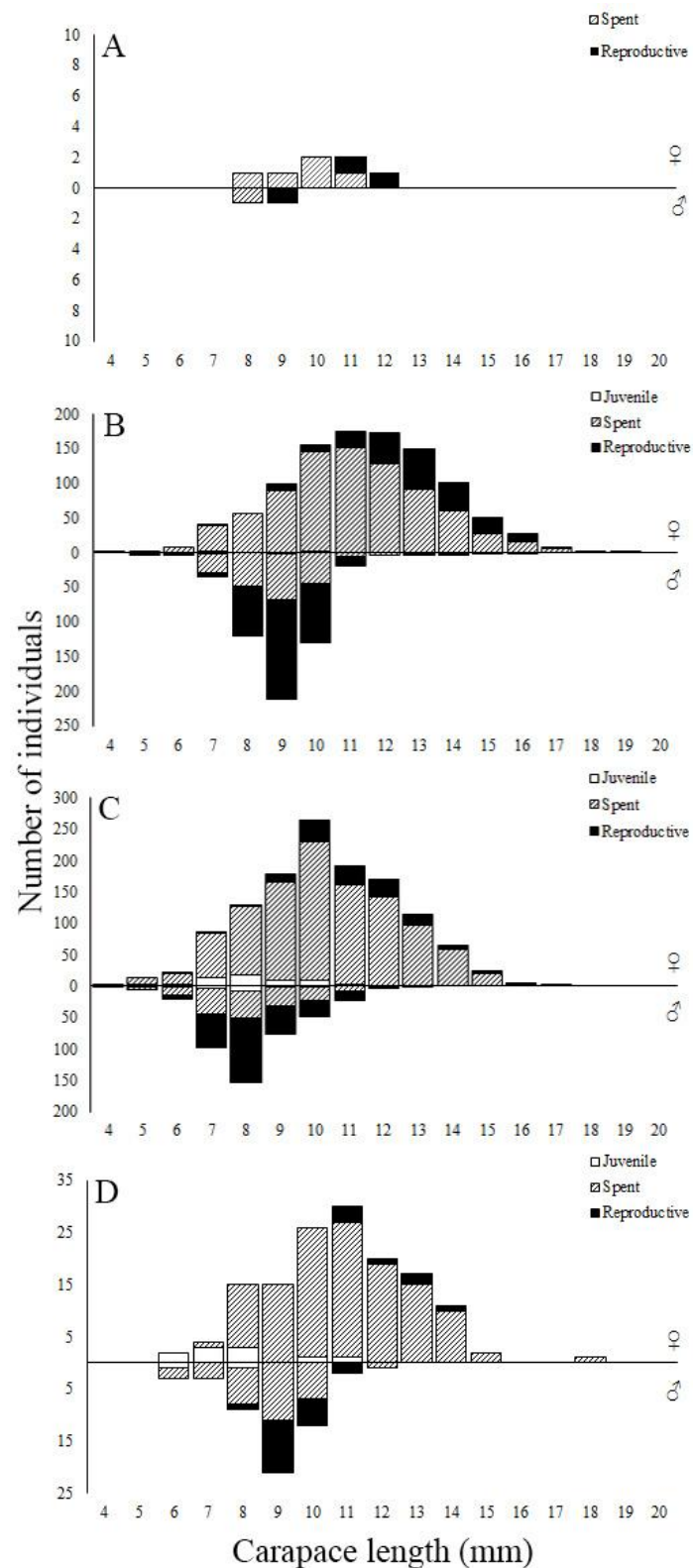


Figure 2: *Rimapenaeus constrictus*: number of individuals per demographic group in each size class, samples taken from: A) Macaé, RJ (from July 2013 through May 2014); B) Ubatuba, SP (from July 2013 through June 2014); C) Cananéia, SP (from July 2012 through May 2014); and D) São Francisco do Sul, SC (from July 2010 through June 2011).

Environmental factors

Annual salinity means showed a decreasing trend as latitude increased. Monthly means of bottom water salinity varied from 34.8 to 38 psu in MA (average mean: 36.7 psu); from 34.3 to 37 psu in UB (average mean: 35.5 psu); from 25.7 to 36.1 psu in CA (average mean: 31.5 psu); and from 31.4 to 35.6 psu in SFS (average mean: 33.4 psu) (Tabs. I-IV).

Annual bottom temperature means showed an increasing trend as latitude increases. Bottom water temperature monthly means varied from 18.5 to 22.3 °C in MA (average mean: 20.5 °C); from 19.9 to 25.5 °C in UB (average mean: 22.5 °C); from 17.5 to 29.3 °C in CA (average mean: 23.3 °C); and from 18.2 to 26.1 °C in SFS (average mean: 22.2 °C) (Tabs. I-IV).

Annual means of O.M. showed a decreasing trend as latitude increases. Its means varied from 10.7 to 14.4% in MA (average mean: 12.7%); from 5.2 to 7.1% in UB (average mean: 6.1%); from 2.4 to 4.9% in CA (average mean: 3.7%); and from 1.4 to 8.0 in SFS (average mean: 3.3%) (Tabs. I-IV).

Finally, Phi annual means showed a decreasing trend as latitude increases. Phi means varied from 4.7 to 6.0 in MA (average mean: 5.4); from 4.1 to 4.5 in UB (average mean: 4.4); from 3.1 to 4.1 in CA (average mean: 3.6); and from 3.7 to 4.5 in SFS (average mean: 4.0) (Tabs. I-IV).

Table I: *Rimapenaeus constrictus*: monthly variation in total abundance, sex ratio, percentage of juveniles and reproductive females, temperature, salinity, phi and organic matter content (O.M.). Samples taken in the Macaé region monthly from July 2013 through May 2014.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|-------------|----------|-----|------|
| Jul/13 | 0 | - | 0 | 0 | 21.8 | 38 | 4.7 | 12.5 |
| Aug/13 | 0 | - | 0 | 0 | 21.5 | 37.5 | 4.7 | 12.5 |
| Sep/13 | 0 | - | 0 | 0 | 21 | 38 | 5.7 | 12.5 |
| Oct/13 | 1 | 0.0 | 0 | 0 | 21.5 | 37.5 | 5.7 | 12.5 |
| Nov/13 | 6 | 0.2 | 0 | 20.0 | 19.5 | 36.8 | 5.7 | 12.5 |
| Dec/13 | 1 | 0.0 | 0 | 0 | 18.5 | 34.8 | 4.7 | 10.7 |
| Jan/14 | 0 | - | 0 | 0 | 19 | 34.9 | 4.7 | 10.7 |
| Feb/14 | 1 | 1.0 | 0 | 0 | 19.9 | 35.6 | 4.7 | 10.7 |
| Mar/14 | 0 | - | 0 | 0 | 21.5 | 36.6 | 6.0 | 14.4 |
| Apr/14 | 0 | - | 0 | 0 | 22.3 | 37.5 | 6.0 | 14.4 |
| May/14 | 0 | - | 0 | 0 | 20.9 | 38 | 6.0 | 14.4 |

*: sex ratio statistically different from 0.5 (Binomial test)

Table II: *Rimapenaeus constrictus*: monthly variation in total abundance, sex ratio, percentage of juveniles and reproductive females, temperature, salinity, phi and organic matter content (O.M.). Samples taken in the Ubatuba region monthly from July 2013 through June 2014.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Inseminated females (%) | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|-------------------------|-------------|----------|-----|------|
| Jul/13 | 297 | 0.4* | 0.7 | 4.0 | 20.3 | 22.7 | 34.8 | 4.5 | 6.9 |
| Aug/13 | 130 | 0.4* | 0 | 0 | 11.4 | 20.3 | 34.3 | 4.5 | 6.9 |
| Sep/13 | 86 | 0.2* | 0 | 20.6 | 5.9 | 19.9 | 34.4 | 4.5 | 6.9 |
| Oct/13 | 38 | 0.3* | 0 | 32.1 | 14.3 | 23.5 | 34.5 | 4.1 | 5.2 |
| Nov/13 | 272 | 0.4* | 1.1 | 10.3 | 21.8 | 23 | 35.8 | 4.1 | 5.2 |
| Dec/13 | 376 | 0.2* | 0 | 48.2 | 8.5 | 22.5 | 37.0 | 4.1 | 5.2 |
| Jan/14 | 30 | 0.5 | 16.7 | 9.1 | 9.1 | 21.4 | 37.0 | 4.4 | 7.1 |
| Feb/14 | 54 | 0.3* | 0 | 15.0 | 42.5 | 20.0 | 36.5 | 4.4 | 7.1 |
| Mar/14 | 10 | 0.3 | 0 | 42.9 | 0 | 22.8 | 36 | 4.4 | 7.1 |
| Apr/14 | 64 | 0.3* | 1.6 | 45.5 | 9.1 | 25.5 | 35.5 | 4.5 | 5.3 |
| May/14 | 31 | 0.3* | 0 | 59.1 | 0 | 25.1 | 35.4 | 4.5 | 5.3 |
| Jun/14 | 196 | 0.4* | 0.5 | 0.8 | 0.8 | 23.9 | 35.1 | 4.5 | 5.3 |

*: sex ratio statistically different from 0.5 (Binomial test)

Table III: *Rimapenaeus constrictus*: monthly variation in total abundance, sex ratio, percentage of juveniles and reproductive females, temperature, salinity, phi and organic matter content (O.M.). Samples taken in the Cananéia region monthly from July 2012 through May 2014.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Inseminated females (%) | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|-------------------------|-------------|----------|-----|------|
| Jul/12 | 57 | 0.3* | 0 | 0 | 2.6 | 19.1 | 30.3 | 3.1 | 3.1 |
| Aug/12 | 117 | 0.3* | 0 | 1.2 | 0 | 20.4 | 30 | 3.1 | 3.1 |
| Sep/12 | 31 | 0.2* | 0 | 7.7 | 0 | 22.8 | 33 | 3.1 | 3.1 |
| Oct/12 | 182 | 0.2* | 0 | 18.2 | 4.7 | 22.6 | 36.1 | 3.9 | 4.9 |
| Nov/12 | 91 | 0.2* | 1.1 | 8.2 | 0 | 24.1 | 32.9 | 3.9 | 4.9 |
| Dec/12 | 35 | 0.1* | 0 | 16.1 | 9.7 | 25.7 | 32 | 3.9 | 4.9 |
| Jan/13 | 60 | 0.2* | 56.7 | 12.5 | 56.3 | 26.3 | 32.7 | 3.3 | 4.0 |
| Feb/13 | 29 | 0.1* | 0 | 57.7 | 0 | 27.6 | 33.3 | 3.3 | 4.0 |
| Mar/13 | 3 | 0.3 | 0 | 0 | 0 | 25 | 20.6 | 3.3 | 2.8 |
| Apr/13 | 38 | 0.3 | 2.6 | 0 | 0 | 24.7 | 33.8 | 3.8 | 4.1 |
| May/13 | 28 | 0.3* | 28.6 | 0 | 0 | 22.5 | 31.8 | 3.8 | 3.9 |
| Jun/13 | 194 | 0.4* | 0.5 | 3.5 | 7.0 | 21.2 | 34.6 | 3.8 | 3.9 |
| Jul/13 | 170 | 0.2* | 4.1 | 0 | 9.9 | 17.5 | 30.6 | 3.6 | 2.6 |
| Aug/13 | 154 | 0.2* | 0 | 0 | 23.6 | 18.3 | 29.2 | 3.6 | 2.6 |
| Sep/13 | 56 | 0.2* | 7.1 | 28.6 | 14.3 | 19.3 | 27.8 | 3.5 | 2.4 |
| Oct/13 | 19 | 0.1* | 5.0 | 70.6 | 17.6 | 22.4 | 28.2 | 3.6 | 3.2 |
| Nov/13 | 37 | 0.2* | 16.2 | 36.0 | 12.0 | 23.1 | 25.7 | 3.6 | 3.2 |
| Dec/13 | 83 | 0.2* | 0 | 7.6 | 9.1 | 24.6 | 27.2 | 3.6 | 3.2 |
| Jan/14 | 210 | 0.3* | 1.9 | 26.2 | 20.1 | 29.3 | 32.9 | 3.5 | 4.1 |
| Feb/14 | 17 | 0.1* | 0 | 12.5 | 31.3 | 27.3 | 33.5 | 3.5 | 4.1 |
| Mar/14 | 3 | 0 | 0 | 33.3 | 0 | 25.3 | 34 | 3.5 | 4.1 |
| Apr/14 | 2 | 0.5 | 0 | 0 | 0 | 24.9 | 34.7 | 3.8 | 3.8 |
| May/14 | 78 | 0.3* | 21.8 | 0 | 2.5 | 22.5 | 32.9 | 4.1 | 4.5 |

*: sex ratio statistically different from 0.5 (Binomial test)

Table IV: *Rimapenaeus constrictus*: monthly variation in total abundance, sex ratio, percentage of juveniles and reproductive females, temperature, salinity, phi and organic matter content (O.M.). Samples taken in the São Francisco do Sul region monthly from July 2010 through June 2011.

| Month | Abundance | Sex ratio | Juveniles (%) | Reproductive females (%) | Inseminated females | Temperature | Salinity | Phi | O.M. |
|--------|-----------|-----------|---------------|--------------------------|---------------------|-------------|----------|-----|------|
| Jul/10 | 30 | 0.3* | 10.0 | 0 | 3.7 | 19.4 | 34.6 | 3.8 | 1.4 |
| Aug/10 | 20 | 0.4 | 10.0 | 0 | 5.6 | 18.2 | 33.4 | 3.8 | 1.6 |
| Sep/10 | 16 | 0.5 | 0 | 0 | 0 | 19.5 | 31.4 | 4.4 | 6.8 |
| Oct/10 | 6 | 0.5 | 0 | 0 | 0 | 20.1 | 32.3 | 4.5 | 8.0 |
| Nov/10 | 3 | 0.3 | 0 | 0 | 0 | 22.4 | 32.4 | 4.2 | 4.6 |
| Dec/10 | 8 | 0.1* | 25.0 | 0 | 0 | 24.6 | 32.3 | 4.2 | 5.0 |
| Jan/11 | 8 | 0.1* | 0 | 0 | 0 | 25.6 | 33.8 | 3.7 | 2.4 |
| Feb/11 | 2 | 0 | 0 | 0 | 0 | 26.1 | 32.2 | 3.7 | 1.8 |
| Mar/11 | 4 | 0 | 0 | 0 | 25.0 | 24.7 | 32.7 | 3.8 | 2.0 |
| Apr/11 | 8 | 0.1* | 0 | 57.1 | 25.0 | 23.2 | 34.8 | 3.8 | 2.0 |
| May/11 | 33 | 0.2* | 9.1 | 0 | 6.7 | 22.3 | 35.2 | 4.3 | 2.4 |
| Jun/11 | 56 | 0.2* | 3.6 | 2.4 | 3.7 | 21 | 35.6 | 4.3 | 2.2 |

*: sex ratio statistically different from 0.5 (Binomial test)

The environmental influence over population dynamics

In MA, the first RDA axis represented approximately 80% of the variation in the abundance of the demographic groups. In this area, only the salinity levels influenced individuals (reproductive males and spent females), while the other environmental parameters did not exert any apparent influence (Tab. V). In UB, the first RDA axis explained 57% of the variance in the abundance of individuals. In this region, spent and reproductive males and spent females were negatively influenced by bottom water salinity, while reproductive and inseminated females were positively influenced by the same parameter. The remaining environmental factors did not significantly influence the demographic groups in this area (Tab. VI). In the CA region, the first RDA axis explained around 96% of the variation in the abundance of demographic groups. In this region, bottom water temperature negatively influenced the distribution of spent males and reproductive and spent females, which, on the other hand, were positively influenced by bottom water salinity. The remaining environmental features and demographic groups did not show any significant correlation to each other (Tab. VII). Finally, in the SFS region, the first RDA axis explained around 90% of the variation in the abundance of the demographic groups. In this area, only spent individuals (both males and females) were significantly influenced, positively by bottom water salinity and negatively by bottom water temperature. The remaining environmental factors and demographic groups did not show any significant relation to each other (Tab. VIII).

Table V: *Rimapenaeus constrictus*: Summary of results of the Redundancy Analysis (RDA) for the abundance of demographic classes (spent and reproductive females, and spent and reproductive males) and environmental factors. Samples taken monthly from July 2013 through May 2014 in the Macaé region, southeastern Brazil.

| | RDA 1 | RDA 2 |
|---|--------------|--------|
| Eigenvalue | 1.4 | 0.3 |
| % of variance | 80.35% | 13.89% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | 0.09 | 0.00 |
| Bottom water salinity | -0.53 | -0.49 |
| Organic matter content | -0.09 | 0.06 |
| Phi | -0.11 | -0.02 |
| <i>Abundance of individuals</i> | | |
| Spent males | 0.34 | 0.33 |
| Reproductive males | -0.50 | 0.16 |
| Spent females | -1.34 | 0.00 |
| Reproductive females | 0.06 | -0.49 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Table VI: *Rimapenaeus constrictus*: Summary of results of the Redundancy Analysis (RDA) for the abundance of demographic classes (juveniles; spent, reproductive and inseminated females; spent and reproductive males) and environmental factors. Samples taken monthly from July 2013 through June 2014 in the Ubatuba region, southeastern Brazil.

| | RDA 1 | RDA 2 |
|---|--------------|--------|
| Eigenvalue | 31.27 | 19.36 |
| % of variance | 57.05% | 35.31% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | 0.24 | 0.57 |
| Bottom water salinity | 0.77 | 0.20 |
| Organic matter content | -0.15 | 0.76 |
| Phi | -0.34 | 0.79 |
| <i>Abundance of individuals</i> | | |
| Juveniles | 0.07 | 0.11 |
| Spent males | -0.52 | 1.14 |
| Reproductive males | -0.53 | 1.23 |
| Spent females | -0.94 | 0.62 |
| Reproductive females | 2.17 | 0.63 |
| Inseminated females | 0.66 | 0.67 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Table VII: *Rimapenaeus constrictus*: Summary of results of the Redundancy Analysis (RDA) for the abundance of demographic classes (juveniles; spent, reproductive and inseminated females; spent and reproductive males) and environmental factors. Samples taken monthly from July 2012 through May 2014 in the Cananéia region, southeastern Brazil.

| | RDA 1 | RDA 2 |
|---|--------------|-------|
| Eigenvalue | 46.40 | 1.41 |
| % of variance | 95.87% | 2.93% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | -0.74 | 0.66 |
| Bottom water salinity | 0.69 | 0.58 |
| Organic matter content | 0.07 | 0.02 |
| Phi | 0.10 | -0.26 |
| <i>Abundance of individuals</i> | | |
| Juveniles | -0.01 | 0.31 |
| Spent males | 0.66 | 0.01 |
| Reproductive males | 0.72 | 0.52 |
| Spent females | 4.50 | -0.05 |
| Reproductive females | -0.36 | 0.50 |
| Inseminated females | 0.00 | 0.19 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Table VIII: *Rimapenaeus constrictus*: Summary of results of the Redundancy Analysis (RDA) for the abundance of demographic classes (juveniles; spent, reproductive and inseminated females; spent and reproductive males) and environmental factors. Samples taken monthly from July 2010 through June 2011 in the São Francisco do Sul region, southeastern Brazil.

| | RDA 1 | RDA 2 |
|---|--------------|-------|
| Eigenvalue | 4.10 | 0.42 |
| % of variance | 89.83% | 9.13% |
| <i>Environmental factors</i> | | |
| Bottom water temperature | 0.47 | 0.83 |
| Bottom water salinity | -0.93 | 0.37 |
| Organic matter content | 0.03 | -0.49 |
| Phi | -0.14 | -0.14 |
| <i>Abundance of individuals</i> | | |
| Juveniles | -0.22 | -0.03 |
| Spent males | -0.43 | -0.53 |
| Reproductive males | -0.13 | -0.16 |
| Spent females | -1.90 | 0.14 |
| Reproductive females | 0.09 | 0.22 |
| Inseminated females | -0.03 | 0.12 |
| Bold values denote the variables which were considered biologically meaningful for that RDA axis (i.e., >0.4 and <-0.4) (Rakocinski et al. 1996). | | |

Reproductive biology

Throughout the studied period, it was possible to observe a clear female-biased sex ratio for all regions. Unfortunately, it was not possible to determine a pattern on sexual proportion for the species in the MA region due to the low number of individuals sampled in this area (Tab. I). In UB, we observed sex ratios statistically different from 0.5 (Binomial test, $p < 0.05$) in 10 out of 12 months (Tab. II). Similarly, in CA we observed statistically female-biased sex ratios in 20 out of 24 studied months (Binomial test, $p < 0.05$) (Tab. III). In SFS, we observed differences from a 0.5 sex ratio in 6 out of 12 sampled months (Binomial test, $p < 0.05$), favoring females mainly in autumn and early winter (Tab. IV).

In MA, the presence of reproductive females was recorded only in November; however, it was not possible to determine the reproductive periodicity for the area due to the low number of sampled individuals. On the other hand, in UB we observed a continuous reproduction for the species. In this area, we recorded the presence of reproductive females in 11 out of 12 sampled months, even though with peaks in their abundance in spring, late summer and autumn. The same is valid for the percentage of inseminated spent females in this area, which showed a continuous distribution throughout the year, with a peak in February, and being absent in March and May (Tab. II), characterizing a continuous mating pattern for the area. In the CA region, the distribution of the percentage of reproductive females was continuous throughout the studied period, despite their absence in some periods (9 out of 23 studied months), with peaks in February and October 2013 and March 2014. In this region, the distribution of inseminated spent females also showed a continuous tendency (peaks in January and August 2013, and February 2014), even though they were not sampled in 9 out of 23 studied months (Tab. III), leading us to suggest a continuous mating pattern for the region. In SFS, the percentage of reproductive females was concentrated in most of the autumn months (April and June), being absent along the remaining months and showing, therefore, a discontinuous pattern. The same is valid for inseminated spent females, which were concentrated in autumn/ winter (Tab. IV), evidencing a seasonal mating periodicity for the area.

Recruitment seemed to be episodic, except for MA (where the low number of sampled individuals did not allow us to define the recruitment period for the species). In UB, the main peak in percentage of juveniles was recorded in January, even though a low abundance was recorded for this month (30 individuals). In this region, the juvenile

presence did not display a clear pattern since it was observed in July, November, April and May (Tab. II). As informed above, the recruitment periods in CA seemed to grow stronger in the spring/ summer months, since recruitment appears to begin during late winter and has its peaks in the subsequent seasons of both years, with juveniles being recorded in 11 out of 23 sampled months (Tab. III). In SFS, recruitment juveniles were recorded in late autumn, winter and summer, assuming an episodic pattern (Tab. IV). In this area, juveniles were sampled in 5 out of 12 sampled months.

Discussion

In our study, we could evidence how local conditions alter the expected patterns for the population dynamics of a bycatch species throughout the southeastern Brazilian coast. We sampled juvenile to reproductive individuals of both sexes in a substantial abundance, evidencing that the species finds favorable conditions to the successful establishment of a population in the area. Such plasticity may be a reflex of the wide geographical range of the species, allowing them to adapt itself to unfavorable conditions.

The environmental influence over population structure

In the study of penaeoideans' population dynamics, it is well known that environmental factors play a crucial role over several aspects of their life cycle (Dall *et al.* 1990, Costa & Fransozo 2004b, Castilho *et al.* 2015b, Grabowski *et al.* 2016). According to Dall *et al.* (1990), the behavior of penaeid shrimps is influenced by environmental factors since they are closely related to their physiological processes.

Bauer (1992) attested that among such factors, growth and reproduction are specially influenced by the variations in the water temperature, which are strongly tied to the latitude in which they are found. If so, higher temperatures at lower latitudes would cause an increase in the growth coefficient through a higher metabolism, which in turn would cause them to attain smaller body sizes. Briefly, the “latitudinal effect paradigm” states that congener or conspecific species tend to grow bigger, and as a consequence, live longer, as latitude increases (Bauer 1992, Castilho *et al.* 2007b, 2012).

Along the Brazilian coast, such pattern has already been confirmed to species such as *A. longinaris* (Castilho *et al.* 2007b, 2015b) and *P. muelleri* (Castilho *et al.* 2012). On the other hand, in this thesis, as in recent studies, we discuss the applicability

of such pattern to penaeoids occurring along the southeastern Brazilian coast. As it was possible to be noted in Chapter 1 and 2, such environmental pattern cannot be attested to happen in this area for *Sicyonia dorsalis* Kingsley, 1878 and *P. muelleri*, respectively. A similar lack in the applicability of this paradigm was also pointed out for *X. kroyeri* (Grabowski *et al.* 2014) and even for the same species as studied in this chapter (Lopes *et al. in press*).

The results here presented for *R. constrictus* proves that the latitudinal effect paradigm cannot explain the variation in the population dynamics aspects such as maximum size and size at the onset of sexual maturity for the species. The medium sizes (males: smallest: CA and largest: SFS; females: smallest: CA and largest: UB) and maximum sizes (males: smallest: MA and largest: UB; females: smallest: MA and largest: UB) variation seems not to follow a clear pattern along the studied areas. It could also be noted when analyzing the size of the smallest reproductive female in each region, which is similar between SFS and MA (11.4 and 11.8 mm CL, respectively), but undergo a decrease in the UB and CA regions (7.5 and 6.8 mm CL, respectively).

The reason why the latitudinal pattern cannot be applied to the all penaeoidean species along the southeastern Brazilian coast can be associated to the geographical features in the area. In a hypothetic general model, it is expected to find higher and homogeneous temperature levels in lower latitudes, and a more evident fluctuation in this parameter as latitude increases. In other words, localities in lower latitudes tend to show continuous temperature levels along the year, while in higher latitudes, temperature tends to increase in summer and decrease in winter (Brown & Lomolino 2006). However, the studied areas are located in a zone known as the Atlantic upwelling zone, comprehended between the latitudes of 23 and 29°S, and it is highly influenced by marine fronts (marine areas in which the characteristics of two or more waters are combined, causing it to present characteristics of a transitional zone). Among the water masses influencing the region, it is possible to name the South Atlantic Central Water (SACW), the Coastal Water (CW) and the Tropical Water (TW). Such mixture of features from different sources can result in increased primary, and consecutively, secondary production. From such ones, the SACW is the one that can get closer to the shallower areas, although being formed in regions far from the coast (Acha *et al.* 2004).

The SACW gets closer to the coast during late spring and early summer, and is characterized by lower salinity and temperature levels (<18 °C and <36 psu, respectively), mixing water from the warm Brazilian current (temperature >20 °C and

salinity >36 psu) and the Falklands current (temperature <15 °C and salinity <34 psu). It emerges in the Cabo Frio region, as an upwelling event (Castro-Filho *et al.* 1987, Castro-Filho & Miranda 1998, Acha *et al.* 2004). In UB, the occurrence of the SACW can be noticed when there is a decrease in the bottom water temperature levels down to 15 °C (Costa *et al.* 2005). The effects of the SACW intrusion can reflect in considerable changes in the inhabiting community, either positive or negative, since there can be observed both increased and decreased number of sampled individuals for different species (for instance, *P. muelleri* and *X. kroyeri*, respectively) (Castilho *et al.* 2008b).

On the other hand, in the southern areas covered by our study, it was possible to observe the presence of large estuarine areas (Grabowski *et al.* 2014, Barioto *et al. in press*, Garcia *et al.* 2016). Thus, the CA region undergo a strong influence caused by the freshwater influx coming from a huge estuarine area (the complex estuarine-lagoon system of Cananeia-Iguape), while SFS is influenced by the influx coming from the Babitonga Bay, one of the main estuarine areas in southern Brazil. (Besnard 1950, DNIT/IME 2004). Therefore, in these areas it was possible to evidence not only the influence of water masses occurring along the coast, but also the influence of local characteristics, which can also be held responsible for the absence of a pattern in the population traits we analyzed.

Although *R. constrictus* is essentially marine, Garcia *et al.* (submitted) sampled a considerable number of individuals close to the estuarine area. The authors state the species' tolerance to temperature ranges, suggesting that they can adapt themselves to the local conditions found along their distributional range. According to the authors, it is also important to remember that the mean salinity in the sampling station in which the specimens were sampled allows one to attest that this is a poly/ mesohaline area (salinity between 15 and 35 psu), presenting good conditions to the establishing of the species at certain periods (high salinity and temperature, for instance).

Such a behavior plasticity was also evident when analyzing the species' abundance variation along the year. Even though we observed periods in which the abundance was higher (mainly winter and spring), the species could be found throughout the entire sampled period in all regions, except for MA. The low number of individuals sampled in MA suggests that even though this is considered a eurythermal species (see Garcia *et al.* submitted), the temperature range in this area can be considered a limiting factor to the successful establishment of the population. Despite MA is located in a tropical region, it undergoes through a strong influence of the Cabo

Frio upwelling, causing it to present cool-temperate regions environmental aspects (Sancinetti *et al.* 2015). Under the influence of such low temperatures, the species may migrate to other areas where the environmental conditions are more favorable for them, and so, the lack of environmental influence (except for salinity) shown by the RDA results may be a reflex of the low number of sampled individuals as well.

Besides being a generalist species concerning temperature, another factor that could induce the presence of the species throughout the year is the amount of nutrients found in each one of the studied regions. During the intrusion of the SACW, besides the thermal seasonality, it is possible to observe higher levels of chlorophyll, reflecting in an increased phytoplankton productivity, which in turn may stimulate the subsequent production of zooplanktonic herbivorous organisms. In marine coastal animals, spawning events generally coincide with the spring phytoplanktonic production, upon which the newly-hatched larvae will feed on (Pires-Vanin *et al.* 1993, Vega-Pérez 1993, Castilho *et al.* 2015b).

According to Léo & Pires-Vanin (2006), the texture of the sediment is one of the main factors influencing the regions and faunistic assemblages, and so the distribution patterns of the communities are closely related to the sediment composition and its O.M. However, no significant correlations were observed between the abundance of individuals and the grain size distribution, nor with the O.M. associated to the substrate, in all the studied areas. It may be an evidence that this species does not show preference for a specific type of sediment, and so this would not be a limiting factor to the individuals, as purposed by Costa & Fransozo (2004b), and reflecting again on the behavioral plasticity displayed by the species. Garcia *et al.* (submitted) also discussed that under adverse conditions, the species may prefer a specific type of sediment, more appropriate for burrowing. Despite the importance of the sediment features over the biology of the species, Castilho *et al.* (2008b) also reported a weak influence of such parameters over the penaeoidean community in the UB region. According to the authors, it is possible that the variation in such factor was not high enough to allow its influence to be clearly visible. Besides that, the benthic communities are also affected by several other factors such as food availability, prey-predator relationships and migration, among other factors that were not considered in our study (Lenihan & Micheli 2001).

Reproductive biology

In our study, females attained greater body sizes, as well as showed higher abundances when compared to males, in all the studied regions. Boschi (1989) states that sex-related differences in body size (specially observing larger females) is considered a general pattern in the study of penaeids. Additionally, Gab-Alla *et al.* (1990) and Yamada *et al.* (2007) consider this sexual dimorphism an evolutionary adaptation in order to benefit reproduction, since larger females could produce an exponentially higher number of eggs. The same pattern on sexual dimorphism was also stated for other Penaeoidea species such as *X. kroyeri* (Grabowski *et al.* 2014, 2016, Castilho *et al.* 2015a), *A. longinarius* (Castilho *et al.* 2007a, 2015b), *P. muelleri* (Castilho *et al.* 2012) and *R. constrictus* (Costa & Fransozo 2004a, Lopes *et al. in press*), among others.

In addition, the female-skewed sex ratio is also a common pattern for penaeoids. As pointed out by Garcia *et al.* (2016), it demonstrates that *R. constrictus* is another exception to the sex allocation theory proposed by Fisher (1930), which attests that in gonochoric species, sex ratio should be 1:1, as parents may produce an equal number of male and female individuals in each offspring. Such a deviation in sex ratio could be caused by many factors, such as migration and differential mortality rates between sexes (Wenner 1972, Gab-Alla *et al.* 1990), among others. Furthermore, Garcia *et al.* (2016) discussed that sex ratio can also be a function of individual size, as it follows. Since males show a higher growth coefficient and consequent lower body size, the chance of finding males of a certain size is lower. It is also believed that high metabolic rates lead to cellular ageing and consequent decreased longevity. If so, males' greater growth investment leads to higher metabolic rates, culminating in decreased longevity and lower body size, also deviating the sex ratio in the largest size classes (Pearl 1928, Garcia *et al.* 2016).

Except for MA, we observed a discontinuous tendency in the reproductive periodicity as latitude increases. Reproductive peaks coincided with the periods of higher abundance of individuals in UB, the same as observed in CA. Such a pattern became even clearer in SFS, where the highest abundances of reproductive females were observed in autumn and winter, while were absent in the rest of the year. The same pattern could be suggested to the mating periodicity, which showed a trend towards continuity in lower latitudes.

In a temperate-subtropical area, within the 28-30°N latitudinal variation, Bauer & Lin (1994) found out that the reproductive activities of the species are restricted to the warmer months. In the southeastern Brazilian coast (UB), Costa & Fransozo (2004a) also observed a higher reproductive activity for the species in summer months. However, these authors sampled breeding females throughout the entire year, suggesting that in UB, the reproductive periodicity of the species is continuous. In our study, temperature was negatively correlated with the number of individuals in CA and SFS, however, with no significant association between both factors in UB.

Every environmental factor (physical or biological) presents a specific variation gradient, and species respond differently to them, according to their tolerance, thus being classified as eurytopic (ecologically tolerant) or stenotopic (ecologically intolerant) (Brown & Lomolino 2006, Cox & Moore 2009). Therefore we agree on the suggestion made by Garcia *et al.* (2016), which states that *R. constrictus* is an eurythermal species, i.e., is able to tolerate a wide range in temperature levels. The same seems to be valid for the populations we studied, since the species could be captured throughout the entire year in all areas (except for MA), and displays a great distributional range, being found along almost all the Western Atlantic (Pérez-Farfante & Kensley 1997). Such a continuity in the species' capture was also stated by Costa & Fransozo (2004a) and Hiroki *et al.* (2011) in the UB region. However, independently of the tolerance level shown by the species, their functional full efficiency may be displayed only in a specific portion of each gradient, and toward any of its limits, the species undergo an increasing physiological stress (Brown & Lomolino 2006, Cox & Moore 2009). This may be the reason why the abundance of the species was so lower in MA when compared to the other regions, since MA showed some of the lowest temperature levels of the entire studied area, despite the absence of statistical relation between the abundance of individuals and the temperature range.

Juvenile individuals did not display a clear pattern in their temporal distribution, what may be a consequence of the continuity in the reproductive periodicity of the species. Since it was discontinuous along studied period, our results confirm the episodic recruitment pattern reported for the species by Costa & Fransozo (2004a) and Bauer & Lin (1994), in UB and Gulf of Mexico, respectively.

Among the events that could explain the episodic recruitment pattern for a given species, one can highlight the variation in the mortality rate of larval and early juvenile stages due to the variation in food availability, physical conditions of the regions or the

presence of predators (Bauer 1989, Castilho *et al.* 2007a, Garcia *et al.* 2016). As discussed by Castilho *et al.* (2015a), recruitment is likely affected by many environmental factors which can influence on the growth, survival and dispersal of the early development stages. Furthermore, Castilho *et al.* (2015a) discuss that teasing out the individual effects of such myriad factors require multidisciplinary studies concerning the biology of the species, as well as the oceanographic conditions in which they live.

Yet Dall *et al.* (1990) have considered the species to have a “type III” life cycle (mating and spawning occur in offshore areas, while juvenile recruitment takes place in inshore regions), in this study, we present evidences that do not agree with such statement. Except for the MA region, we sampled juvenile to reproductive individuals throughout the entire sampled area, in a substantial abundance. On the other hand, our findings are similar to the ones discussed by Bauer & Lin (1994), which attest that the entire life portion from juveniles to spawning adult stages of the species may occur in inshore waters. The results here presented hence show the absence of distributional segregation of the species life stages, and how it can adapt to different environmental conditions in order to obtain success in their establishment.

In our study, we refute the hypothesis that the “latitudinal effect paradigm” is applicable when explaining the geographical variation in the population dynamics of *R. constrictus*. Furthermore, this study brings relevant information in order to improve the fisheries management along the Brazilian coast, since even though not commercialized, this species plays a substantial role in the food web chain along the southern Brazilian coast. According to Bauer (1992), generalizations are oversimplifications that do not hold up as more studies are conducted on the biological phenomenon, and contradictory results are found. In this sense, further studies are welcome to be carried out along the Brazilian coast, in order to understand in a clearer way how the oceanographic conditions can affect the life history of important economic resources such as the Penaeoidean shrimp, as well as their bycatch fauna.

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Considerações finais

Em seu estudo clássico, Bauer (1992) afirma que generalizações sobre fenômenos biológicos são uma ferramenta útil e necessária para sumarizar informações a respeito dos mesmos, e neste sentido, atuam como modelo ou paradigma para se propor e testar hipóteses sobre fatores responsáveis pelos padrões observados. Há de se lembrar, contudo, que frequentemente as generalizações são demasiadamente simplificadas, e não se mantêm imutáveis à medida que mais estudos são realizados, e resultados contraditórios são encontrados. Então, o paradigma é descartado ou modificado; porém, ao longo do processo, frequentemente novas e importantes informações vêm à tona, aumentando o nosso entendimento acerca do mundo biológico.

Considerando o produto final desta tese, faz-se legítimo o raciocínio apresentado pelo autor, uma vez que, analisando os resultados obtidos para as três espécies, conclui-se de que nenhuma delas apresenta um padrão que valide o “paradigma do efeito latitudinal” para a dinâmica de peneídeos na costa brasileira. De maneira geral, duas frentes de pensamento podem ser seguidas para explicar os padrões biológicos obtidos:

A primeira delas baseia-se no fato de que, além do padrão geográfico generalizado observado na variação dos fatores ambientais (especialmente temperatura, i.e., temperaturas altas e homogêneas em latitudes baixas e temperaturas frias e mais heterogêneas em altas latitudes), existem individualidades locais que são capazes de modificar tal cenário. Em outras palavras, os paradigmas tidos como norteadores no estudo de determinados fenômenos biológicos têm seu mérito, porém, são generalizações que devem ser tomadas com cautela, uma vez que sua aplicabilidade se restringe a estudos em larga escala, e por isso nem sempre descrevem de maneira adequada os eventos em menor amplitude. Vale salientar que o “paradigma do efeito latitudinal” desconsidera tais ações locais, tais como as observadas ao longo da região abordada no presente estudo. Como visto ao longo dos capítulos, as espécies apresentam, sim, uma tendência nos padrões apresentados em seus parâmetros do ciclo de vida, os quais por sua vez podem, de fato, ser associados à variação nos fatores ambientais atados à latitude local. Porém, as características oceanográficas observadas ao longo da costa brasileira fazem com que o padrão climático se inverta no Sudeste do Brasil (i.e., temperaturas baixas são observadas nas regiões mais próximas ao equador), levando as espécies a adaptarem seus ciclos de vida conforme as suas necessidades.

Em segundo lugar, há de se ponderar questões particulares a cada espécie, considerando também os processos evolutivos que permearam o estabelecimento das populações para que apresentem-se da maneira que conhecemos hoje. Para entender este

raciocínio, é necessário retomar as conclusões obtidas ao analisar os parâmetros populacionais de *Pleoticus muelleri* (Spence Bate, 1888) e *Rimapenaeus constrictus* (Stimpson, 1874).

Estudos sugerem que *P. muelleri* tipicamente habite regiões temperadas frias, sendo inclusive considerada uma espécie indicadora da presença de massas de água frias na costa sudeste do Brasil. Contudo, ainda que os organismos apresentem determinada tolerância à variação em fatores ambientais, só é possível atingir a eficiência plena de suas funções biológicas em uma porção mais ou menos limitada deste gradiente, e em direção a qualquer um dos limites, a espécie sofre um crescente estresse fisiológico. Partindo deste pressuposto, presume-se que as espécies, e *P. muelleri*, em especial, apresentem maiores tamanhos corpóreos, bem como tendência à continuidade reprodutiva, nas regiões mais ao norte da área estudada (especialmente Macaé), em virtude desta localidade apresentar características de regiões temperadas. Logicamente, esta situação é construída a partir da ação de massas de água ao longo da região costeira, sendo este efeito ampliado substancialmente devido à proximidade de Macaé com a Ressurgência de Cabo Frio. Desta maneira, é possível, sim, afirmar que o ciclo de vida desta espécie é regido pela ação de um fator ambiental em especial que, em uma situação generalizada, apresenta níveis elevados em menores latitudes, e níveis baixos em maiores latitudes. Neste caso, são então as forças ambientais locais que fazem com que este gradiente de temperatura seja invertido na costa sudeste do país, tendo o mesmo efeito sobre a dinâmica populacional de *P. muelleri*, bem como sobre as demais.

Por outro lado, os parâmetros reprodutivos de *R. constrictus* não pareceram apresentar um padrão claro quando comparados entre as regiões estudadas. Obviamente, seus processos reprodutivos e de recrutamento também são regidos pela influência de fatores ambientais, porém a espécie apresenta determinado grau de plasticidade fenotípica, o que a torna mais generalista tratando-se de condições ambientais.

Neste contexto, testadas as hipóteses propostas, propõe-se as principais conclusões obtidas:

- As espécies se comportaram de formas diferentes quanto à variação na periodicidade reprodutiva observada. *Sicyonia dorsalis* Kingsley 1878 apresentou uma maior sazonalidade reprodutiva em todas as regiões, ainda que com um maior número de meses reprodutivos em menores latitudes. Já *P. muelleri* e *R. constrictus* apresentaram uma tendência à reprodução contínua em menores latitudes, e uma maior sazonalidade em latitudes maiores.

Provavelmente, tal tendência está relacionada não apenas à temperatura nestes locais, mas também ao aporte de nutrientes oferecido pela ação de correntes marinhas e do fenômeno da ressurgência;

- A estrutura populacional das espécies seguiu um padrão contrário ao que é esperado considerando o “paradigma do efeito latitudinal”, de acordo com o qual, as espécies de peneóides tendem a atingir maiores tamanhos corpóreos e maturidade sexual tardia em maiores latitudes. Do mesmo modo, analisando as estimativas obtidas nas análises de crescimento populacional, foi possível notar o mesmo padrão contrário ao esperado, com menores constantes de crescimento e maiores comprimentos assintóticos observados nas áreas ao norte da área abordada. Provavelmente, as espécies comportam-se desta maneira na costa sudeste do Brasil devido ao fato de que as regiões ao norte da região estudada apresentam características ambientais similares àsquelas observadas em latitudes mais altas, em virtude da ação de massas de água nestas localidades. Tal característica parece atuar com uma intensidade ainda maior sobre *P. muelleri*, uma vez que a história de vida da espécie é historicamente associada a temperaturas baixas;
- As forças locais observadas ao longo da costa do Brasil são, de fato, capazes de alterar os padrões historicamente propostos para os padrões da dinâmica populacional dos camarões Penaeoidea. Dentre eles, grandes áreas estuarinas, a presença de massas de água e eventos de ressurgência regem o ciclo de vida dos camarões.

Os dados apresentados nesta tese são de suma importância na busca por um sistema de gerenciamento pesqueiro eficiente, que proteja não apenas as espécies de interesse comercial, mas também aquelas que sofrem as consequências da pesca excessiva de camarões, mesmo sem apresentar interesse econômico.

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