UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – CÂMPUS DE BOTUCATU
PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
ÁREA DE CONCENTRAÇÃO: ZOOLOGIA

TESE DE DOUTORADO

# COMPOSIÇÃO, BIOLOGIA REPRODUTIVA E DINÂMICA POPULACIONAL DA TAXOCENOSE DE PORTUNOIDEA (CRUSTACEA, DECAPODA): VARIAÇÕES TEMPORAIS AO LONGO DO GRADIENTE LATITUDINAL E FENÔMENO DA RESSURGÊNCIA

**LUCIANA SEGURA DE ANDRADE**

Orientador: Dr. Adilson Fransozo
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Botucatu – SP
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Tese apresentada ao curso de pós-graduação em Ciências Biológicas: Zoologia, do Instituto de Biociências, Universidade Estadual Paulista (UNESP), Campus de Botucatu, como parte dos requisitos para a obtenção do título de Doutor em Ciências Biológicas – Área de Concentração: Zoologia

**Botucatu – SP**
**2014**

FICHA CATALOGRÁFICA ELABORADA PELA SEÇÃO TÉC. AQUIS. TRATAMENTO DA INFORM.
DIVISÃO DE BIBLIOTECA E DOCUMENTAÇÃO - CAMPUS DE BOTUCATU - UNESP
BIBLIOTECÁRIA RESPONSÁVEL: ROSEMEIRE APARECIDA VICENTE - CRB 8/5651

Andrade, Luciana Segura.

Composição, biologia reprodutiva e dinâmica populacional da taxocenose de portunoidea (crustacea, decapoda): variações temporais ao longo do gradiente latitudinal e fenômeno da ressurgência / Luciana Segura Andrade. - Botucatu, 2014

Tese (doutorado) - Universidade Estadual Paulista, Instituto de Biociências de Botucatu

Orientador: Adilson Fransozo

Coorientador: Fúlvio Aurélio de Morais Freire

Capes: 20406002

1. Caranguejo - Distribuição geográfica. 2. Decapode (Crustáceo). 3. Dinâmica Populacional. 4. Massas de água.

Palavras-chave: Biologia populacional; Dinâmica das massas d'água; Dinâmica populacional; Portunoidea.

# Dedicatória

*Aos meus pais José Carlos e Ivanir, pela*
*criação baseada em carinho e dedicação.*

*Aos meus filhos Rayan e Laís, por me*
*ensinarem o verdadeiro significado do amor.*

*Ao meu amado esposo Israel, por me dar o*
*conforto do seu ombro todas as noites.*

# Agradecimentos

À Deus, que me carrega no colo em todos os momentos difíceis e me coloca no chão cheia de forças para alcançar meus objetivos.

Ao meu “prof amado”, Dr. Adilson Fransozo, por todo incentivo desde a época em que eu fazia parte dos Cursos de Biologia apenas como ouvinte. Por ter me recebido de braços abertos quando cheguei a Botucatu. Por ter confiado a mim valiosas planilhas, pois eu cresci em cima de cada uma delas. Por esquecer-se da hora quando discutíamos fervorosamente os nossos resultados. Você, como meu pai científico, transmitiu a mim a paixão pelos crustáceos, pela ecologia, pela pesquisa de campo. Serei eternamente grata!

Ao meu coorientador, Dr. Fúlvio Aurélio de Moraes Freire, pelas discussões durante as disciplinas de multivariada, as quais foram imprescindíveis para o desenvolvimento de trabalhos consistentes. Obrigado por ter me apresentado o Cadu (Carlos Eduardo Alencar), que também se mostrou ser um grande amigo e excelente crítico.

À Professora Lúcia (Maria Lúcia Negreiros-Fransozo na comunidade científica), por todo apreço comigo e com meus filhos. Por ter acreditado em mim e no meu trabalho. Por receber-nos em sua casa com todo carinho do mundo. Pelas colheres de pau cheias de brigadeiro, deliciosas, que adoçam qualquer amargura das dificuldades!

Aos professores Dr. Antonio Leão Castilho e Dr. Rogério Caetano da Costa. Sem vocês o desenvolvimento da tese que eu havia objetivado não seria possível. Obrigado por confiar em mim valiosos dados. Obrigada por todas as sugestões, críticas e conselhos. O meu crescimento profissional também se deve a vocês.

À Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP (2009/54672-4; 2010/50188-8; 2011/50411-1), por todo suporte financeiro que garantiu o desenvolvimento dessa pesquisa e pela bolsa de estudos concedida. À Pró-Reitoria em Pesquisa (Primeiros Projetos, UNESP) FUNDUNESP (no. 1214/2010-DFP) pelo apoio financeiro nas coletas de São Fransico do Sul.

Às meninas do ponto de apoio Fapesp: Marluci, Niva e Rosângela. Vocês são um exemplo de profissionalismo e competência, obrigada por todas as dicas e apoio.

Ao IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais e Renováveis)/SISBIO, por conceder a licença para a coleta do material nas áreas estudadas.

Ao NEBECC - Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos, por toda infraestrutura de laboratórios e materiais utilizados. Aos companheiros “Nebeccianos” e funcionários envolvidos, que de alguma forma contribuiram para a execução do projeto. Aos amigos que estão ou passaram pelo NEBECC desde a minha chegada. A todos aqueles que participaram das coletas (pessoal de Bauru e pessoal do Tony), e em especial ao Gustavo Sancinetti, que sempre tirava minhas dúvidas à respeito de Macaé, Raphael Grabowski e Milena Wolf, que me ajudaram na identificação dos juvenis provenientes de São Francisco do Sul.

Ao curso de pós-graduação em Ciências Biológicas (Zoologia) e ao Departamento de Zoologia, incluindo seus competentes e atenciosos funcionários: André Arruda, Carolina Lopes, Davi Müller, Flávio da Silva, Hamilton Rodrigues, Herivaldo Santos, Juliana Ramos, Luciana Campos e Silvio Almeida.

Aos meus co-autores que não fizeram parte dessa tese, mas contribuíram para meu crescimento profissional na área de crustáceos por meio de críticas que jamais serão esquecidas e sugestões que serão sempre acatadas: Prof$^{a}$ Dr$^{a}$ Giovana Bertini, Prof. Dr. Gustavo Teixeira, Prof$^{a}$ Dr$^{a}$ Laura Lópes-Greco, Prof$^{a}$ Dr$^{a}$ Maria Lúcia Negreiros-Fransozo, Prof$^{a}$ Dr$^{a}$ Vívian Fransozo, e Prof. Dr. Valter Cobo. Vocês foram verdadeiros professores.

À professora Janet Reid, que além de fazer as emendas na tradução sempre deu valiosas sugestões na escrita dos trabalhos.

Ao meu queridíssimo amigo Passarinho (Djalma Rosa), que me levou para uma coleta noturna inesquecível, me deixou no comando do barco e fez questão de gravar tudo! Foi com você que eu aprendi muito dos meus animais. O conhecimento (científico e pessoal) que ganhei com você é ímpar. Obrigada por me levar para dentro de sua casa e dar a oportunidade de conhecer sua família, que tanto adoro.

À minha amiga Paloma Lima, que ao longo do tempo se tornou minha irmã e confidente. Mesmo você vindo em churrasco para não comer carne, eu te adoro! Obrigada pelo carinho com meus filhos e apoio nas horas mais difíceis.

À minha sogra Lena e vó Mafalda, pela educação do homem que me ajuda a lidar com dificuldades e me dá as mãos para conquistarmos juntos nossos objetivos. À minha vó Auri, tios, tias, primos e primas, por fazerem companhia aos meus pais desde quando resolvi me mudar de Maringá.

Ao meu ex-aluno, sempre professor (eu aprendo com ele todos os dias) e eterno amor, Israel Fernandes Frameschi de Lima. Obrigada por me mostrar que fiz a diferença quando lecionei com paixão. Obrigada por todas as longas discussões com relação às análises de dados e biologia dos animais. Obrigada pela paciência, mesmo quando eu te acordava muito cedo e questionava sobre bioestatística. Obrigada pelo cuidado e carinho com meus filhos, principalmente nos momentos em que eu me concentrava em escrever e esquecia de fazer café da manhã, almoço, janta... Obrigada por cuidar de mim, das crianças e da nossa casa!

Aos meus filhos amados, Laís e Rayan. Vocês são tudo prá mim! Obrigada por me receber morrendo de saudades e com bilhetes espalhados pela casa todas as vezes que tive de estar fora. Obrigada por entender toda a falta de paciência da mamãe quando o trabalho era intenso. Obrigada por fazer cafuné em mim todas as vezes que ao ficar com vocês, eu acabava dormindo... Vocês foram e sempre serão o meu combustível!

Aos meus pais Ivanir e José Carlos, por suportarem novamente a dor em ficar longe de mim e das crianças para me incentivar nos meus objetivos. Obrigada pelas viagens que acalentavam a saudade e me dava ânimo em continuar. Obrigada pelos longos telefonemas, pela eterna paciência e por sempre trazer o resultado das pescarias. Mãe, obrigada por cozinhar prá mim todas as vezes que você vem me ver, adoro ter a sensação de estar morando com você novamente; obrigada por ler e conferir referências dos meus trabalhos, você é o meu “dedinho especial”. Pai, obrigada por me ensinar a ter fé, a ver a “fresca passar”, a “morder a língua”, e a “chorar no banheiro”. Tais atitudes são indispensáveis para o meu crescimento pessoal. Amo vocês.

# Sumário

Effect of geographical variation in the Brazilian tropical/subtropical domain on the fitness of populations of the swimming crab *Callinectes ornatus*

Reproductive strategy of two coexisting swimming crabs (Decapoda: Brachyura) associated with hydrogeographic variation

Does the swimming crab Achelous spinimanus (Crustacea: Decapoda) show a modified life strategy in an upwelling region off the Brazilian coast?

# Considerações iniciais

A composição e estrutura de uma taxocenose, bem como os parâmetros populacionais das espécies tendem a variar conforme a sua localização latitudinal. Tal paradigma é usualmente utilizado para gerar hipóteses sobre estímulos ambientais específicos e pressões seletivas que podem agir sobre a dinâmica das comunidades e populações, avaliando se as flutuações em determinados parâmetros seriam respostas às alterações ambientais locais ou a gradientes latitudinais (Whiteley et al 1997; Brante et al 2004). Todavia, as características ambientais das regiões podem ser tão diferentes que, mesmo estando próximas latitudinalmente, os organismos podem responder de maneira discrepante (Connolly et al 2001). Nestes casos, as particularidades do ambiente sobrepõem o efeito da latitude.

Variações na história de vida das populações podem ser explicadas como uma resposta ao ambiente para garantir o sucesso reprodutivo sob condições ambientais favoráveis (Sastry 1983). Animais marinhos podem ter sua sobrevivência e distribuição limitadas quando sujeitos às variações dos parâmetros ambientais (Moore 1958). Esta afirmativa é válida também para decápodos, que seguem um determinado padrão de ocorrência, principalmente em relação à salinidade, temperatura, teor de matéria orgânica do sedimento onde vivem, massas d' água, disponibilidade de alimento e abrigo (Fransozo et al 1992; Costa et al 2000; Bertini e Fransozo 2004; Fransozo et al 2008; Furlan et al 2013; Andrade et al 2013 *herein*). Neste contexto, os limites de distribuição dos organismos marinhos são determinados pela ação do complexo ambiental, sobre todos os estágios do ciclo de vida das espécies.

A infraordem Brachyura (Crustacea: Decapoda), representada por siris e caranguejos, é um dos grupos mais relevantes da comunidade bêntica marinha, tanto por fatores evolutivos (Ng et al 2008) quanto por ter apresentar notável biomassa em relação aos demais grupos (Bertini e Fransozo 2004). Tal biomassa pode ser justificada pela conquista de habitats extremamente diversificados, sendo encontrados em ambientes terrestres, dulcícolas, estuarinos e marinhos (Bowman e Abele 1982; Melo 1996, 2003; Ng et al 2008).

Em especial no ambiente marinho, esses invertebrados bênticos são importantes agentes estruturadores, pela participação efetiva na cadeia trófica demersal (Pires 1992). É nesta função que se constituem em substancial fonte de energia para espécies ecológicas e economicamente relevantes e que atuam dentro e/ou fora do meio bêntico, tais como Portunoidea.

A ordem Portunoidea é representada por siris de hábitos distintos. Em levantamentos realizados por diversos autores (Lavrado et al 2000; Bertini e Fransozo 2004; De Léo e Pires-Vanin 2006; Bertini et al 2010; Di Beneditto et al 2010) é possível observar que os representantes desta taxocenose[1] estão distribuídos de forma bem diferenciada ao longo do litoral brasileiro. Buchanan e Stoner (1988) afirmam que os padrões distribucionais são resultado da interação das preferências de habitat e interações intra e interespecíficas entre os siris; sendo que a variação dos fatores ambientais ou biológicos pode limitar a ocorrência de espécies particulares, onde as baixas tolerâncias para cada condição, ou o conjunto delas, faz com que as espécies apareçam mais localizadas ou endêmicas. Além dos padrões de composição e abundância, a variação temporal na produtividade planctônica também é um fator essencial na sazonalidade reprodutiva de organismos marinhos, sendo os períodos de reprodução e desova vinculados àqueles com maior disponibilidade de alimento (Thorson 1950). Em regiões onde existe flutuação da temperatura, fotoperíodo e/ou da disponibilidade de alimento a reprodução pode variar entre as estações, de forma que o aumento da abundância larval na coluna de água tende a coincidir com o aumento da temperatura e da produtividade primária (Sastry 1983; Hereu e Calazans 2001).

Tais condições estão diretamente associadas às três áreas da costa brasileira escolhidas neste estudo: (1) à zona de ressurgência (Macaé, Rio de Janeiro), uma vez que esta promove o transporte de nutrientes (N e P) aprisionados nas camadas inferiores pela

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[1] *Taxocenose* refere-se ao grupo de espécies com mesma identidade taxonômica que pode ou não possuir similaridade em suas distribuições geográficas ou papéis ecológicos. Tal definição difere do termo *Assembleia*, o qual se restringe a um grupo de espécies filogeneticamente relacionadas que possuem similaridade em sua distribuição (Lincoln e Clark 1987; Krebs 2001).

Água Central do Atlântico Sul (ACAS) para as zonas eufóticas, influenciando diretamente a produtividade primária (Odebrecht e Castello 2001; Lopes et al 2006); (2) à região de transição faunística (Ubatuba, São Paulo), onde além de haver um regime oceanográfico de transição entre águas costeiras e de plataforma continental, a drenagem tem um padrão bastante incipiente, e os processos de troca de água e material sedimentar entre a região costeira e a plataforma adjacente são relativamente pequenos (Mahiques 1995); e (3) à região de grande aporte terrestre (São Francisco do Sul, Santa Catarina), onde atividades de dragagem nos canais de navegação interferem no transporte de sedimentos ao longo da costa, não permitindo a decantação das partículas finas em suspensão (Laybauer e Bidone 2001).

Desta maneira, levantamos a hipótese de que a composição de Portunoidea, bem como a estrutura e dinâmica populacional (levando em consideração o recrutamento e reprodução) das espécies representantes desse táxon, possam se diferenciar entre regiões que diferem quanto aos aspectos biológicos e hidro-geográficos. O resultado dessa investigação foi dividido em cinco capítulos. O primeiro, “The assemblage composition and structure of swimming crabs (Portunoidea) along a gradient with geographical variations”, foi encaminhado para apreciação da revista Continental Shelf Research, e avaliou a composição e estrutura da assembléia de Portunoidea em três locais ao longo da costa brasileira caracterizados pela ocorrência de fenômenos naturais contrastantes. O segundo capítulo “Can the pattern of juvenile recruitment and population structure of the speckled swimming crab *Arenaeus cribrarius* (Decapoda: Brachyura) be determined by geographical variations?” foi aceito para publicação na revista Marine Ecology – an Evolutionary Perspective, e trata sobre a estrutura de recrutamento juvenil de *A. cribrarius*. O terceiro capítulo, intitulado “Effect of geographical variation in the Brazilian tropical/subtropical domain on the fitness of populations of the swimming crab *Callinectes ornatus*”, está sendo revisado pela Estuarine and Coastal Shelf Science e abordou como as características de estrutura e recrutamento da espécie se ajustam a estímulos específicos e pressões seletivas que variam ao longo do tempo e do espaço. O capítulo quatro “Reproductive strategy of two coexisting swimming crabs (Decapoda: Brachyura) associated with hydrogeographic variation” inquiriu se portunídeos que coexistem seguem um padrão em sua estratégia reprodutiva, levando em consideração a periodicidade reprodutiva e a relação das variáveis ambientais com fêmeas e machos reprodutivos de *A. cribrarius* e *C. ornatus*. Enfim, o último capítulo “Does the swimming crab *Achelous spinimanus* (Crustacea: Decapoda) show a modified life strategy in an upwelling region off the Brazilian coast?” discutiu sobre estratégias de vida da referida espécie em uma região afetada pelo fenômeno da ressurgência, e está sendo avaliado pela revista Population Ecology.

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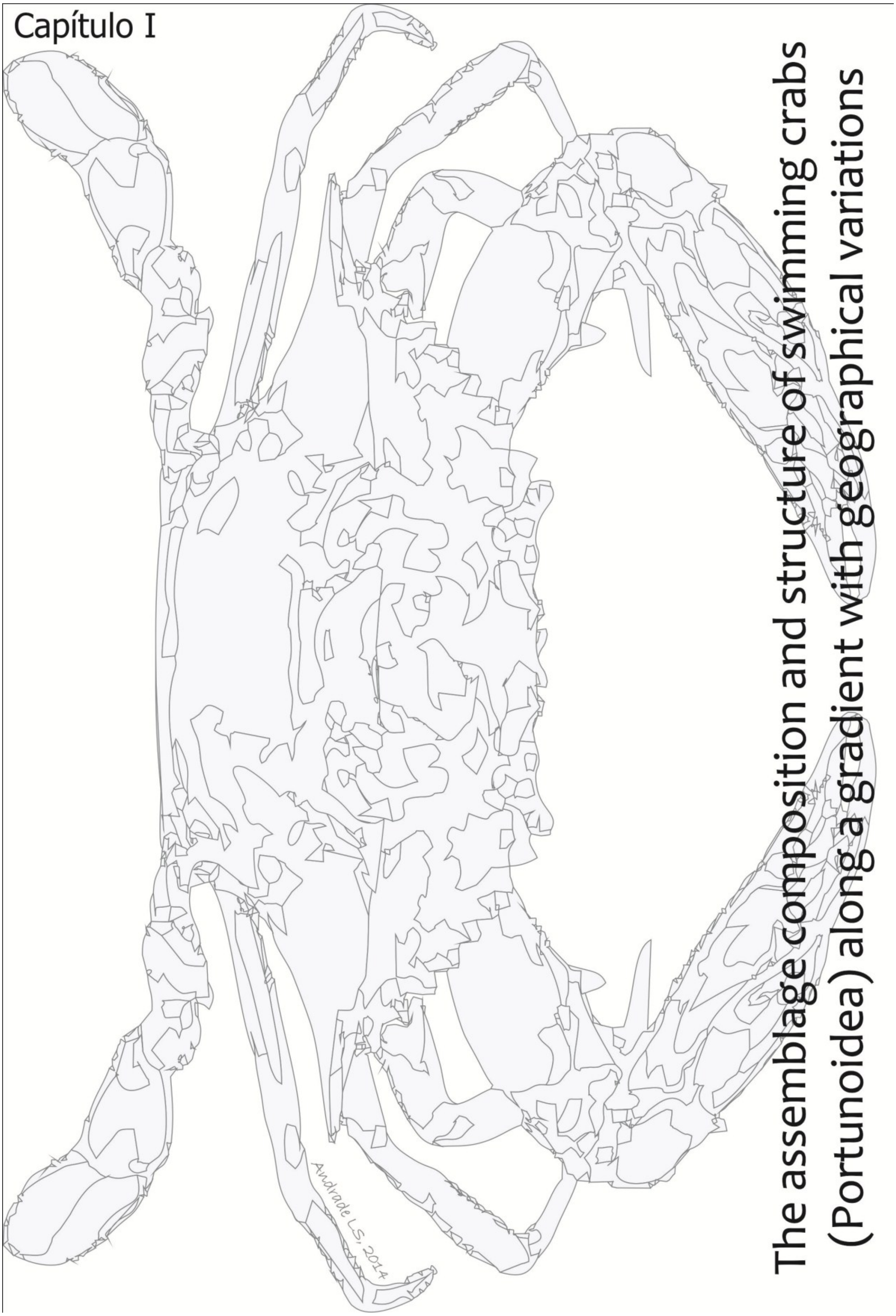
Capítulo I



# The assemblage composition and structure of swimming crabs (Portunoidea) along a gradient with geographical variations

## Abstract

Three regions along the Brazilian coast characterized by the occurrence of contrasting natural phenomena, such as upwellings and continental input, were surveyed to determine the composition and structure of the assemblage of swimming crabs. Twelve monthly collections were performed (July 2010 to June 2011) in Macaé, Rio de Janeiro (MAC) (22º47'S, 41º45'W); Ubatuba, São Paulo (UBA) (23º 27'S, 44°58'W); and São Francisco do Sul, Santa Catarina (SFS) (26º08'S, 48º34'W). The lowest values of the phi sediment grain size measure and bottom temperature and the highest values of organic matter and salinity were measured in MAC. In all, 10,686 individuals were collected, belonging to six species of Portunoidea: *Arenaeus cribrarius*, *Callinectes danae*, *Callinectes ornatus*, *Callinectes sapidus*, *Achelous spinicarpus* and *Achelous spinimanus*. A Multiple Response Permutation Procedure (MRPP) test indicated that the species composition differed significantly among the sampling sites, showing substantial heterogeneity in the composition and abundance of species among regions. Differences among the ecological indexes of this assemblage associated with the regions were also detected. A redundancy analysis showed that environmental factors explained 38.3% of the total variance in the abundance of swimming crabs. We conclude from these findings that areas affected by different phenomena produce changes in the composition and abundance of the assemblage of Portunoidea. Although the strength of eutrophication differs between UBA and MAC, the substantial continental inflow affecting SFS favors the development of species that complete their life cycle in the estuary.

**Keywords** Biological structure · Continental waters · Decapoda · Dynamics of water masses

## 1. Introduction

The responses of species to environmental gradients allow us to explain the relative importance of abiotic and biological factors in structuring assemblages (Stevenson and Lauth 2012). The coexistence of different species can be explained by alternations in the peaks of temporal abundance and spatial differences in the uses of the habitat, the influence of environmental factors and the requirements imposed by the habits of each species (Bauer and Rivera Vega 1992). According to Abele (1974), the diversity of decapod crustaceans responds to historical and regional factors that uniquely influence speciation and dispersal as well as to contemporary events and continuous predation, competition, adaptation and local environmental events. Thus, the presence and survival of an organism or group of organisms in a given area depends on various complex conditions, and any condition that is close to or exceeds the tolerance limits can be considered a limiting factor (Vernberg and Vernberg 1970).

The relationship between dominance and diversity, resulting from spatial heterogeneity and environmental perturbations, can be investigated by quantifying the interactions between species (Magurran 1988). Additionally, surveys conducted in various regions worldwide, such as North and South America, the southeastern coast of Africa, South Asia (Sanders 1968) and southwestern Europe (Abelló et al. 1988; Farigña et al. 1997; Cartes et al. 2007) have shown that the effects of environmental factors such as temperature, salinity, the texture and organic matter content of the sediment and the latitude and occurrence of water masses are important in controlling the distribution of marine organisms. One of the principal sources of environmental variability and biological heterogeneity on the continental shelf is the proximity of the shelf to the mainland. Mainland sources are responsible for substantial inputs of freshwater, nutrients and sediments, which alter the chemical composition of the water (Braga et al. 2006). Mahiques (1995) has noted that the sediment dynamics of bays shows variations over seasons and years, expressed by a significant contribution of continental sediments to the coastal region during the period of greatest rainfall. Another important factor in shelf environments is depth, which can allow light to reach virtually the entire water column. Due to the relatively shallow depth (75-120 m), the shelf is strongly influenced by winds, waves and currents (Castro et al. 2006). The water movements generated by winds and currents resuspend organic material and nutrients deposited on the bottom, making them available for recycling. In this way, light intensity and nutrients can sustain a high level of productivity on the continental shelf (Braga et al. 2006).

Seasonal variations in primary productivity have been reported by several authors (see Fariña et al. 1997; Cartes et al. 2007). In regions affected by upwelling phenomenon, such enrichment effects are pronounced (Fariña et al. 1997). The Brazilian shelf can be classified as shallow and not highly productive, although enriched waters occur in areas affected by upwelling. This phenomenon is typically observed during the summer in the region of Cabo Frio, RJ (De Léo and Pires-Vanin 2006). Enrichment also occurs in sites near estuaries due to the export of dissolved or particulate organic material (Lana et al. 1996). Both upwelling events and continental input are of great significance for the benthic and planktonic community, as the availability of food for the benthos is controlled by several physical and biological factors (Lana et al. 1996; De Leo and Pires-Vanin 2006; Braga et al. 2006). Thus, it becomes evident that studies on the fauna of these regions are important for understanding the biological processes that occur there. Moreover, a temporal evaluation may identify relationships between seasonal productivity and the composition and structure of the Portunoidea assemblage. Benthic invertebrates are important due to the influence of these species as structuring agents or their effective participation in the demersal trophic chain. These important roles, associated with the functioning of a cyclic stability-adjustment mechanism, can help to explain the dynamics of the megabenthos (Pires 1992). For this reason, a substantial energy source is available to supply ecologically and economically important species. This energy input affects species both within and outside the benthic environment.

Portunid crabs occur in the benthic environment and are affected by this energy source, both in terms of the energy available to portunids and the role of portunids as a source of energy for other species. The superfamily Portunoidea includes crabs with a variety of habits. Surveys by various authors (see Lavrado et al. 2000; Bertini and Fransozo 2004; Bertini et al. 2004; De Leo and Pires-Vanin 2006; Bertini et al. 2010; Di Beneditto et al. 2010) have shown that the representatives of this assemblage are distributed in a well-differentiated manner along the Brazilian coast. Buchanan and Stoner (1988) have claimed that the distributional patterns of crabs are a result of the interaction of habitat preferences with intra/interspecific interactions occurring among the crabs. Variations in biological or environmental factors may limit the occurrence of particular species (see Cartes et al. 2007). In such cases, a low tolerance for each condition or set of conditions makes the species appear more localized or endemic.

Abelló et al. (1988) have shown that the principal assemblages are related to several hydrological characteristics that vary seasonally. According to Sanders (1968), one of the fundamental characteristics of a community is its diversity, namely, the number of species and the numerical composition represented by these species. In this context, Sanders (1968) cites the higher diversity of communities of tropical regions relative to that of communities of higher-latitude regions. This latitudinal effect paradigm is usually used to generate hypotheses about specific environmental stimuli and selective pressures that can act on the composition, abundance and adaptations of crustaceans at different latitudes (Whiteley et al. 1997). However, exceptions to this paradigm can be found in regions affected by certain natural phenomena such as upwellings and substantial continental input. Accordingly, the aim of this study was to evaluate the composition and structure of the assemblage of Portunoidea at three locations along the Brazilian coast characterized by the occurrence of contrasting natural phenomena.

## 2. Materials and Methods

### 2.1 Study areas

The samples were collected according to a defined schedule from July 2010 to June 2011. Monthly, an area of 108,000 $m^2$ was sampled, covering depths ranging from 5-20 m at three Brazilian coastal localities: Macaé, Rio de Janeiro state (22º47'S and 41º45'W);

Ubatuba, São Paulo state (23º 27'S and 44°58'W); and São Francisco do Sul, Santa Catarina state (26º08'S and 48º34'W) (Fig. 1). A hydrological phenomenon known as coastal upwelling occurs in the Macaé (MAC) region. This phenomenon is caused by atmospheric circulation associated with the center of high pressure in the South Atlantic. Three principal water masses are present in the area. North of MAC, Tropical Water (TW), which is warm (T > 20°C) and saline (S > 36), covers the entire shelf, forming the main stream of the Brazilian Current (BC). To the south, a mixture of TW and South Atlantic Central Water (SACW), a relatively cold (< 20°C) and less saline (< 36) water mass, is predominant. The third water mass is Coastal Water (CW), which results from the mixture of continental runoff and Shelf Water (SW) (Castro-Filho and Miranda 1998).

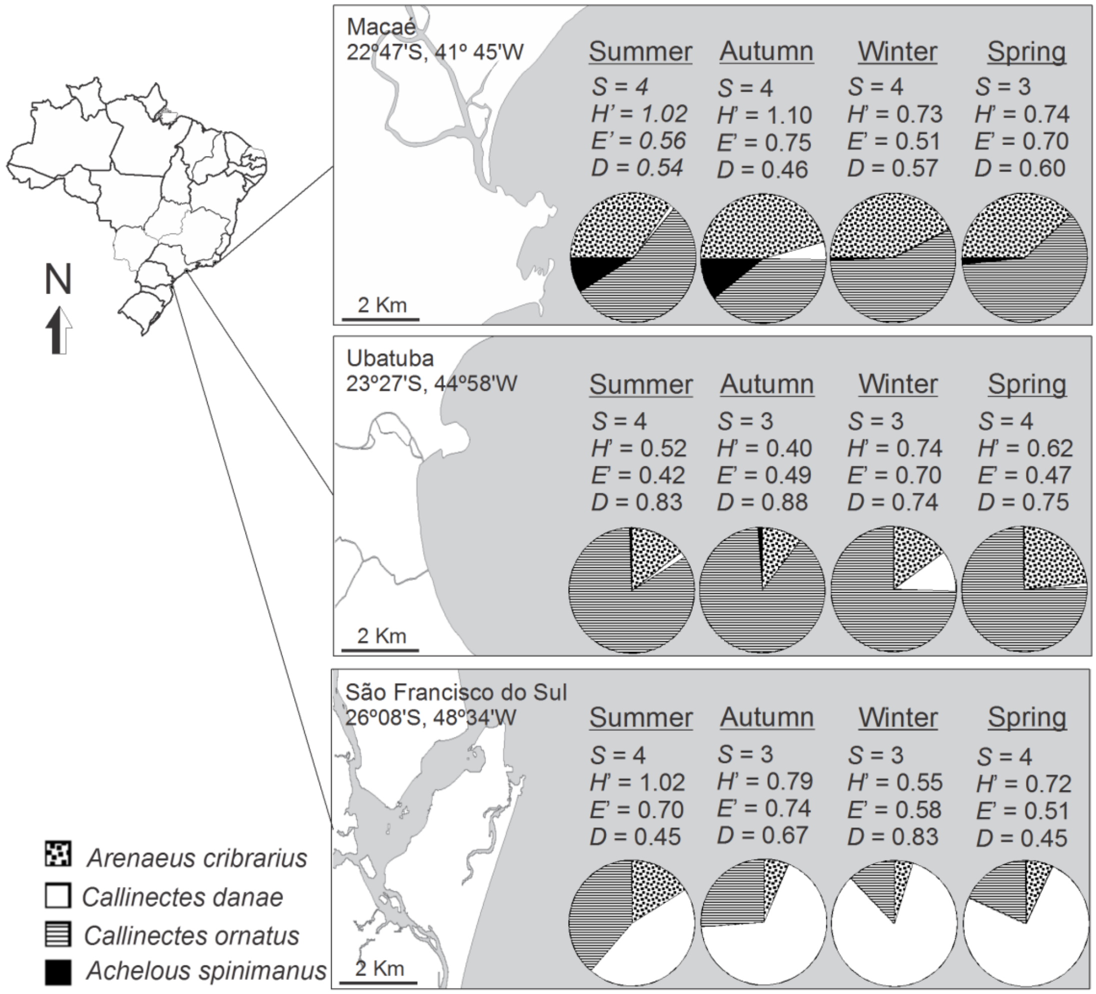


**Fig. 1** Location of the study areas and composition of the assemblage of Portunoidea in three regions of the South-Southeast coast of Brazil. S richness, H' diversity, E' evenness, D dominance

The region of Ubatuba (UBA), along the northern coast of São Paulo state, is characterized by the Serra do Mar, a mountain range that extends into the marine environment to form a highly jagged coastline with several semi-confined coves. The dynamics of the water masses in Ubatuba differs from that found in the MAC region because the SACW thermal front, observed during the summer months, remains at subsurface depths, so that upwelling events are rarely observed (Castro-Filho and Miranda 1998). The drainage pattern in this area is relatively undifferentiated, and the exchange of water and sedimentary material between the coastal region and the adjacent slope is relatively minor (Mahiques 1995). The UBA oceanographic regime represents a transition between coastal waters and the continental shelf. The distribution of the water mass in the region shows distinct patterns (Castro-Filho et al. 1987) because the dynamics of the water mass depends primarily on wind, currents and submarine relief.

The region of São Francisco do Sul (SFS) has a relatively straight coastline and is the location of the largest estuarine complex in Santa Catarina state, with an area of 1,567 km$^2$ (Angulo et al. 2006) (Fig. 1). Note that the region has been extensively modified by human activity due to repeated episodes of dredging, especially in connection with the development of the estuary and the harbor area. The dredging of navigation channels to accommodate vessels of greater load displacement has interfered with sediment transport along the coast and may be responsible for severe erosion problems in the coastal zone (Angulo et al. 2006). The sites most exposed to water movement do not allow fine particles to settle. For this reason, only coarser-grained particles are deposited in areas with intense hydrodynamic activity (Laybauer and Bidone 2001).

## 2.2 Data collection

Nonconsecutive 3-hr monthly hauls were performed for each region studied during each month. This approach ensured that the analysis would not be influenced by local variation. All field work was conducted with a commercial fishing vessel (10 m long) with an otter trawl. The opening between the trawl doors was 4.5 m, and the net mesh size and cod end mesh size were 20 and 18 mm, respectively. After the end of each trawl operation, the nets were collected, and the material was screened on the boat and packed in plastic bags. The bags were labeled and stored in a freezer prior to analysis. The crabs were identified in the laboratory according to Melo (1996).

### 2.3 Environmental variables

For each site, the bottom and surface water temperature and salinity were recorded using a thermometer attached to a Van Dorn bottle and an optical refractometer, respectively. An ecobathymeter coupled with a GPS was used to record the depth at the sampling sites. Sediment samples were collected during each season using a Van Veen grab. A bottom area of 0.06 $m^2$ was sampled to determine the organic matter content (%) and sediment grain size. In the laboratory, the sediment was dried at 70°C for 72 hr in an oven. The sediment organic matter content (%) was obtained by ash weighing. Three 10-g aliquots per station were placed in porcelain crucibles and incinerated for 3 hr at 500°C. The samples were then weighed to determine the organic matter content. In general, these procedures followed those of Fransozo et al. (2012). The sediment grain size composition was also analyzed according to Fransozo et al. (2012), and the sediment remaining after analysis of the organic matter was redried and passed through a series of sieves with graduated mesh sizes following the Wentworth (1922) scale.

### 2.4 Data analyses

The bottom temperature (BT), surface temperature (ST), bottom salinity (BS), surface salinity (SS), organic matter (OM) and a central measure of sediment grain size (phi) were plotted on a matrix of six environmental factors for 36 hauls (12 months in three regions). A one-way permutational analysis of variance (PerMANOVA) was used to assess the significance of environmental variation at different spatial scales (Anderson 2001, 2005). A one-way ANOVA was used to assess the significance of the environmental variation among seasons for each region (Zar 1996).

To determine the ordering of the species among the regions relative to the seasons, a dissimilarity matrix based on species abundance by location and season was analyzed using a Correspondence Analysis (CA). The original matrix of six species in 36 hauls was reduced by eliminating the species with a frequency of occurrence of less than 1% in a given season. A CA was used to simultaneously order sampling units and species based on the patterns of redundant co-occurrence in the species data (McCune and Grace 2002). The CA process begins by randomly assigning scores to sampling units. These scores are used as the weights in a weighted average to calculate species scores. New sampling unit scores are then calculated using these species scores as weights. Both sets of scores are thus refined through many back-and-forth (i.e., reciprocal) iterations, using a measure equivalent to a chi-squared distance measure. The sampling unit scores reflect the major patterns in the species data, whereas the species scores approximate the locations of the maximal abundances (optima). The eigenvalues are calculated to measure the amount of variation in the responses along the ordination axis. These values reflect the degree of correspondence shown between the responses and the sampling unit scores. The sum of the eigenvalues for all axes is termed the “total inertia”. From this sum, the percentages of the total variance represented by each axis (% of variance explained) are calculated as the ratio of the eigenvalue for each axis to the total inertia (Hill 1973; Peck 2010).

The abundance data (Sorensen distance) were tested for variation in the species composition of each site using a Multiple Response Permutation Procedure (MRPP). The differentiation of assemblages in this statistical analysis is represented by the variable A, which expresses the similarity of the samples of each region corrected by the similarity observed in randomly distributed samples. The value of A varies from zero to 1, where zero represents no difference between the heterogeneity observed in the group and that expected by chance, and 1 represents equivalence between all elements of the group (McCune and Grace 2002). A Mantel test with 9999 iterations was used to verify correlations between the matrices (local-season *vs.* species). Subsequently, a nonparametric permutational analysis of variance (two-way PerMANOVA) was used to assess the significance of changes in the structure of the associations among different spatial scales and seasons (Anderson 2001, 2005). A cluster analysis (cluster distance measure: Bray-Curtis, linkage method: Group Average) of the same data matrix used in the CA was performed to verify the grouping of locations according to species abundance.

The total abundance, richness of species (*S*), Shannon diversity (*H'*) (Shannon 1948), evenness (*E'*) (Pielou 1975) and Berger-Parker dominance index (*D*) (Magurran 1988) were estimated to furnish ecological indexes describing the monthly samples from each region. These indicators were contrasted using a two-way orthogonal PerMANOVA (Anderson 2001) to test the null hypothesis of no differences in ecological indexes associated with the factors “site” and “season”. A pairwise *t* statistic was used as an a posteriori method for detecting groups. A redundancy analysis (RDA) was used to order regions based on linear relationships (Pearson correlation) between the patterns of redundant co-occurrence of the portunids (4 species) and environmental factors: organic matter, phi, water temperature (surface and bottom) and salinity (surface and bottom). Thus, the RDA produced final ordination scores that summarized the linear relationships between the environmental factors and each species’ response (Peck 2010). Randomization tests (Monte Carlo test, 999 permutations), which provided p-values, were performed to check the linear relationship between the response and explanatory matrices and the association between the first and second set of sample unit ordination scores in RDA analyses (ter Braak 1986). The p-values from these randomization tests indicate the confidence level associated with the predictions (Peck 2010). All multivariate analyses and group comparisons were performed using PC-ORD 6.0 software. The ecological indexes were estimated using PAST 2.09 software.

## 3. Results

**Table 1** PerMANOVA for environmental factors at three Brazilian coastal sites. *df* degrees of freedom, *Sum S* sum of squares, *MS* mean square. *MAC* Macaé, *UBA* Ubatuba, *SFS* São Francisco do Sul

PAIRWISE COMPARISONS for environmental factors

| Bottom temperature - BT | *t* | *P* |
|---|---|---|
| MAC *vs.* UBA | 3.39 | 0.0027 |
| MAC *vs.* SFS | 1.47 | 0.1425 |
| UBA *vs.* SFS | 1.29 | 0.2122 |
| Surface temperature - ST | | |
| MAC *vs.* UBA | 2.56 | 0.0199 |
| MAC *vs.* SFS | 0.47 | 0.6410 |
| UBA *vs.* SFS | 2.35 | 0.0277 |
| Bottom salinity - BS | | |
| MAC *vs.* UBA | 6.33 | 0.0001 |
| MAC *vs.* SFS | 7.63 | 0.0001 |
| UBA *vs.* SFS | 0.03 | 0.9897 |
| Surface salinity - SS | | |
| MAC *vs.* UBA | 7.15 | 0.0001 |
| MAC *vs.* SFS | 7.70 | 0.0001 |
| UBA *vs.* SFS | 0.06 | 0.9488 |
| Organic matter - OM | | |
| MAC *vs.* UBA | 4.34 | 0.0001 |
| MAC *vs.* SFS | 3.96 | 0.0005 |
| UBA *vs.* SFS | 0.24 | 0.9385 |
| Phi | | |
| MAC *vs.* UBA | 5.62 | 0.0001 |
| MAC *vs.* SFS | 1.35 | 0.1847 |
| UBA *vs.* SFS | 4.93 | 0.0001 |

*Mean and standard deviation of environmental variables*

| | | OM (%) | Phi | ST ($^oC$) | BT ($^oC$) | SS | BS |
|---|---|---|---|---|---|---|---|
| MAC | Sum | 8.8 ± 1.9 | 4.3 ± 0.6 | 23.7 ± 1.6 | 20.2 ± 0.9 | 36.9 ± 0.9 | 36.8 ± 0.5 |
| | Aut | 10.3 ± 2.8 | 4.7 ± 0.1 | 23.0 ± 0.8 | 22.0 ± 0.4 | 36.2 ± 1.0 | 37.4 ± 0.6 |
| | Win | 4.4 ± 1.9 | 3.4 ± 0.9 | 20.7 ± 0.5 | 20.0 ± 0.5 | 36.4 ± 0.6 | 37.0 ± 0.3 |
| | Spr | 11.8 ± 1.0 | 4.6 ± 0.6 | 23.3 ± 1.3 | 21.2 ± 1.5 | 36.5 ± 1.3 | 36.3 ± 0.8 |
| UBA | Sum | 3.6 ± 3.3 | 2.2 ± 1.2 | 27.8 ± 2.6 | 24.3 ± 3.9 | 31.3 ± 1.0 | 33.3 ± 1.8 |
| | Aut | 2.0 ± 2.5 | 2.4 ± 1.3 | 24.7 ± 2.4 | 24.2 ± 2.1 | 33.6 ± 1.1 | 33.6 ± 1.6 |
| | Win | 2.4 ± 1.1 | 2.0 ± 1.1 | 22.6 ± 1.1 | 21.9 ± 1.1 | 34.5 ± 0.4 | 34.7 ± 0.8 |
| | Spr | 4.4 ± 4.7 | 3.0 ± 1.4 | 25.7 ± 1.1 | 24.5 ± 2.0 | 31.6 ± 0.9 | 32.4 ± 1.5 |
| SFS | Sum | 1.9 ± 1.2 | 3.3 ± 1.0 | 25.9 ± 1.0 | 25.7 ± 0.8 | 31.4 ± 1.2 | 32.6 ± 1.3 |
| | Aut | 2.3 ± 1.1 | 4.0 ± 0.7 | 22.2 ± 1.0 | 22.4 ± 1.0 | 34.6 ± 0.9 | 35.2 ± 0.6 |
| | Win | 3.0 ± 4.0 | 4.1 ± 0.5 | 19.1 ± 0.5 | 19.0 ± 0.8 | 33.1 ± 1.4 | 33.8 ± 1.3 |
| | Spr | 6.4 ± 4.7 | 4.3 ± 0.6 | 22.8 ± 1.8 | 22.0 ± 1.8 | 32.1 ± 0.4 | 32.5 ± 0.6 |

The BT, ST, BS, SS, OM and phi values differed among the studied regions (Table 1). The lowest BT values were found in MAC and SFS (mean ± standard deviation, 20.76 ± 1.21°C, 22.13 ± 2.74°C, respectively), whereas the highest ST values were observed in

UBA (25.03 ± 2.82°C). High salinities were observed in MAC throughout the study period (BS = 36.88 ± 0.56, SS = 36.72 ± 0.75). These values differed significantly from those found for the other regions. The content of organic matter was higher in MAC (8.83 ± 2.89), accompanied by smaller grain sizes in this region (4.25 ± 0.56). Only UBA showed no seasonal variation in the values of the environmental factors (BT: $F_{(3,8)} = 0.63$, $P = 0.5867$; ST: $F_{(3,8)} = 3.41$, $P = 0.0846$; BS: $F_{(3,8)} = 1.08$, $P = 0.4206$; OM: $F_{(3,8)} = 0.48$, $P = 0.7541$; phi: $F_{(3,8)} = 1.17$, $P = 0.378$) except for SS ($F_{(3,8)} = 10.3$, $P < 0.00$). In MAC, neither BT ($F_{(3,8)} = 2.47$, $P = 0.1376$) nor BS and SS ($F_{(3,8)} = 2.85$, $P = 0.0555$; $F_{(3,8)} = 0.16$, $P = 0.936$, respectively) differed among the seasons, whereas ST ($F_{(3,8)} = 5.18$, $P = 0.0378$), OM ($F_{(3,8)} = 114.21$, $P < 0.00$) and phi ($F_{(3,8)} = 70.31$, $P < 0.00$) varied throughout the year. Almost all the environmental factors evaluated varied throughout the year in SFS (BT: $F_{(3,8)} = 11.27$, $P < 0.00$; ST: $F_{(3,8)} = 10.47$, $P < 0.00$; BS: $F_{(3,8)} = 5.28$, $P = 0.0311$; SS: $F_{(3,8)} = 5.80$, $P = 0.032$; phi: $F_{(3,8)} = 7.38$, $P = 0.0117$) with the exception of OM ($F_{(3,8)} = 2.77$, $P = 0.0817$).

**Table 2** Abundance of Portunoidea assemblage at three Brazilian coastal sites. *MAC* Macaé, *UBA* Ubatuba, *SFS* São Francisco do Sul. *Sum* Summer, *Aut* Autumn, *Win* winter, *Spr* spring. A cri *A. cribrarius*, C dan *C. danae*, C orn *C. ornatus*, C sap *C. sapidus*, A. sca *A. spinicarpus*, *A spi A. spinimanus*

| Season | | *A cri* | *C dan* | *C orn* | *C sap* | *A sca* | *A spi* | Total |
|---|---|---|---|---|---|---|---|---|
| MAC | Sum | 247 | 8 | 386 | - | 10 | 63 | 714 |
| | Aut | 429 | 42 | 367 | - | - | 99 | 937 |
| | Win | 255 | 2 | 340 | - | - | 3 | 600 |
| | Spr | 141 | - | 221 | - | - | 6 | 368 |
| | Total | 1072 | 52 | 1314 | - | 10 | 171 | 2619 |
| UBA | Sum | 80 | 9 | 463 | - | - | 3 | 555 |
| | Aut | 63 | - | 535 | - | - | 7 | 605 |
| | Win | 48 | 34 | 239 | - | - | - | 321 |
| | Spr | 92 | 5 | 298 | - | - | 1 | 396 |
| | Total | 283 | 48 | 1535 | - | - | 11 | 1877 |
| SFS | Sum | 348 | 970 | 830 | 1 | - | 1 | 2150 |
| | Aut | 85 | 894 | 348 | 1 | - | - | 1328 |
| | Win | 61 | 1060 | 155 | - | - | - | 1276 |
| | Spr | 99 | 1075 | 260 | - | - | 2 | 1436 |
| | Total | 593 | 3999 | 1593 | 2 | - | 3 | 6190 |

We collected a total of 2619 individuals in MAC, 1877 in UBA and 6190 in SFS. Six species of Portunoidea were found: *Arenaeus cribrarius* (Lamarck, 1818), *Callinectes danae* Smith, 1869, *Callinectes ornatus* Ordway, 1863, *Callinectes sapidus* Rathbun, 1896, *Achelous spinicarpus* (Stimpson, 1871) and *Achelous spinimanus* Latreille, 1819 (Table 2). Two species were excluded from the analysis of the ecological indexes because few individuals were captured (*C. sapidus*, 2 individuals captured during the summer in SFS, and *A. spinicarpus*, 10 individuals captured during the summer in MAC). *Arenaeus cribrarius* and *C. ornatus* were the principal species in MAC, whereas the principal species in UBA and SFS were *C. ornatus* and *C. danae,* respectively.

The ordering of the sites by CA showed an evident separation of the areas on Axis 1, explaining 78% of the observed variance among the locations. Axis 2 represented 17% of the observed variance among the locations (Table 3). This analysis showed that *A. spinimanus* was better correlated with summer and autumn in MAC, whereas *A. cribrarius* was found in all seasons in this region. *Callinectes danae* was strongly correlated with SFS, whereas *C. ornatus* did not show strong associations with regions or periods of study. An MRPP test indicated that species composition differed significantly among the sampled sites (Table 3). The composition and abundance of species showed substantial heterogeneity among the sites (Fig. 1). The results of a cluster analysis based on abundance showed a separation of the observations into two dissimilar groups (A and B) represented by MAC-UBA and SFS, respectively. Group A was further divided into two subgroups (I and II) with a similarity of approximately 50%. These groups were represented by MAC and UBA, respectively; during the spring, these regions were even more similar (Fig. 2). This heterogeneity among localities was reaffirmed by the Mantel test, which showed no association between the arrays of species abundance for different locations (MAC *vs.* UBA, $r = 0.10$, $P > 0.25$; MAC *vs.* SFS, $r = -0.21$, $P > 0.10$; UBA *vs.* SFS, $r < 0.00$, $P > 0.41$). The PerMANOVA analysis of variance showed differences among locations and among seasons. An a posteriori multiple comparison provided by the analysis showed that the three locations were distinct ($P < 0.00$) relative to the composition and abundance of the species of Portunoidea. The summer abundance also differed from that in winter and spring ($P < 0.02$) (Table 4).

**Table 3** Summary of correspondence analysis (CA) and average within-group distance (MRPP) analyses of the associations among three Brazilian coastal sites and the abundance of the Portunoidea assemblage. *MAC* Macaé, *UBA* Ubatuba, *SFS* São Francisco do Sul

**Correspondence Analysis**

| Species | Axis 1 | Species | Axis 2 |
|---|---|---|---|
| *Achelous spinimanus* | 230 | *Achelous spinimanus* | 478 |
| *Arenaeus cribrarius* | 123 | *Arenaeus cribrarius* | 134 |
| *Callinectes ornatus* | 94 | *Callinectes danae* | 18 |
| *Callinectes danae* | -171 | *Callinectes ornatus* | -95 |
| Ranked 1 | | Ranked 2 | |
| MAC - Summer | 113 | MAC - Autumn | 75 |
| MAC - Autumn | 110 | MAC - Summer | 37 |
| MAC - Spring | 107 | SFS - Winter | 9 |
| MAC -Winter | 106 | SFS - Spring | 6 |
| UBA - Autumn | 99 | MAC -Winter | 5 |
| UBA - Spring | 98 | MAC - Spring | 1 |
| UBA - Summer | 95 | SFS - Autumn | -4 |
| UBA - Winter | 70 | SFS - Summer | -6 |
| SFS - Summer | -20 | UBA - Spring | -39 |
| SFS - Autumn | -82 | UBA - Winter | -49 |
| SFS - Spring | -102 | UBA - Summer | -57 |
| SFS - Winter | -125 | UBA - Autumn | -64 |
| Inertia 0.59 | | | |
| | Axis 1 | | Axis 2 |
| Eigenvalue | 0.46 | | 0.10 |
| % of Variance | 0.78 | | 0.17 |

**MRPP**

| Multiple comparisons (Euclidean) | *T* | *A* | *P* |
|---|---|---|---|
| MAC *vs.* UBA | -2.155 | 0.199 | < 0.04 |
| MAC *vs.* SFS | -4.056 | 0.444 | < 0.01 |
| UBA *vs.* SFS | -4.089 | 0.444 | < 0.01 |

The ecological indexes for this assemblage were dissimilar among the sampling sites. Total abundance, diversity, evenness and dominance differed significantly among MAC, UBA and SFS (Table 5). However, seasonal disparities were not found for these indexes. Species richness did not diverge among sites or seasons. A pairwise *t* test between sites for evenness and diversity detected two groups, whereas three groups were detected for abundance and dominance (Table 6). The evenness for UBA ($E'_{year}$ = 0.44) differed from that for MAC and SFS ($E'_{year}$ = 0.66; $E'_{year}$ = 0.60, respectively), showing that the species were more evenly distributed in MAC and SFS (Fig. 1). A similar result was found for diversity: UBA ($H'_{year}$ = 0.57) differed from MAC and SFS ($H'_{year}$ = 0.97; $H'_{year}$ = 0.86, respectively), showing that the diversity of species was higher throughout the year in MAC and SFS. These findings are consistent with the significantly greater value of dominance in UBA ($D_{year}$ = 0.82) than in MAC and SFS.

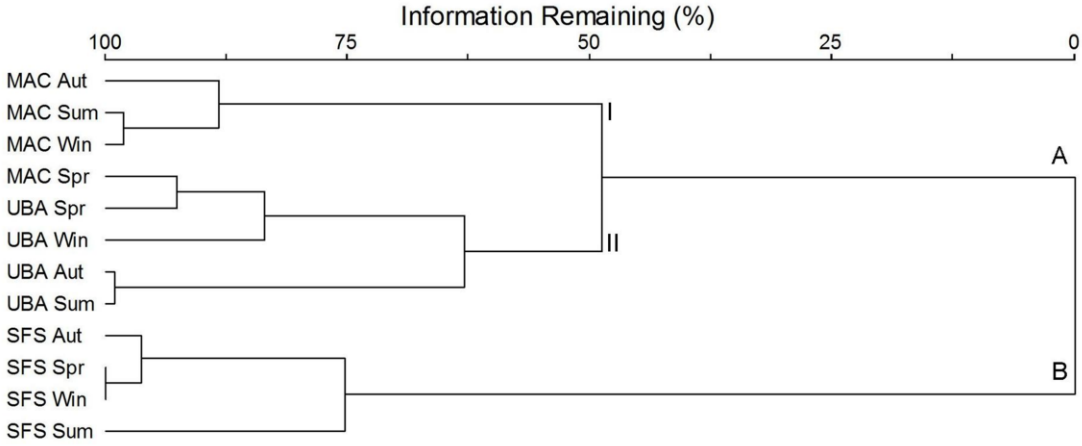


**Fig. 2** Cluster analysis (Bray-Curtis) for three regions of the Brazilian coast. *MAC* Macaé, *UBA* Ubatuba, *SFS* São Francisco do Sul. *Sum* Summer, *Aut* Autumn, *Win* winter, *Spr* spring

A redundancy analysis showed two axes representing the influence of environmental factors on the abundance of swimming crabs, with a total variance of 38.3% (Table 7). The correlation between environmental factors and abundance, represented by the first axis, was statistically significant (Monte Carlo permutation test, $P < 0.00$) (Table 7). This axis explained 26.2% of the variance among species according to sites. Bottom and surface salinity and organic matter were the variables best correlated with axis 1 (Table 7), as well as *C. danae* (Pearson, $r = -0.66$) and *A. spinimanus* ($r = 0.61$). These results suggest that *C. danae* had a negative correlation with the variables cited above, showing a greater abundance in waters with a lower salinity and lower organic matter content. In contrast, *A. spinimanus* was positively correlated with these factors, showing a greater abundance under the opposite conditions. The phi measure was negatively correlated with axis 2 (Table 7) as well as with *A. cribrarius* (*r* = -0.86), *C. danae* (*r* = -0.99) and *A. spinimanus* (*r* = -0.53), indicating that higher abundances were found at higher phi values or a smaller sediment grain size (Fig. 3). *Callinectes ornatus* was poorly correlated with the variables measured (Table 7) and appeared not to show strong selectivity for particular habitat characteristics (Fig. 3). In an ordination analysis, the variables are represented as arrows, and the arrow length indicates the relative importance of each variable (ter Braak 1986). The angle between the arrows indicates the correlation among the environmental variables, and the arrangement of sites or species relative to the arrow represents the characteristics of the site or species preferences (Palmer 1993).

**Table 4** PerMANOVA for the abundance and composition of the Portunoidea assemblage for three Brazilian coastal sites in relationship to the seasons. *MAC* Macaé, *UBA* Ubatuba, *SFS* São Francisco do Sul. *df* degrees of freedom, *Sum S* sum of squares, *MS* mean square

| Source of variation | df | Sum S | MS | Pseudo-F | *P* |
|---|---|---|---|---|---|
| Site | 2 | 3.279 | 1.639 | 33.873 | 0.0001 |
| Season | 3 | 0.344 | 0.115 | 2.371 | 0.0332 |
| Site *vs*. Season | 6 | 0.353 | 0.059 | 1.216 | 0.2789 |
| Residual | 24 | 1.162 | 0.048 | | |
| Total | 35 | 5.138 | | | |
| PAIRWISE COMPARISONS for factor "site" | | | | | |
| Sites | | | *t* | | *P* |
| MAC *vs.* UBA | | | 3.028 | | 0.0001 |
| MAC *vs.* SFS | | | 7.830 | | 0.0001 |
| UBA *vs.* SFS | | | 6.159 | | 0.0001 |
| PAIRWISE COMPARISONS for factor "season" | | | | | |
| Season | | | *t* | | *P* |
| winter *vs.* spring | | | 0.871 | | 0.4850 |
| winter *vs.* summer | | | 2.090 | | 0.0145 |
| winter *vs.* autumn | | | 1.414 | | 0.1414 |
| spring *vs.* summer | | | 2.173 | | 0.0115 |
| spring *vs.* autumn | | | 1.681 | | 0.0600 |
| summer *vs.* autumn | | | 0.434 | | 0.9065 |

## 4. Discussion

The environmental factors analyzed in this study are crucial determinants of the composition and abundance of crabs in each region. *Callinectes ornatus* is reported by several authors as the main representative of the family Portunidae in the bycatch of the artisanal fishery for sea-bob shrimp (Branco and Fracasso 2004) and as the most abundant species of Portunidae in the inshore regions of the Brazilian coast (Pires 1992; Bertini and Fransozo 2004; Bertini et al. 2010; De Leo and Pires-Vanin 2006; Di Benedito et al. 2010; Lavrado et al. 2000). Carvalho and Couto (2011) have shown that the abundance of *C. ornatus* is positively correlated with high salinity on the northeast coast of Brazil. This species has also been found to be abundant in estuarine regions with high salinities ranging from 20 to 35 (see Teixeira and Sa 1998). Such euryhaline behavior corroborates the statement of Mantelatto and Fransozo (1999) that although the life cycle of this species is marine, the adults can eventually enter estuaries in search of food. The present study showed that the species is a habitat generalist and that its absolute abundance is similar in the three regions studied.

The highest relative abundance of *C. ornatus* was found in UBA (generally greater than 75% of the total abundance of the species). This result increased the level of dominance of this species in the region. The equity and species richness of UBA were less than the corresponding values for MAC and SFS. In the studied regions north and south of UBA, the relative frequency of *C. ornatus* was reduced by the presence of other species. SFS showed a greater abundance of the congener *C. danae*, which predominated during the entire study period. Pita et al. (1985) studied the biology of *C. danae* in the complex bay-estuary of Santos, SP. Their study showed that this species is positively associated with freshwater inputs. The same result was found in this study, as SFS has the largest terrestrial freshwater supply of the regions studied here. This same species showed a very low relative frequency in MAC, where it was recorded only in summer and autumn and represented less than 2% of the total species throughout the study period. This low frequency supports the hypothesis that *C. danae* has a relatively low tolerance to high values of salinity. Such high values were observed frequently in MAC, especially during the winter and spring. In UBA, the relative frequency of *C. danae* was greater than 2.5% of the total abundance of species. The supply of freshwater at this site was the lowest recorded in the study, explaining the lower abundance of *C. danae* found in this case. *C. sapidus* occurred in SFS. This environment favors the development of species that complete their life cycle in the estuary; indeed, *C. sapidus* is seldom found at sites with a depth greater than 5 m (Bertini and Fransozo 2004).

**Table 5** PerMANOVA for the abundance, richness (*S*), diversity (*H'*), evenness (*E'*) and dominance (*D*) of the Portunoidea assemblage for three Brazilian coastal sites. *df* degrees of freedom, *Sum S* sum of squares, *MS* mean square

| Source of Variation | df | Sum S | MS | Pseudo-F | *P* |
|---|---|---|---|---|---|
| Total abundance | | | | | |
| Site | 2 | 1.521 | 0.760 | 21.523 | *0.0001* |
| Season | 3 | 0.249 | 0.083 | 2.345 | 0.0593 |
| Site *vs.* season | 6 | 0.272 | 0.045 | 1.283 | 0.2775 |
| Residual | 24 | 0.848 | 0.035 | | |
| Total | 35 | 2.889 | | | |
| Richness (S) | | | | | |
| Site | 2 | 0.002 | 0.008 | 1.826 | 0.1748 |
| Season | 3 | 0.014 | 0.005 | 1.019 | 0.4111 |
| Site *vs.* season | 6 | 0.072 | 0.012 | 2.648 | *0.0332* |
| Residual | 24 | 0.108 | 0.005 | | |
| Total | 35 | 0.210 | | | |
| Diversity (H') | | | | | |
| Site | 2 | 0.223 | 0.112 | 8.058 | *0.0015* |
| Season | 3 | 0.046 | 0.015 | 1.117 | 0.3579 |
| Site *vs.* season | 6 | 0.260 | 0.043 | 3.130 | *0.0162* |
| Residual | 24 | 0.333 | 0.014 | | |
| Total | 35 | 0.863 | | | |
| Evenness (E') | | | | | |
| Site | 2 | 0.061 | 0.031 | 6.112 | *0.0075* |
| Season | 3 | 0.006 | 0.002 | 0.408 | 0.7595 |
| Site *vs.* season | 6 | 0.110 | 0.018 | 3.660 | *0.0102* |
| Residual | 24 | 0.120 | 0.005 | | |
| Total | 35 | 0.298 | | | |
| Dominance (D) | | | | | |
| Site | 2 | 0.160 | 0.080 | 14.800 | *0.0002* |
| Season | 3 | 0.013 | 0.004 | 0.800 | 0.4969 |
| Site *vs.* season | 6 | 0.061 | 0.010 | 1.869 | 0.1266 |
| Residual | 24 | 0.130 | 0.005 | | |
| Total | 35 | 0.363 | | | |

In MAC, *A. cribrarius* was relatively abundant but did not replace *C. ornatus*. At this location, *A. cribrarius* represented more than 40% of the total abundance of species. Several studies of the composition of the Brachyura have reported a low frequency of *A. cribrarius* relative to other species of Portunidae, e.g., 0.17% (Lavrado et al. 2000) and 4.31% (Severino-Rodriguez et al. 2002) of the Portunoidea assemblage. Bertini and Fransozo (2004) conducted a survey of Brachyura in Ubatuba and identified *A. cribrarius* as the fifth most abundant species of Portunoidea, with an extremely low number of individuals captured relative to the other species. Anderson et al. (1977) and Pinheiro et al. (1996) reported a preference of *A. cribrarius* for cooler and saline waters. The present study found that these characteristics distinguished MAC from the other regions. In addition, the level of organic matter found in MAC was significantly higher than that found in SFS, and the grain size of the sediment in MAC was significantly less than that in UBA. According to Melo (1996), *A. cribrarius* has a thin granular carapace with small white spots (hence the name "speckled swimming crab") and usually remains in a burrow during the day. These characteristics, combined with the characteristics of the sediment in MAC, appear to contribute to the opportunities for the species to remain camouflaged, reducing the risk of predation, which may explain the substantial abundance of this crab in the region.

**Table 6** Results of pairwise tests for abundance, diversity (*H'*), evenness (*E'*) and dominance (*D*) of the Portunoidea assemblage for three Brazilian coastal sites. *MAC* Macaé, *UBA* Ubatuba, *SFS* São Francisco do Sul

| Groups | *t* | *P* |
|---|---|---|
| Abundance | | |
| MAC *vs.* UBA | 2.127 | < 0.04 |
| MAC *vs.* SFS | 5.553 | < 0.00 |
| UBA *vs.* SFS | 5.401 | < 0.00 |
| Evenness (E') | | |
| MAC *vs.* UBA | 3.170 | < 0.00 |
| MAC *vs.* SFS | 0.204 | > 0.85 |
| UBA *vs.* SFS | 2.649 | < 0.02 |
| Diversity (H') | | |
| MAC *vs.* UBA | 3.560 | < 0.00 |
| MAC *vs.* SFS | 1.679 | > 0.11 |
| UBA *vs.* SFS | 2.419 | 0.021 |
| Dominance (D) | | |
| MAC *vs.* UBA | 5.097 | < 0.00 |
| MAC *vs.* SFS | 3.237 | < 0.00 |
| UBA *vs.* SFS | 2.251 | 0.039 |

The low temperatures and the fine-grained sediment in MAC also explain the presence of *A. spinimanus* and *A. spinicarpus* (in lower numbers). These species were found in greater abundance only during summer and autumn. These months have colder water temperatures due to the upwelling and upwelling entry of ACAS. Santos et al. (1994), Branco et al. (2002) and Ripoli et al. (2007) have shown that the abundance of *A. spinimanus* is strongly related to low temperatures. The same relationship has been demonstrated for the congener *A. spinicarpus*, found in abundance at depths greater than 40 m in the region of Cabo Frio (De Leo and Pires-Vanin 2006).

Variation among regions in the composition and abundance of species may reflect regional differences and environmental phenomena that act on each species. According to Sumida and Pires-Vanin (1997), changes in the benthic fauna along a latitudinal gradient may be due primarily to the stability of sediments and water masses. The three regions studied here differ significantly in these characteristics. In MAC, the high sensitivity to wind systems found in the area causes rapid alternations between seasonal upwelling phenomena and subsidence as well as unstable inorganic nutrient inputs (Purcell 2005), which influence the biological structure of the area. The bottom temperature is one of the strongest influences on this structure because it remains below 20°C during most of the year. Consistent with the temperature, salinity also exhibits values above 36, reaching 38 during the fall months. Such variations are due to the high thermal variation caused by the entry and exit of ACAS in addition to mechanical disturbances generated by incoming waves and cold fronts (see Pires 1992). This author also states that the intrusion of ACAS also elevates new primary production, which increases the benthic biomass when exported to the bottom. Pires (1992) has demonstrated that one of the principal factors that serve to maintain and regulate the structure of the benthic macrofauna on the continental shelf of UBA is the dynamics of the water masses. The north central coast of Santa Catarina harbors three types of distinct water masses, and the nearest coastal region is marked by the occurrence of Coastal Water (CW) with low salinity (<34) and temperatures varying seasonally between 19 and 28°C. The latter water mass depends on the water supply from the continent, extending dozens of kilometers into the Atlantic during periods of maximum rainfall (Schettini et al. 1998). Two other water masses, the Water Platform (AP) and ACAS, occur farther offshore and show higher salinities (> 35). These masses do not reach the areas sampled in this study. For this reason, given their salinity and temperature characteristics, they were not included in the analyses (see Schettini et al. 1998).

**Table 7** Statistical summary of axes generated by redundancy analysis with final scores of species and correlations for environmental variables. Monte Carlo test for species-environment correlations based on 9999 runs. Coefficients ≥ ± 0.4 are considered ecologically important and are in bold text

| Axis statistical summary | Axis 1 | Axis 2 |
|---|---|---|
| Eigenvalue | 1.05 | 0.49 |
| % of variance explained | 26.2 | 12.10 |
| Final Scores | | |
| *A. cribrarius* | 0.38 | **-0.86** |
| *C. danae* | **-0.66** | **-0.99** |
| *C. ornatus* | 0.00 | -0.24 |
| *A. spinimanus* | **0.61** | **-0.53** |
| Organic matter | **0.71** | -0.26 |
| Mean grain size – phi | 0.22 | **-0.78** |
| Surface temperature | 0.22 | 0.09 |
| Bottom temperature | -0.09 | -0.04 |
| Bottom salinity | **0.72** | -0.23 |
| Surface salinity | **0.70** | -0.15 |
| Monte Carlo test results<br>Species-Environment correlations | | |
| Pearson correlation | **0.80** | **0.66** |
| Mean | 0.53 | 0.40 |
| Minimum | 0.29 | 0.17 |
| Maximum | 0.79 | 0.69 |
| *P* | < 0.00 | |

However, beyond this pattern of temporal variation determined by the fluctuations governed by the water masses, there are other more stable factors that are active on a spatial scale and that influence the distribution and structure of the fauna. One of these factors is the grain size of the sediment. Mahiques et al. (2002) studied the sedimentation of the outer continental shelf and upper slope between São Sebastião and Cabo Frio. Their study found that the upwelling area is one of the regions showing a higher rate of sedimentation, as also observed in the present study. The authors of that study related their findings to the interaction between changes in the topography of the coast and winds that induce upwelling and act on the dynamics of water masses and, hence, cause high rates of deposition of organic matter and fine sediments. According to Moore (1958), sites with a substrate composed primarily of finer granules have a higher organic content than coarser-grained deposits. This characteristic is the most important determinant of the amount of life that can be supported in MAC.

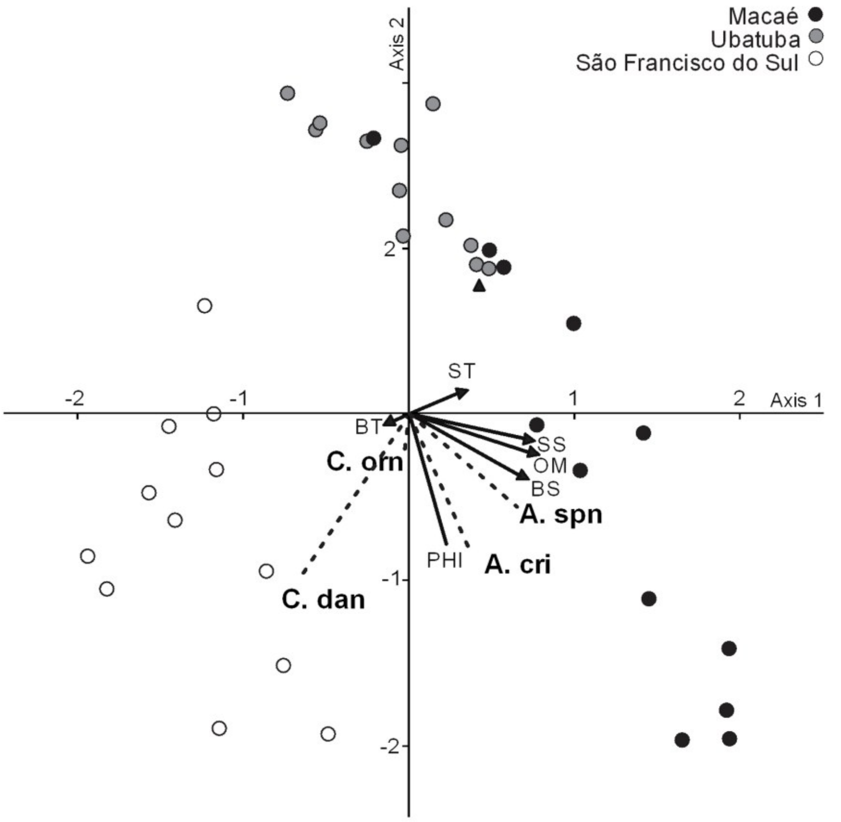


**Fig. 3** RDA ordination plot. **a** Sites and environmental variables. Each point represents a single sample site (month). **b** The association of a species with each axis is represented by its score (plotted), and the correlation between the environmental variables and the axes are represented by the length and angle of the arrows. *MAC* Macaé, *UBA* Ubatuba, *SFS* São Francisco do Sul. *OM* organic matter, *PHI* measure of the central tendency of sediment grain size, *ST* surface temperature, *SS* surface salinity, *BT* bottom temperature, *BS* bottom salinity. *A cri A. cribrarius*, *C dan C. danae*, *C sap C. sapidus*, *A spi A. spinimanus*

The organic matter found in UBA is primarily the result of the concentration of waste transported from the continent (Pires 1992), particularly from the large number of human residences. In SFS, a substantial proportion of the organic matter is furnished by a terrestrially associated source, Babitonga Bay. Braga et al. (2006) stated that continental input produces high concentrations of organic matter in the outfall to the bay. However, high-energy events occur periodically due to exposure to wave trains in the region, providing conditions that allow the resuspension and transport of previously deposited fine sediments. Braga et al. (2006) also state that the volume of inflow of fresh water is associated with substantial variations in salinity through the gradual dilution of the seawater and that the biota is adapted to these variations. An example is the marked abundance of *C. danae* in SFS, which contributed substantially to the higher abundance of species in the region. The finding that the lowest values of salinity occur in spring and summer can be explained by the greater contribution of continental waters resulting from the rains, which are more frequent during these seasons.

## 5. Conclusions

The present study demonstrates that areas affected by different phenomena show abrupt changes in the composition and abundance of key species of the Portunoidea assemblage. *Callinectes ornatus* was the principal species found in MAC and UBA, whereas *A. cribrarius* predominated only in MAC and *C. danae* was highly abundant only in SFS. Although the strength of eutrophication in UBA and MAC appears to differ, SFS includes an extensive estuarine complex, favoring the development of species that complete their life cycle in the estuarine environment. Thus, the observed differences in diversity, equity and species dominance primarily reflect the sediment composition and salinity and the water masses that reach the regions studied.

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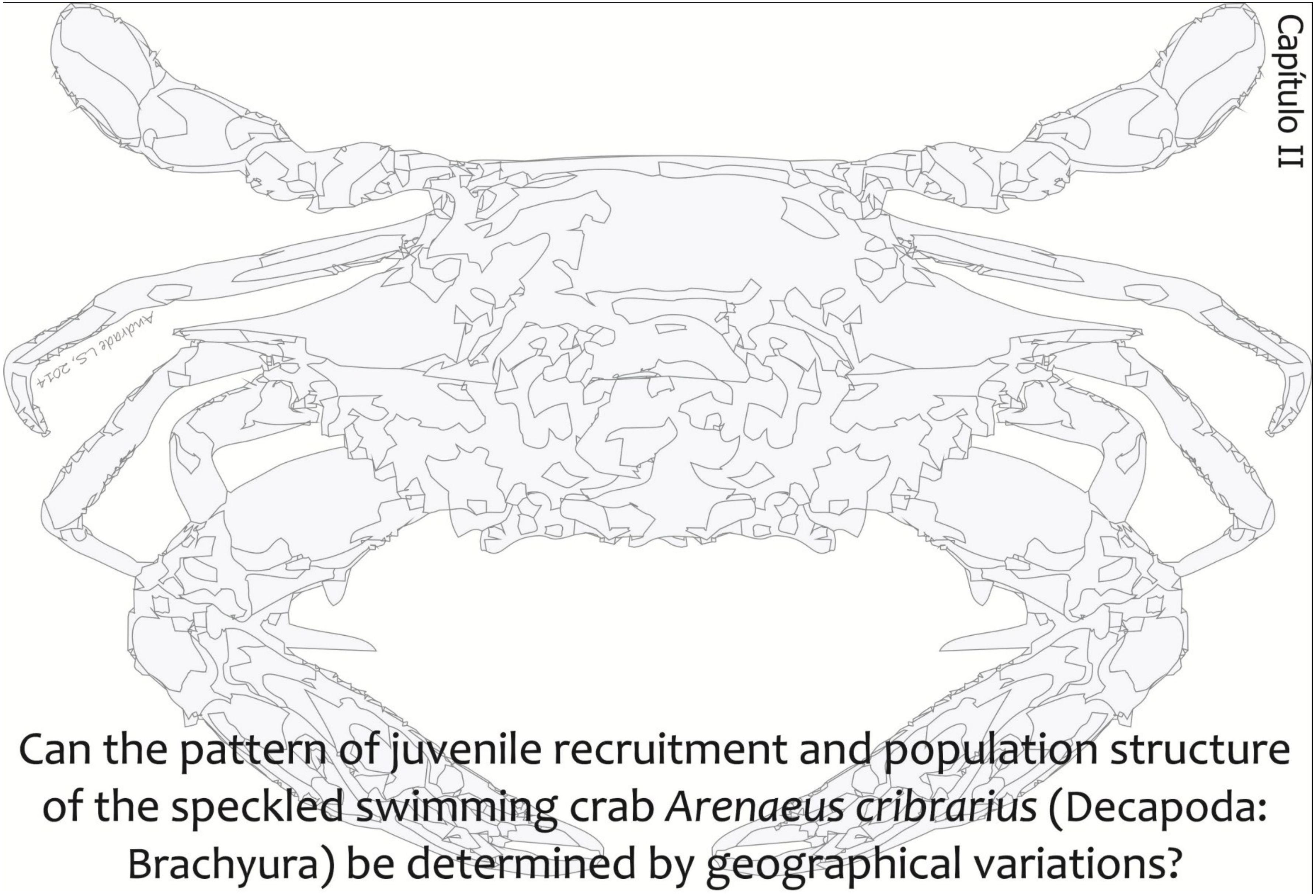
Capítulo II



# Can the pattern of juvenile recruitment and population structure of the speckled swimming crab *Arenaeus cribrarius* (Decapoda: Brachyura) be determined by geographical variations?

## Abstract

This study evaluated the effect of environmental stimuli and selective pressures in different geographical areas along a latitudinal gradient, on the juvenile recruitment, population structure, and sex ratio of the speckled swimming crab *Arenaeus cribrarius*. Samples were collected monthly during one year in three locations along the Brazilian coast: Macaé, state of Rio de Janeiro (MAC, 22º47'S and 41º45'W), Ubatuba, São Paulo (UBA, 23º 27'S and 44°58'W) and São Francisco do Sul, Santa Catarina (SFS, 26º08'S and 48º34'W). The specimens of *A. cribrarius* were identified, counted, sexed, and measured for maximum carapace width (CW). The largest juvenile found was in UBA (47.7 ± 1.36 mm); and the largest adult females and males in MAC (74.26 ± 0.93 mm and 77.04 ± 0.79 mm, respectively). Recruitment in MAC was continuous, while in UBA and SFS, recruitment showed seasonal characteristics. The sex ratio was skewed toward females only in UBA; in MAC and SFS, males and females were present in equal proportions. These results indicate that geographical variations can cause differences in the recruitment and population structure of *A. cribrarius*. These regional differences call attention to the necessity for improved management plans and control of shrimp fishing, which can affect population patterns such as juvenile recruitment, population structure and life history of the target species and species that are caught in bycatch from shrimping, such as the swimming crab *A. cribrarius*.

**Key-words** *Arenaeus cribrarius* · Crustacea · Latitudinal trends · Population patterns · Portunid · Size rate.

## 1. Introduction

The speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) is found in the western Atlantic Ocean from Massachusetts, United States to La Paloma, Uruguay (Melo 1996). This crab has been recorded from the tidal zone of sandy beaches to 70 m depth, although it is more common in shallower areas (Avila & Branco 1996; Pinheiro *et al*. 1996; Carmona-Suárez & Conde 2002; De Leo & Pires-Vanin 2006); it is rarely found in estuaries and coastal lagoons (Melo 1996). The few investigations of population features of *A. cribrarius* are limited to one region in Venezuela (Carmona-Suárez & Conde 2002; Guerra-Castro *et al.* 2007), and two in Brazil (states of Santa Catarina, Avila & Branco 1996; and São Paulo, Pinheiro & Fransozo 1993; 1998, Pinheiro *et al*. 1996). The information obtained in these studies differs in several respects, including the depth in which the crabs were found, reproduction and recruitment periods, size of individuals, etc., which led us to inquire about the factors that might contribute to these variations.

Environmental stimuli and selective pressures originating from different latitudes and upwelling zones have been widely used to generate hypotheses about the causes of differences in population life history of crustaceans. Several studies on crustaceans have found that individual size generally increases with latitude, e.g., copepods (Lonsdale & Levinton 1985) and *Artemesia longinaris* Bate, 1888 (Castilho *et al*. 2007). This feature is believed to be related to temperature regimes, with cooler waters (more common farther from the equator) producing larger individuals, and warmer temperatures (usually closer to the equator) producing smaller individuals. However, other factors may interact with temperature to determine individual size. Population density and predation have been hypothesized to contribute to slower individual growth as it increases intraspecific encounters, reducing food intake per individual and resulting in smaller-sized individuals (Sanders 1968; Chittleborough 1976; Wallerstein & Brusca 1982; Jones & Simons 1983; Lonsdale & Levinton 1985; Connolly *et al*. 2001; Defeo & Cardoso 2002; Castilho *et al*. 2007; Mantelatto *et al*. 2010; Terossi *et al*. 2010; Viegas *et al*. 2012).

The population structure and recruitment period of a population are the result of adaptation to specific environmental stimuli (proximate factors) and selective pressures (final factors) that vary along a gradient. Seasonal changes in water temperature, as well as in the salinity, photoperiod, and food supply may be critical proximate factors that cause changes in population patterns. Our question was whether the classical paradigm of continuous recruitment and smaller body size in the tropics, and seasonal recruitment and larger size at higher latitudes would be supported by the results of a study of *A. cribrarius* in locations at different latitudes, affected by different water masses and with distinct geographical features. This study investigated the juvenile recruitment and population structure of *A. cribrarius* in three regions of the Brazilian coast, in order to assess if the geographical variations might determine: a) the abundance of demographic groups; b) the ratio of males to females; c) the size of individuals; and d) the period when juveniles enter the population.

## 2. Material and Methods

### 2.1 Study areas

We analyzed three localities of the Brazilian coast (Fig. 1): two in the southeast region (Macaé, state of Rio de Janeiro, 22º47'S and 41º45'W; Ubatuba, state of São Paulo, 23º 27'S and 44°58'W) and one in the southern region (São Francisco do Sul, state of Santa Catarina, 26º08'S and 48º34'W). Macaé (MAC) is near Cabo Frio, where coastal upwelling occurs due to atmospheric circulation associated with the center of the South Atlantic High Pressure. This occurs intensively during the summer months, when prevailing winds blow from the E–NE quadrant and the South Atlantic Central Water (SACW) rises from 300 m depth and reaches the surface in a coastal current 5 km wide, bringing large amounts of nutrients up to the euphotic zone (Valentin *et al*. 1987). Three main water masses are present in the area. North of MAC, the warm (T > 20 °C) and saline (S > 36) Tropical Water (TW) covers the entire shelf, constituting the main stream of the Brazilian Current (BC). To the south, a mixture of TW and SACW, a relatively cold (< 20 °C) and less saline (< 36) water mass, is predominant. The third type is the Coastal Water, a mixture of continental runoff and the Shelf Water (SW) (Castro-Filho & Miranda 1998). During summer, the TW lay on the surface and the SACW on the bottom, creating a thermal front 15 km long that lasted for several days. In the winter, the SACW thermal front retreats to the outer shelf; and in the spring, due to favorable wind conditions, it is possible to observe the beginning of the progressive intrusion of the SACW (De Leo & Pires-Vanin 2006).

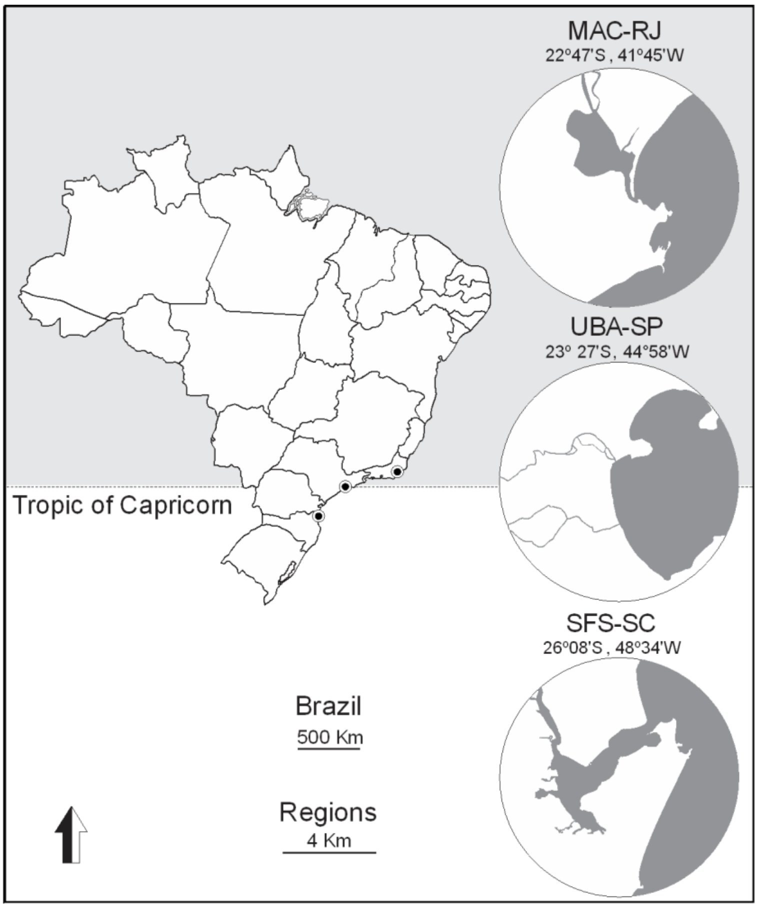


Fig. 1. Locations of three Brazilian regions where swimming crabs *Arenaeus cribrarius* were collected. MAC-RJ = Macaé, Rio de Janeiro, UBA-SP = Ubatuba, São Paulo, SFS-SC = São Francisco do Sul, Santa Catarina. Scale applies to maps of regions

In the region of Ubatuba (UBA), along the northern coast of São Paulo state, the Serra do Mar mountain range extends into the sea to form a jagged coastline with several semi-confined coves. The water-mass dynamics in UBA differs from MAC because the SACW thermal front, observed during the summer months, remains at subsurface depths, so that upwelling is rarely observed (Castro-Filho & Miranda 1998). Drainages in this area are small and local, with limited exchange of water and sediment between the coastal region and the adjacent shelf (Mahiques 1995). The UBA oceanographic system forms a transition between coastal waters and the continental shelf (Mahiques 1995). The distribution of water masses has distinct patterns (Castro-Filho *et al*. 1987), since the dynamics of the local water masses depend mainly on the wind, currents and sea-floor relief. Thus, during winter when the SACW thermal front retreats to the outer shelf, warm bottom temperatures (20-22 °C) and low salinities (34-35) indicate the presence of the Coastal Water in the coastal zone. With the approach of spring, different water masses are observed, with lower salinity and higher temperatures. In the summer, the thermal front is located on the inner shelf, with bottom temperatures of 18°C (De Leo & Pires-Vanin 2006).

The coast of São Francisco do Sul (SFS) is generally linear and houses the largest estuarine complex in the state of Santa Catarina, with an area of 1567 km² (see Fig. 1). In this region are four distinct water masses: Coastal Water, Shelf Water, Tropical Water and South Atlantic Central Water. The Coastal Water is closest to the coastal region and covers the study area; this water mass has low salinity (< 34) and temperatures varying seasonally between 19 and 28 ºC in winter and summer, respectively (Schettini *et al.* 1998). The occurrence of the Coastal Water and its salinity depend on the continental contribution, extending tens of kilometers toward the ocean during periods of maximum rainfall (Emílsson 1961). The Shelf Water occurs farther from the coast and is formed by mixing of Coastal Water, SACW and TW, as well as through heating by solar radiation, with salinity > 35 and temperature between 20 and 23 $^{o}$C (Emílsson 1961). In this region, SACW is observed only in greater depths and during the spring and summer months (Schettini *et al*. 1998).

## 2.2 Data collection

The samples were collected in a systematic way, from July 2010 through June 2011, covering 5-20 m depths. For each study region, one-hour hauls were conducted in three different areas for a total of three hours monthly. The crabs were collected from a shrimp-fishing boat equipped with double-rig nets, with the following net specifications: length 10 m, mouth 4.5 m, body mesh diameter 20 mm, cod-end mesh diameter 18 mm. At the end of each trawl, the material was screened on the boat, packed in labeled plastic bags, and kept in a freezer until the specimens were examined.

### 2.3 Laboratory procedures

The specimens of *A. cribrarius* were identified according to Melo (1996). The crabs were counted, sexed, and measured for maximum carapace width (CW), disregarding the lateral teeth, using a caliper (0.01 mm). Males were distinguished by the inverted-T shape of the abdomen and the presence of the first two pairs of pleopods, and females by the semicircular abdomen and four pairs of pleopods (Pinheiro & Fransozo 1998). All individuals obtained were grouped in the following demographic categories: adult males, adult females, and immatures (checked by the adherence of the abdomen to the thoracic sternites, following the procedures adopted by Pinheiro & Fransozo 1998).

### 2.4 Data analyses

Differences in the carapace width of the demographic groups from MAC, UBA and SFS were compared using a Kruskal-Wallis test followed by Dunn’s multiple comparison tests. To evaluate sexual dimorphism by size, in each region, the Mann-Whitney test was used. In these tests, each crab was used as a sample, without ranking them by size class, since the aim was to evaluate the mean by region, as performed by Andrade *et al.* (2013).

From the maximum and minimum size of the crabs, size classes were defined following the method suggested by Sturges (1926), which was adapted to standardize the comparison of different demographic groups collected in the three regions. A one-way permutational analysis of variance (PerMANOVA) (Anderson 2001, 2005) was used to assess the significance of the distribution of size classes among seasons. The same test was used to assess the significance of the abundance of immature crabs between semesters and regions (percentage of recruits over the total number of individuals captured in each region, the same protocol followed by Connolly *et al*. 2001). The Binomial test (Wilson & Hardy

2002) was applied to samples from populations constituted by only two categories, here used to evaluate the proportion between males and females in each season and region.

## 3. Results

A total of 1948 specimens of *A. cribrarius* were caught during the study period: 1072 in MAC, 283 in UBA and 593 in SFS. Individuals collected in MAC measured from 16.0 to 107.4 mm, in UBA from 21.4 to 99.6 mm, and in SFS from 13.7 to 92.3 mm CW.

The mean size of the immatures was significantly larger (H = 44.74, p = 0.00) in UBA (mean ± standard error: 47.7 ± 1.36 mm), followed by immatures in MAC (41.9 ± 0.43 mm) and in SFS (38.8 ± 0.44 mm) (Fig. 2A). The mean size of adult females also differed significantly between regions (H = 32.53, p = 0.00; Fig. 2B); the largest adult females were found in MAC (74.26 ± 0.93 mm), followed by females in UBA (71.39 ± 0.79 mm) and in SFS (66.25 ± 1.13 mm). Significantly (H = 6.23, p = 0:00) larger adult males were found in MAC (77.04 ± 0.79 mm) and UBA (76.75 ± 1.33 mm) than in SFS (68.36 ± 1.55 mm) (Fig. 2C).

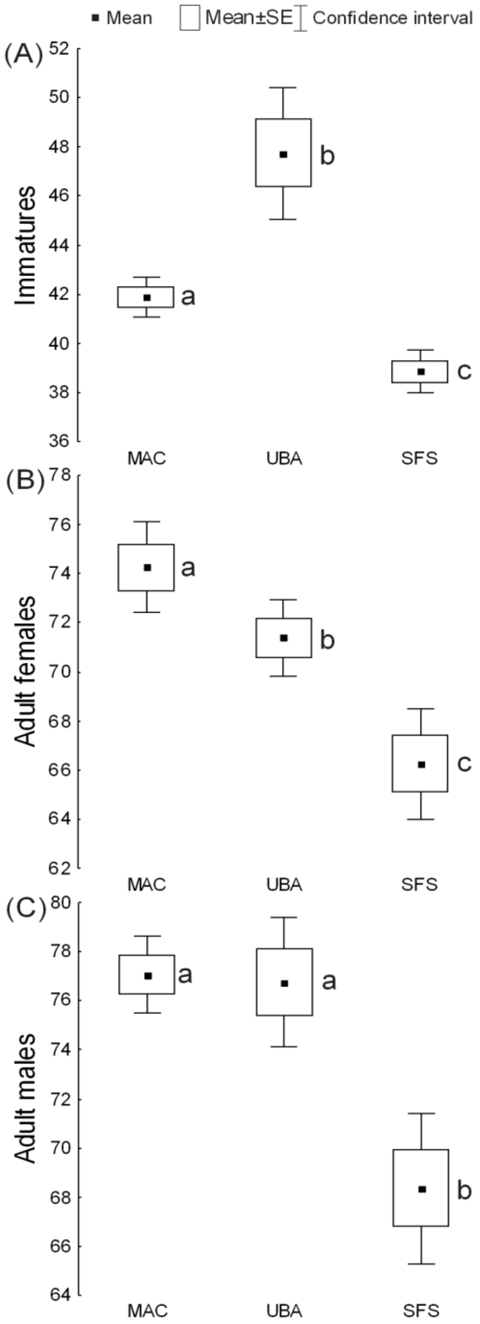


Fig. 2. Mean size, standard error and confidence interval for immature individuals (A), adult females (B) and adult males (C) of *Arenaeus cribrarius* collected from July 2010 through June 2011 in three regions of the Brazilian coast. MAC = Macaé-RJ, UBA = Ubatuba-SP, SFS = São Francisco do Sul-SC. Same letter in common indicates no significant difference in post-hoc Dunn test (p > 0.05)

The number and size (maximum carapace width) of immatures (IM), adult males (AM) and adult females (AF) were recorded, and the crabs were grouped in 12 size classes of 8 mm each. In MAC and UBA (Fig. 3, A and B) the size-class distribution was uniform throughout the seasons (perMANOVA, MAC: F = 1.804, p = 0.144; UBA: F = 1.378, p = 0.149). In SFS (Fig. 3 C), there were peaks of abundance in the first size classes (entrance of smaller juveniles) during the summer, differing significantly from the other seasons (F = 26.31, p = 0.00), when no juveniles entered the population.

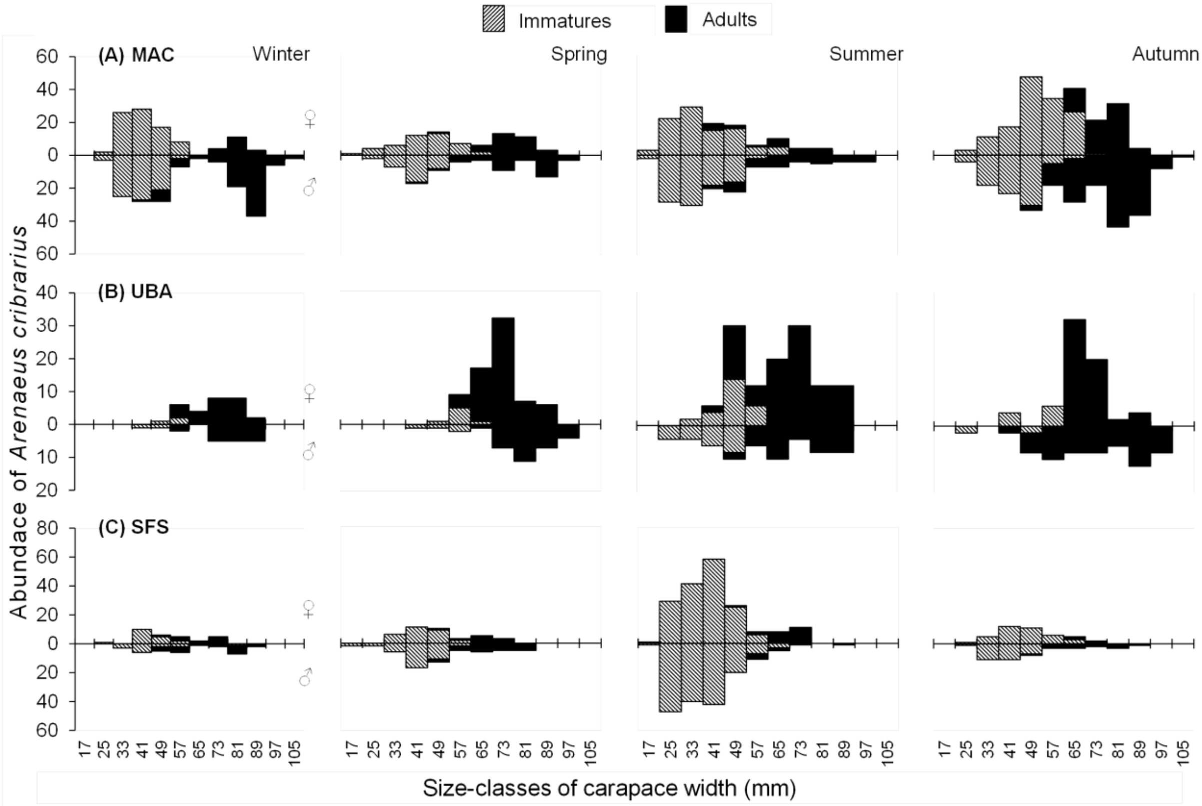


Fig. 3. Size-class frequency distribution for the total number of individuals *Arenaeus cribrarius* sampled from three regions of the Brazilian coast. MAC = Macaé-RJ, UBA = Ubatuba-SP, SFS = São Francisco do Sul-SC. ♀ = females (above X axis); ♂ = males (below X axis)

In MAC and UBA the populations showed sexual dimorphism in size, with males significantly larger than females (MAC: Z = -4.54, p = 0.00; UBA: Z = -2.58, p = 0.00). In SFS the sexes showed no significant difference in size (Z = 1.28, p = 0.20). The sex ratio followed the Mendelian proportion for the populations in SFS and MAC, in all seasons. In

UBA, females outnumbered males during the spring and summer, and the overall sex ratio during the study period was 1 female to 0.45 males (Fig. 3, Table 1).

Table 1. Sex ratio for populations of *Arenaeus cribrarius* collected from July 2010 through June 2011 in three regions of the Brazilian coast. MAC = Macaé-RJ, UBA = Ubatuba-SP, SFS = São Francisco do Sul-SC. *significant differences detected by Binomial test.

| Region | Season | Females | Males | *P* | Confidence intervals (95%) |
|---|---|---|---|---|---|
| MAC | Autumn | 176 | 147 | 0.11 | 129.2 < 147.0 < 165.1 |
| | Spring | 59 | 53 | 0.60 | 42.3 < 53.0 < 63.8 |
| | Summer | 112 | 121 | 0.56 | 05.6 < 121.0 < 136.3 |
| | Winter | 84 | 98 | 0.30 | 84.3 < 98.0 < 111.5 |
| | **total** | **431** | **419** | **0.69** | **390.5 < 419.0 < 447.5** |
| UBA | Autumn | 29 | 19 | 0.15 | 12.4 < 19.0 < 26.3 |
| | Spring | 49 | 12 | 0.00* | 6.5 < 12.0 < 19.4 |
| | Summer | 41 | 22 | 0.01* | 14.7 < 22.0 < 30.2 |
| | Winter | 20 | 10 | 0.08 | 5.2 < 10.0 < 15.8 |
| | **total** | **139** | **63** | **0.00*** | **50.2< 63.0 < 77.0** |
| SFS | Autumn | 42 | 40 | 0.83 | 30.8 < 40.0 < 49.2 |
| | Spring | 38 | 56 | 0.06 | 46.0 < 56.0 < 65.4 |
| | Summer | 180 | 167 | 0.47 | 148.4 < 167.0 < 185.7 |
| | Winter | 29 | 26 | 0.69 | 18.5 < 26.0 < 33.7 |
| | **total** | **289** | **289** | **0.98** | **265.5 < 289.0 < 312.5** |

Juvenile recruitment was significantly higher in MAC and SFS than in UBA (Table 2). The percentage of recruits was higher from January to June (PerMANOVA, F = 4.047, P = 0.01) in all three regions (Fig. 4).

## 4. Discussion

The populations of *A. cribrarius* from southeastern and southern Brazil showed different characteristics in terms of carapace width, sex ratio and recruitment period among locations studied. The larger individuals were found at locations with cooler waters, such as MAC (which is affected by upwelling) and UBA (which in summer is influenced by the lower temperatures of the South Atlantic Central Water thermal front). Adults found in the area affected by upwelling were larger than those from the intermediate latitude, which contains a high abundance of females. Apparently, the location at lower latitude, affected by upwelling, has the best conditions for the continuous establishment of juveniles; while higher latitude seems to have seasonal characteristics, i.e., the occurrence of Coastal Water and South Atlantic Central Water, which favor recruitment during the summer. A similar pattern was reported by Connolly *et al*. (2001), who observed transitions in recruitment patterns of barnacles and mussels along a latitudinal gradient that included regions that were affected and others that were not affected by upwelling.

Table 2. PerMANOVA for abundance of recruits of *Arenaeus cribrarius* in three regions of the Brazilian coast. MAC = Macaé-RJ, UBA = Ubatuba-SP, SFS = São Francisco do Sul-SC. *significant differences

| Recruitment between semesters in the three regions | | | | | |
|---|---|---|---|---|---|
| Source of variation | Df | SS | MS | Pseudo-F | *P* |
| Site | 1 | 0.271 | 0.271 | 4.047 | 0.015* |
| Residual | 10 | 0.669 | 0.067 | | |
| Total | 11 | 0.939 | | | |
| Recruitment among regions | | | | | |
| Source of variation | Df | SS | MS | Pseudo-F | *P* |
| Site | 2 | 1.926 | 0.963 | 19.144 | 0.000* |
| Residual | 33 | 1.660 | 0.050 | | |
| Total | 35 | 3.586 | | | |
| Pairwise comparisons between regions | | | | | |
| | | | t | *P* | |
| Macaé *vs.* Ubatuba | | | 4.428 | 0.0001* | |
| Macaé *vs.* São Francisco do Sul | | | 0.545 | 0.6004 | |
| São Francisco do Sul *vs.* Ubatuba | | | 4.672 | 0.0001* | |

The individual size of *A. cribrarius* has been found to vary among populations: 9.5 to 56.5 mm, in depths not exceeding 1.5 m, in Venezuela (11°27'N, 69°34'W; Carmona-Suárez & Conde 2002), 21.1 to 112.0 mm in Ubatuba (Pinheiro *et al*. 1996), and 18.0 to 119.0 mm (including lateral spines) in the region of Santa Catarina (27°29'S, 48°23'W; Avila & Branco 1996). The differences in CW between the populations studied here and the previously studied populations mentioned above is probably due to different temperature regimes. Populations found in greater depths (such as those from Santa Catarina, studied by Avila &

Branco 1996) or in areas with upwelling (such as MAC) generally reach larger sizes, while populations in regions with higher temperatures such as SFS have smaller individuals. Several factors may explain this: (1) The region influenced by upwelling is richer in nutrients, which may increase the rate of growth during early development (De Leo & Pires-Vanin 2006). Likewise, there are also several reports of entry of South Atlantic Central Water in the region at intermediate latitude (UBA), which increases primary productivity during spring and early summer (Castro-Filho *et al*. 1987; Vega-Pérez 1993); this coincides with the season of larval dispersal prior to the recruitment of juveniles caught in this study (see Fig. 4). (2) The higher-latitude region studied (SFS) is strongly influenced by Coastal Water (during winter and summer) and continental inflows, which reduce the local salinity (see Braga et al. 2006), promoting the dominance of estuarine species and euryhaline species such as *Callinectes danae* Smith, 1869 (Andrade *et al*. unpublished observations), which may compete for food and space with A. cribrarius (Pinheiro *et al*. 1997). (3) The movement of the largest individuals to areas farther off the coast in search of better environmental conditions. The temperature and salinity can affect the characteristics of marine decapods (Lonsdale & Levinton 1985). Carmona-Suárez & Conde (2002) sampled *A. cribrarius* in harsh environmental conditions in Venezuela, where the rainfall is sparse and seasonal, with temperature, salinity and oxygen varying temporally. Thus, the size patterns observed in this study may be associated with differences in temperature and salinity among the localities, although still within the requirements of the species.

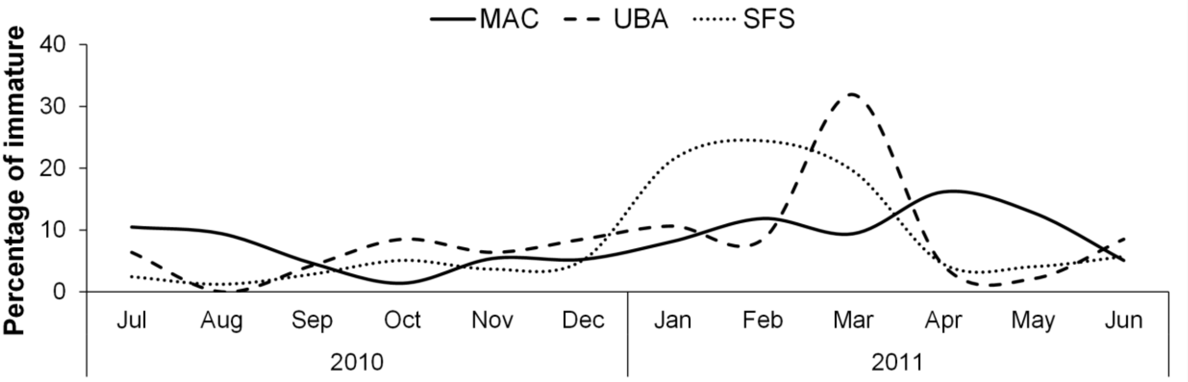


Fig. 4. Juvenile recruitment of *Arenaeus cribrarius* collected in three regions of the Brazilian coast. MAC = Macaé-RJ, UBA = Ubatuba-SP, SFS = São Francisco do Sul-SC

The highest abundance of *A. cribrarius* in the higher-latitude region, mainly represented by juveniles, occurred during the summer. Normally, the South Atlantic Central Water intrudes into the region during this season (Schettinni *et al*. 1998; Borzone *et al*. 1999). If we consider that the greater abundance of *A. cribrarius* in the region influenced by upwelling may indicate a preference for colder and more-saline water (see Andrade *et al*. 2013), i.e., with the characteristics of the South Atlantic Central Water, it seems reasonable to infer that individuals of SFS are farther off the coast, since the Tropical Water and South Atlantic Central Water occur farther offshore (Borzone *et al*. 1999). Areas farther from the coast were not sampled in this study, and may harbor larger individuals of *A. cribrarius*.

Sexual dimorphism may indicate differences in growth patterns between the genders, as in most species of Crustacea (Hartnoll 1985). Pinheiro & Fransozo (1993; 1998), Avila & Branco (1996) and Carmona-Suárez & Conde (2002) have all described this pattern for *A. cribrarius*. The lack of dimorphism in size observed in the location at higher latitude may be related to more-stressful social and energy-demanding activities at the lower- and intermediate-latitude populations, since these regions have larger numbers of adults that compete for food and partners, which result in a larger size and improved ability to compete for potential mates. It is also possible that this profile is acting in combination with differences in food limitations among the three areas. The optimum physiological performance of the species should be reached in the center of the geographical distribution, and will become suboptimal near the geographical extremes (Sorte & Hofmann 2004). Another factor that may have led to the absence of dimorphism in SFS is the high percentage of immature individuals in relation to adults (82.8%), since this dimorphism is apparent only in adult individuals (Pinheiro & Fransozo 1993). This same factor may account for the 1:1 sex ratio found in the same region, since the Mendelian ratio is reported for juvenile marine crustaceans (Wenner 1972).

Differences in the pattern of the sex ratio along the latitudinal gradient are not commonly studied in Decapoda. In this study, the lower- and higher-latitude populations showed a sex ratio of 1:1, which can be explained by the considerable percentage of recruits found in the region. According to Wenner (1972), differential mortality may contribute to an unequal sex ratio, although the quality of food, more-active behavior of one sex than the other, and the possibility of differential distribution between the sexes, among other factors, also must be considered. In this case, we consider that the high percentage of immature individuals accounts for the balanced sex ratio.

Recruitment has been found to be higher in regions where intraspecific competition for space is more intense (e.g., mussels and intertidal barnacles, Connolly *et al*. 2001). Our observations appear to concord with this, since juveniles of *A. cribrarius* were more abundant in MAC, the region at the highest latitude and richer in nutrients, coming from upwelling. Comparing the abundance of recruits between UBA and SFS indicated a higher percentage of immatures in the region farther south. However, it was apparent that the latitudinal effect may act in opposition to the effect of the upwelling zone (MAC), since the abundance of recruits in this region did not differ significantly from the population at 4 degrees farther south (SFS). This concords with the investigations of Connolly & Roughgarden (1998), who stated that the transitions marked by upwelling regions can cause differences in the recruitment of several species by interposing the effect of latitude. Connolly *et al*. (2001) also observed the influence of an upwelling zone, where a stronger offshore current flow may have transported the recruits from the intertidal zone to farther off the coast where food was more available.

The increase of juveniles was more seasonal in the southern region, i.e., the abundance of juveniles peaked from January to March. However, the percentage of recruits at this location did not differ from the other regions, and was consistently higher from January to June. Shoji *et al*. (2001) evaluated the effect of latitude during recruitment in fish, and observed the most prominent seasonal effects at higher latitudes. Terossi *et al* (2010) also observed greater seasonality in the reproduction of *Pagurus exilis* (Benedict, 1892) caught at higher latitudes. The most pronounced evidence of this variability is apparent from a comparison of the classical studies with the growing literature suggesting that, at some sites, recruitment rates largely determine adult distribution and abundance, and that recruitment rates may determine the strength of interspecific interactions (Connolly & Roughgarden 1998). The results presented here indicate that the upwelling and the latitudinal effect can lead to differences in the recruitment and population structure of *A. cribrarius*. In the location at lower latitude and affected by upwelling, recruitment was continuous and with similar intensity among the months; while in the intermediate and highest latitudes, the recruitment showed seasonal characteristics, occurring mainly during the occurrence of South Atlantic Central Water, which increases nutrient availability. Bauer & Rivera Vega (1992) found similar patterns of reproduction and recruitment in two sicyoniid shrimp species. Andrade *et al*. (2013) observed seasonal breeding in UBA, which also confirms the recruitment season in this region.

## 6. Conclusions

Regional characteristics such as an upwelling area may cause transitions in the population pattern, as observed by evaluating the abundance of demographic groups and the size of individuals. Local oceanographic conditions in different geographical areas can control the population patterns of *A. cribrarius*, such as population structure and juvenile recruitment, since the latitudinal gradient seems to exert a powerful effect on the period of recruitment, and the upwelling phenomenon affects the abundance and size of individuals.

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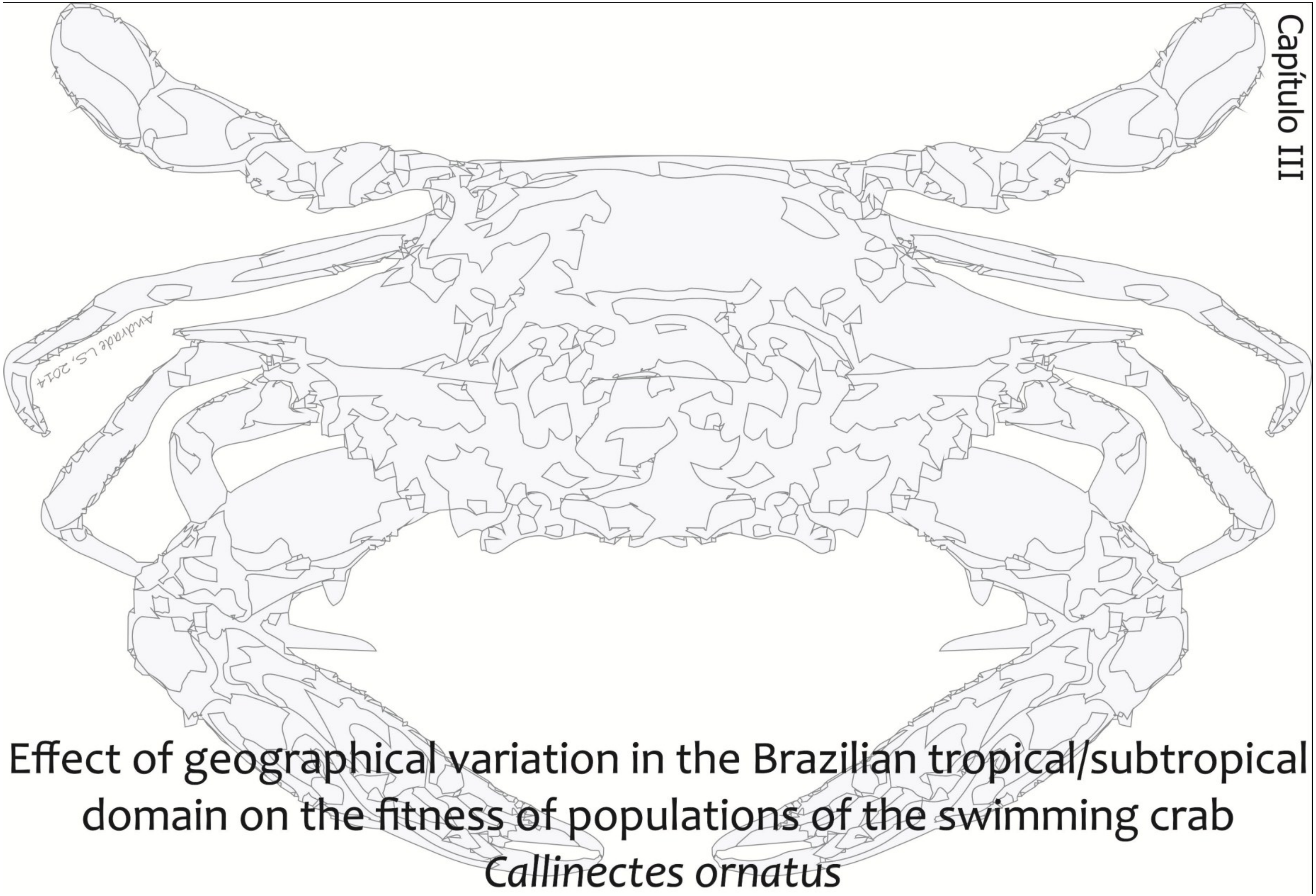
Capítulo III



# Effect of geographical variation in the Brazilian tropical/subtropical domain on the fitness of populations of the swimming crab *Callinectes ornatus*

## Abstract

The population structure and recruitment period of a species result from fitness to specific stimuli and selective pressures that may vary over time and space. The objective of this study was to evaluate the population patterns of the crab *C. ornatus* in three sites located in tropical and subtropical regions along the Brazilian coast in order to investigate whether geographical variations such as upwelling and high continental input affect the population fitness of the species. Thus, were sampled: Macaé (MAC, 22º47'S and 41º45'W), which is influenced by upwelling; Ubatuba (UBA, 23º27'S and 44°58'W), a region of faunal transition; and São Francisco do Sul (SFS, 26º08'S and 48º34 'W), which has a large estuary. The total abundance of specimens was similar in the three regions, as was the sex ratio. Juvenile recruitment was continuous throughout the study period. Larger individuals were found in the higher-latitude SFS region; however, independently of the maximum size attained by the species, the onset of sexual maturity did not change among the regions. These results suggest that *C. ornatus* is an r-strategist species, since it does not show major changes in population patterns due to environmental variations, and maximizes its effort to produce offspring.

**Keywords** Biological properties · Coastal inlets · Coastal upwelling · Latitudinal variations · Quantitative distribution

## 1. Introduction

One group of marine invertebrates that is most affected by shrimp fishing is the decapod crustaceans, which comprise 10% of the total bycatch (Silva et al., 2013). According to these authors, problems such as reduced juvenile recruitment and biomass of populations are among the strong impacts of harvesting unwanted species (bycatch). This may lead some species to respond functionally in their life-history patterns related to fitness, such as body growth, number of molts prior to reproduction, reproductive period, and number of clutches, among others (Childress, 1972). Porter et al. (1983) stated that the ability of genotypes to persist and increase from year to year (e.g., fitness) in cyclical environments of variable duration is likely to be most affected by the factors that influence rapid population growth.

Six species of brachyuran crabs of the genus *Callinectes* Stimpson, 1860 have been recorded on the Brazilian coast (Melo, 1996): *C. bocourti* Edwards, 1879; *C. danae* Smith, 1869; *C. exasperatus* (Gerstaecker, 1856); *C. larvatus* and *C. ornatus* Ordway, 1863; and *C. sapidus* Rathbun, 1896. In general, these species have wide geographic distributions, inhabiting ponds, mangroves, estuaries, and the open sea.

Studies of the abundance of Portunoidea from northern to southern Brazil have revealed the presence of *C. ornatus* at all sampling sites (Branco, 1991; Sankarankutty et al., 1991; Lavrado et al., 2000; Mantelatto and Fransozo, 2000; Almeida and Coelho, 2008; Nevis et al., 2009; Bertini et al., 2010). In some regions, this species is significantly more numerous than other crabs (Bertini et al., 2010; Junior et al., 2010; Andrade et al., unpublished results). Because of its ecological importance (Mantelatto and Fransozo, 1999), and abundance in the bycatch from shrimp fisheries (Di Beneditto et al., 2010), *C. ornatus* has received special attention regarding its juvenile development (Bolla Jr et al., 2008), growth (Keunecke et al., 2008), feeding habits (Mantelatto and Christofoletti, 2001; Branco et al., 2002), physiology (Garçon et al., 2007, 2009), reproduction (Mantelatto and Fransozo, 1997, 1999; Branco and Fracasso, 2004; Andrade et al., 2013a), and distribution and population structure (Negreiros-Fransozo and Fransozo, 1995; Fernandes et al., 2006; Andrade et al., 2013b).

The population structure and recruitment period of a species result from its fitness for specific stimuli and selective pressures, which may vary over time and space. Changes in environmental parameters such as water temperature, salinity, photoperiod and food availability may be critical factors that contribute to changes in population patterns. Our question here was: Do populations of *C. ornatus* from regions with different geographical characteristics show differences in abundance? Does the size of the individuals, as well as a reduction in the number of stages to reach sexual maturity, generated from the ecological fitness defines the same? Does the frequency of recruitment of young correspond better in larger populations? Using the abundance of demographic groups, sex ratio, size of individuals, period of entry of young into the population and estimation of sexual maturity, it may be possible to generate a set of tools that will help to answer these questions. This study describes the population patterns of the crab *C. ornatus* in three sites located in tropical and subtropical regions along the Brazilian coast (Boltovskoy, 1999) in order to investigate whether geographical variations such as upwelling and high continental input affect the population fitness of the species.

## 2. Materials and Methods

### 2.1 Study areas

The samples were performed in three localities of the Brazilian coast (Fig. 1): two in the southeast region (Macaé, state of Rio de Janeiro, 22º47'S and 41º45'W; Ubatuba, state of São Paulo, 23º 27'S and 44°58'W) and one in the southern region (São Francisco do Sul, state of Santa Catarina, 26º08'S and 48º34'W). The collections were made in four seasons, i.e., austral winter (July-September), spring (October-December), summer (January-March) and autumn (April-June).

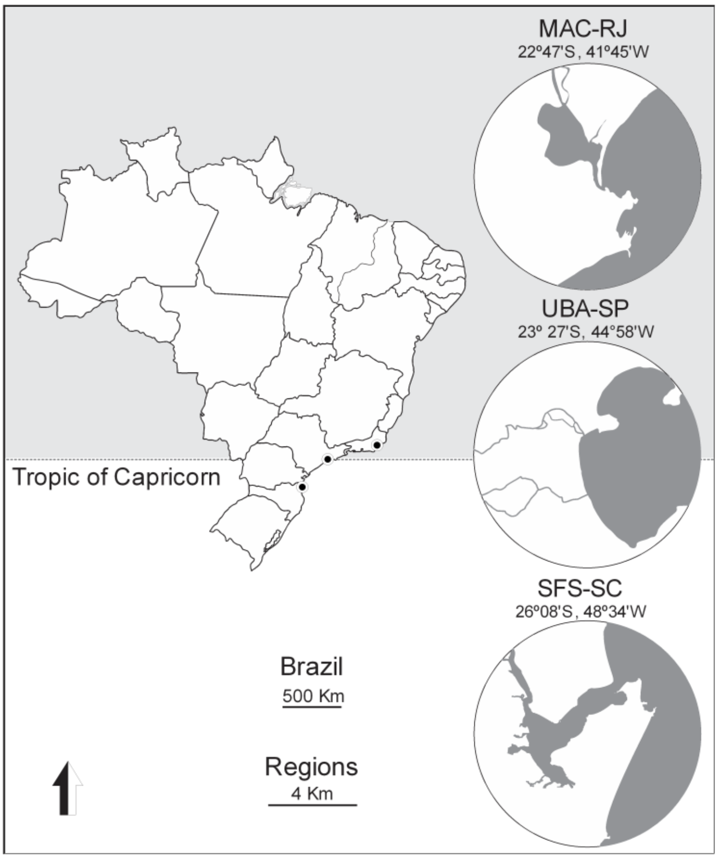


**Fig. 1.** Locations of three Brazilian regions where swimming crabs *Callinectes ornatus* were collected. MAC-RJ = Macaé, Rio de Janeiro; UBA-SP = Ubatuba, São Paulo; SFS-SC = São Francisco do Sul, Santa Catarina

Macaé (MAC) is near Cabo Frio, where coastal upwelling occurs due to atmospheric circulation associated with the center of the South Atlantic High Pressure. Three main water masses are present in the area. North of MAC, the warm (T > 20 °C) and saline (S > 36) Tropical Water (TW) covers the entire shelf, constituting the main stream of the Brazil Current. To the south, a mixture of TW and the South Atlantic Central Water (SACW), a relatively cold (< 20 °C) and less saline (< 36) water mass, is predominant. The third type is the Coastal Water (CW), a mixture of continental runoff and the Shelf Water (SW) (Castro-Filho and Miranda, 1998).

In the region of Ubatuba (UBA), along the northern coast of São Paulo, the Serra do Mar mountain range extends into the sea to form a jagged coastline with several semi-confined coves. The water-mass dynamics in UBA differs from MAC because the SACW thermal front remains at subsurface depths in summer, so that upwelling is rarely observed (Castro-Filho and Miranda, 1998). Drainages in this area are small and local, with limited exchange of water and sediment between the coastal region and the adjacent shelf (Mahiques, 1995). The UBA oceanographic system forms a transition between coastal waters and the continental shelf (Mahiques, 1995). The distribution of water masses has distinct patterns (Castro-Filho et al., 1987), since the dynamics of the local water masses depend mainly on the wind, currents and sea-floor relief.

The coast of São Francisco do Sul (SFS) is generally linear and houses the largest estuary complex in the state of Santa Catarina, with an area of 1567 km² (see Fig. 1). The region has been extensively modified by human activity due to repeated periods of dredging, especially in connection with the development of the estuary and the harbor area. The dredging of navigation channels to accommodate vessels of greater load displacement has affected sediment transport along the coast and may be responsible for serious erosion problems in the coastal zone (Angulo et al., 2006), which receives high continental inputs (Braga et al., 2006). In this region are four distinct water masses: Coastal Water, Shelf Water, Tropical Water and South Atlantic Central Water. The CW is closest to the coastal region and covers the study area; this water mass has low salinity (< 34) and temperatures varying seasonally between 19 and 28 ºC (Schettini et al., 1998).

## 2.2 Data collection

The samples were collected systematically from July 2010 through June 2011, covering 5-20 m depths. For each study region, one-hour hauls were conducted in three different areas for a total of three hours monthly. The swimming crabs were collected from a shrimp-fishing boat equipped with double-rig nets, with the following net specifications: length 10 m, mouth 4.5 m, body mesh diameter 20 mm, cod-end mesh diameter 18 mm. At the end of each trawl, the material was screened on the boat, packed in labeled plastic bags, and kept in a freezer until the specimens were examined.

## 2.3 Laboratory procedures

The specimens of *C. ornatus* were identified according to Melo (1996). The crabs were counted, sexed, and measured for maximum carapace width (MCW), disregarding the lateral teeth, using a caliper (0.01 mm). All specimens were grouped in the following demographic categories: adult males, adult females, and immatures (following the procedures adopted by Mantelatto and Fransozo, 1996).

## 2.4 Data analyses

The premises of normality and homoscedasticity were tested by the Levene's and Shapiro-Wilk tests (Shapiro and Wilk, 1965). The evaluation tests were adopted according to the response for the data normality A One-way permutational analysis of variance (PerMANOVA) (Anderson, 2001) was used to assess the significance of the abundance of total crabs, males, females and immature crabs between regions. Immature crabs also were used to assess the significance between semesters (percentage of recruits over the total number of individuals caught in each region, the same protocol followed by Connolly et al., 2001). From the maximum and minimum size of the crabs, size classes were defined following the method suggested by Sturges (1926), which was adapted to standardize the comparison of different demographic groups collected in the three regions.

Differences in the MCW of the demographic groups from MAC, UBA and SFS were compared using a Kruskal-Wallis test followed by Dunn’s multiple comparison test. To evaluate sexual dimorphism by size, in each region, the Mann-Whitney test was used. To estimate sexual maturity for males and females by region, the relative frequency (%) of adult size classes was plotted on graphs, which were fitted by the method of least squares to a sigmoid curve (as adopted by Andrade et al., 2013c). The slope and the intersections of curves for maturity estimated for males and females from three sites were tested with the aid of an analysis of covariance (ANCOVA), using a 95% confidence interval (Zar, 1996).

The Binomial test (Wilson and Hardy, 2002) was applied to samples from populations constituted by only two categories, here used to evaluate the proportion between males and females in each season and region.

## 3. Results

Of the 4442 individuals collected, 1314 were in MAC, 1535 in UBA and 1593 in SFS. The abundance of all individuals as well as those of males and females did not differ between regions (PerMANOVA, *Pseudo-F* = 0.24, $P < 0.01$) (Table 1). Juveniles were more abundance in MAC (59.7% of total individuals) and SFS (46.1% of total individuals), differing significantly from that found in UBA (26.4% of total individuals) (PerMANOVA, *Pseudo-F* = 12.22, $P < 0.00$). The number and size (maximum carapace width) of immature swimming crabs were grouped in 12 size classes of 5 mm each, starting with 13 mm (Fig. 2). Recruitment was continuous in all three regions; however, there was a higher percentage of juveniles during the period from January to June in SFS (PerMANOVA, *Pseudo-F* = 2.78, $P < 0.03$) (Fig. 2). In the other regions, this percentage did not differ ($P > 0.15$).

**Table 1** Number of individuals (N), size as carapace width (mm), and sex ratio of *Callinectes ornatus* collected in three regions of the Brazilian coast from July 2010 through June 2011. SD = standard deviation, Win = winter, Spr = spring, Sum = summer, Aut = autumn, M = males, F = females. Bold number = did not differ significantly, $P > 0.05$

| | Macaé | | | | Ubatuba | | | | São Francisco do Sul | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Season | Win | Spr | Sum | Aut | Win | Spr | Sum | Aut | Win | Spr | Sum | Aut |
| Abundance | 118 | 85 | 157 | 117 | 50 | 95 | 220 | 258 | 43 | 71 | 451 | 113 |
| Sex ratio | 1:0.5 | 1:0.6 | 1:0.7 | 1:0.5 | 1:0.3 | 1:0.5 | **1:0.9** | **1:0.9** | 1:0.4 | 1:0.4 | 1:1.2 | 1:0.5 |
| (M:F) | 1:0.6 | | | | 1:0.7 | | | | 1:0.7 | | | |
| Minimum | 16.6 | | | | 14.8 | | | | 14.7 | | | |
| Maximum | 71.9 | | | | 72.3 | | | | 79.1 | | | |
| Mean ± SD | 38.1 ± 9.0 | | | | 47.4 ± 9.6 | | | | 47.3 ± 10.6 | | | |

The results showed that crabs from MAC measured from 14.3 to 78.0 mm MCW. In UBA the size range was 14.8 - 80.0 mm MCW, while in SFS this range was 13.5 - 79.3 mm MCW (Table 1). Adult females collected from UBA (52.1 ± 5.0 mm MCW) and SFS (52.1 ± 5.2 mm MCW) were significantly larger (Kurskall-Wallis, *H* = 20.92, $P < 0.00$) than females from

MAC (50.0 ± 4.5 mm MCW) (Fig. 3a). The largest adult males were found in SFS (64.2 ± 6.1 mm MCW), and these were significantly larger (Kurskall-Wallis, $H$ = 93.86, $P$ < 0.00) than males from UBA (61.3 ± 6.5 mm MCW) and MAC (60.3 ± 6.8 mm MCW) (Fig. 3b). Following this pattern, also larger juveniles (Kurskall-Wallis, $H$ = 6.72, $P$ < 0.03) were found in SFS (36.8 ± 9.1 mm MCW) and UBA (36.2 ± 8.8 mm MCW) than in MAC (35.6 ± 8.0 mm MCW) (Fig. 3c).

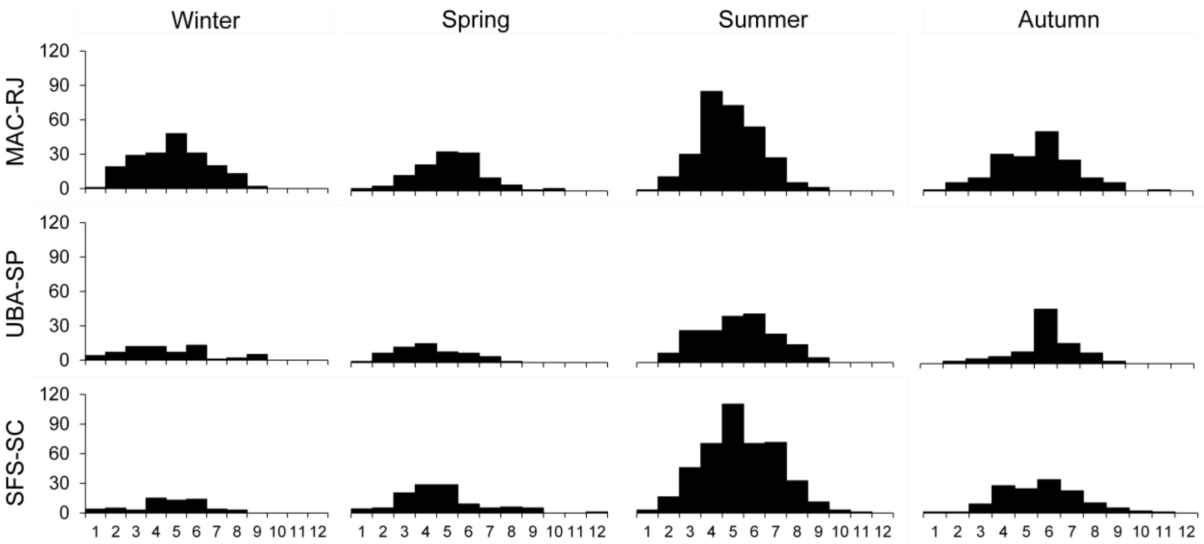


**Fig. 2.** Size-class frequency distribution for juveniles of *Callinectes ornatus* sampled from three regions of the Brazilian coast. The number and size (carapace width) of juvenile crabs were grouped in 12 size classes of 5 mm each, starting with 13 mm (Fig. 2). MAC-RJ = Macaé, Rio de Janeiro; UBA-SP = Ubatuba, São Paulo; SFS-SC = São Francisco do Sul, Santa Catarina

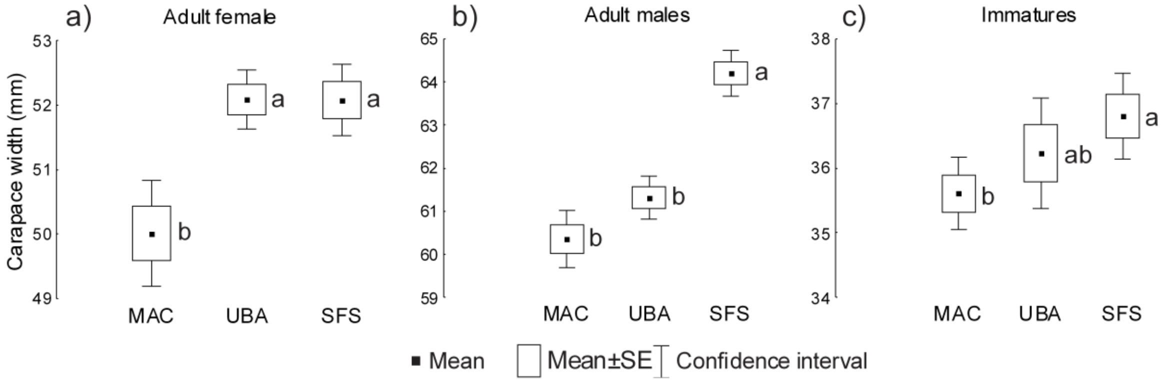


**Fig. 3.** Mean size, standard error and confidence interval for adult females (A), adult males (B), and juveniles (C) of *Callinectes ornatus* collected from July 2010 through June 2011 in three regions of the Brazilian coast. MAC = Macaé, Rio de Janeiro; UBA = Ubatuba, São Paulo; SFS = São Francisco do Sul, Santa Catarina. Same letter in common indicates no significant difference in post-hoc Dunn test ($P$ > 0.05)

Sexual dimorphism in size was evident in all three regions; males were significantly larger than females (Mann-Whitney, MAC: $Z$ = 12.88 and $P$ < 0.00, UBA: $Z$ = 14.92 and $P$ <0.00, SFS, $Z$ = 14.17 and $P$ < 0.00) (Table 1). The major difference in the mean sizes of males and females was observed at MAC, approximately 10 mm MCW. This difference decreased with increasing latitude, and was around 8 mm at UBA and 6 mm at SFS (Table 1).

The size at which males reached sexual maturity varied little among the regions (ANCOVA: $F$ = 0.37, $P$ = 0.70; $F$ = 0.07, $P$ = 0.93; respectively for males and females) (Fig. 4). The sex ratio favored males in all three regions. However, at SFS, during the summer, this ratio favored females at a ratio of 1.2 females to 1 male (Table 1).

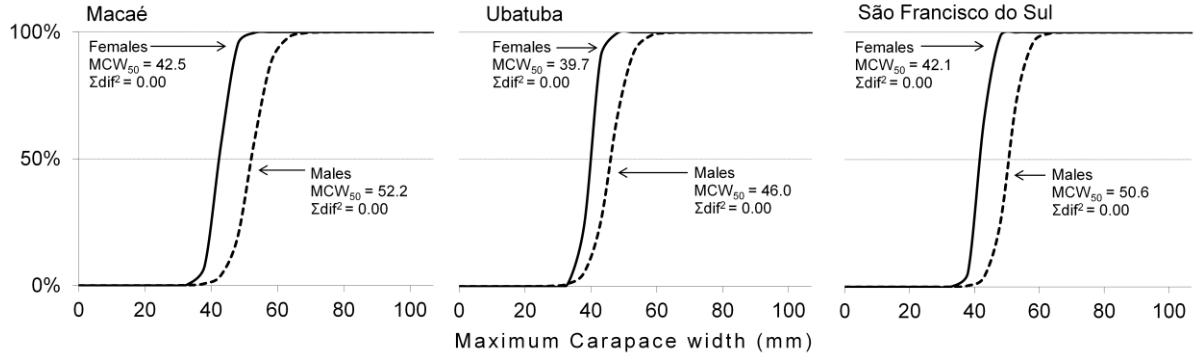


**Fig. 4.** Adjustment of the logistic equation indicating the maximum carapace width (MCW) for males and females of *Callinectes ornatus*, in which 50% of the crabs are mature according to analyses of gonadal development

## 4. Discussion

The ratio between reproductive and maintenance energy varies with the size of the organisms, their population density, and the support capacity of the environment (Du Preez and McLachlan, 1984). According to Pianka (1970), environments with low population density and selective pressure favor species with a high reproductive potential (“r-selection”), whereas high-density conditions favor organisms with a lower reproductive potential, but with a better capacity to utilize and compete for resources (“k-selection”). Pianka (1970) also stated that no organism is completely "r-selected" or completely "k-selected", but all must reach some compromise between the two extremes. Thus, r-strategist species are found in a variety of environments, have densities independent of the mortality rate, invest in many offspring, develop rapidly and do not reach large sizes.

Among other factors that will be discussed later, a similar abundance of C*. ornatus* found in such diverse environments provides evidence of "optimality theories" in the life history of the species. The total abundance of *C. ornatus* was very similar in all three localities. The entry of juveniles occurred throughout the entire study period, indicating a maintenance strategy of the species in the environment. The presence of large estuaries appeared to directly influence the size of individuals, since larger individuals were found in São Francisco do Sul, a region with large continental inputs. Because its population patterns did not change with wide environmental variations and in all situations the species maximized effort to produce offspring, results of this study seem to indicate that *C. ornatus* is an r-strategist.

The abundance of *C. ornatus* in the three study sites showed a wide adaptability of this species in habitats with very different environmental characteristics (Andrade et al., unpublished results), particularly regarding salinity, since SFS receives large inputs from the continent, reducing the local salinity (Figure 1). Congeners of *C. ornatus* such as *C. danae* and *C. sapidus* are abundant in regions of low salinity, since they are estuary-dependent (Hines, 1987, Carvalho and Couto, 2011). However, *C. ornatus* is not selective for the presence of estuaries to complete its life cycle, but may occasionally be found in less-saline areas (Melo 1996, Mantelatto and Fransozo, 1999). Brues (1927) recorded the presence of young *C. ornatus* at the Harvard Biological Station at Soledad, near Cienfuegos, Cuba, in the Rio Caonao at Belmonte, seven miles above the point where the river enters Cienfuegos Bay. Brues stated that when he found the specimens, they were in perfect health, with good locomotor activity and were aggressive when disturbed. This record can be explained by the study of Garçon et al. (2009) of the ionic and osmotic regulatory ability of *C. ornatus*. These authors observed a modest regulatory capacity in relation to salinity variations, in which alterations in membrane composition may favor acclimation to different biotopes. This regulatory capacity may be a selective factor in the permanence of the species.

Regardless of the region and latitude, the results of this study showed a continuous influx of juveniles in all three populations, which also shows that *C. ornatus* is an r-strategist. Branco and Fracasso (2004) in Santa Catarina, and Negreiros-Fransozo et al. (1999) and Andrade et al. (2013b) in São Paulo also reported continuous recruitment for the species, resulting from a reproductive pattern also continuous (Keunecke et al., 2012; Andrade et al., 2013a). However, this pattern along a latitudinal gradient is not a model for all Portunoidea. Andrade et al. (unpublished results) found seasonal recruitment of *Arenaeus cribrarius* (Lamarck, 1818) in higher latitudes (SFS, 26º08'S and 48°34'W) and continuous in lower latitudes (MAC, 22º47'S and 41º45'W), where also upwelling events were observed. Decapod species vary widely in their periods of reproduction and subsequent recruitment along the latitudinal gradient. Bauer and Rivera Vega (1992) compared reproductive patterns of *Sicyonia parri* (Burkenroad, 1934) and *Sicyonia laevigata* (Stimpson, 1871) with patterns of sicyoniid species from other latitudes, and suggested continuous breeding, at the population level, in tropical sicyoniids and an increase of restriction and seasonality in species from higher latitudes. Terossi et al. (2010) analyzed reproductive characteristics of two populations of the hermit crab *Pagurus exilis* (Benedict, 1892) in geographical extremes and found that at lower latitudes, reproduction occurs throughout the year, whereas at higher latitudes, reproduction only occurs in the spring and summer.

However, although the entry of juveniles was continuous in the three regions, the percentage of juveniles in relation to the total number of individuals was higher in MAC and SFS than in UBA. MAC is a region of cold water, rich in nutrients due to the presence of upwelling (De Leo and Pires-Vanin, 2006). These nutrients increase primary production and the availability of food for zooplankton, which in turn favors the abundance of predators and the establishment of large numbers of juveniles. Similarly, SFS also has nutrient-rich waters due to the presence of a large continental supply, which according to Braga et al. (2006) leads to high concentrations of organic matter. UBA also features favorable conditions for the establishment of juveniles at certain times of year, due to the entry of SACW in the region, which increases primary productivity during spring and early summer (Castro-Filho et al., 1987; Vega-Pérez, 1993). However, this region has a very jagged coastline, with many semi-confined coves. These coves (not sampled in this study) have sheltered areas with an abundance of young individuals, due to the predominance of fine sediments and higher levels of organic matter (Andrade et al., 2013b). According to Andrade et al. (2013b), besides the abundance of juveniles, large numbers of adult males may also be captured in this area.

**Table 2** Maximum carapace width (MCW) of species of the genus *Callinectes* found on the Brazilian coast. * = MCW including lateral spines, ** = MCW excluding lateral spines. Abbreviations for states: RJ, Rio de Janeiro; SP, São Paulo; SC, Santa Catarina

| Author | Region | Species | Results (mm) |
|---|---|---|---|
| Keunecke et al., 2008 | Guanabara Bay, RJ | *C. danae* | 120* |
| | | *C. ornatus* | 110* |
| Present study | Macaé, RJ | *C. ornatus* | 78** |
| Costa and Negreiros-Fransozo 1998 | Ubatuba, SP | *C. danae* | 102.7** |
| Present study | Ubatuba, SP | *C. ornatus* | 80** |
| Pereira et al., 2009 | Babytonga Bay, SC | *C. danae* | 110* |
| | | *C. sapidus* | 160* |
| Branco and Fracasso 2004 | Armação, SC | *C. ornatus* | 100* |
| Present study | São Francisco do Sul, SC | *C. ornatus* | 79.3** |

As well as recruitment, the sex ratio was also similar in the three regions. Differences in sex ratio along the latitudinal gradient are not commonly studied in Decapoda, and most often an unequal ratio can be explained by other factors, such as differential mortality between the sexes, behavior, and differential occupation of the habitat, among others (Wenner, 1972). In this study, the higher abundance of males than females can be explained by the reproductive behavior of females. According to Andrade et al. (2013a), egg-bearing females of *C. ornatus* migrate to outlying areas from the coast in order to maximize larval dispersal. Andrade et al. (2013b) found the greatest abundance of females at 25 m depth, whereas in the present study the sampling extended only to 20 m. Fernandes et al. (2006) also found a sex ratio favoring males; in this case, the sampled area had depths of less than 2 m, which further supports the findings of this study, since larger numbers of males can be found in areas up to 10 m deep (Andrade et al., 2013b).

Despite their abundance, the period of entry of recruits and sex ratio of *C. ornatus* was not affected by different hydrographic and geomorphological characteristics of the study regions. The mean size of individuals in each demographic group differed significantly among the regions. The lowest means for MCW males, females and juveniles were found in individuals from MAC, the lowest-latitude region. Sankarankutty et al. (1991), who assessed sizes of different species of *Callinectes* on the tropical Brazilian Northeast coast, found that *C. ornatus* was the smallest of its congeners, with 71 mm MCW (7 mm less than the largest individual found in MAC). This result appears to indicate that latitude can influence the size of this species. Another factor to be considered is the low temperature of the water at MAC, due to upwelling events (see De Leo and Pires-Vanin, 2006). Experimental studies by Cadman and Weinstein (1988) showed slower growth of *C. sapidus* at low temperatures.

**Table 3** Sexual maturity (SM) of species of the genus *Callinectes* found on the Brazilian coast. * = SM including lateral spines, ** = SM excluding lateral spines. Abbreviations for states: RJ = Rio de Janeiro; SP = São Paulo; SC = Santa Catarina

| Author | Region | Species | Results (mm) |
|---|---|---|---|
| Present study | Macaé, RJ | *C. ornatus* | 42.5 (F)**<br>52.2 (M)** |
| Keunecke et al., 2012 | Guanabara Bay, RJ | *C. danae* | 79.9 (F)* |
| | | *C. ornatus* | 67.4 (F)* |
| Present study | Ubatuba, SP | *C. ornatus* | 39.7 (F)**<br>46.0 (M)** |
| Present study | São Francisco do Sul, SC | *C. ornatus* | 42.1 (F)**<br>50.6 (M)** |
| Pereira et al., 2009 | Babytonga Bay, SC | *C. danae* | 71 (F)*<br>86 (M)* |
| | | *C. sapidus* | 102 (F)*<br>89 (M)* |
| Branco and Fracasso 2004 | Armação Itapocoroí, SC | *C. ornatus* | 52 (F)*<br>58 (M)* |

Environmental stimuli in different latitudes have been widely used in evaluating different characteristics of crustaceans, including body size. Lonsdale and Levinton (1985), working with copepods, and Castilho et al. (2007) with *Artemesia longinaris* Spence Bate, 1888, observed an increase in the size of individuals with the increase in latitude. These researchers attributed the differences in size to water temperature, in other words, smaller individuals were found in warmer water. According to Gonzalez-Rodriguez et al. (1992), upwelling regions in the western Atlantic have cold, nutrient-rich water mainly in summer, when the prevailing winds are north-east (NE). On the other hand, winter cold fronts reverse the upwelling and lead to a condition of seasonal subsidence, with a concentration of warm tropical waters (Gonzalez-Rodriguez et al., 1992). The Ubatuba region is also influenced by SACW during the summer (Castro and Miranda Filho, 1998), which may explain the change in size of the crabs between MAC and SFS.

Independent of the maximum size attained by the species, the onset of sexual maturity did not change. There was no significant difference in estimates of sexual maturity among the three regions; however, maturation was reached at smaller sizes in the UBA region. Studies by Teshima and Kanazawa (1983) showed that the onset of maturity is closely related to the nutritional value of the diet, which indicates that higher concentrations of triglycerides and phospholipids can accelerate gonadal maturation. This may explain the findings for individuals from Ubatuba. Being a region of faunistic transition, UBA presents a wide range of components that may be part of the diet of *C. ornatus* during their development (see Mantelatto and Christofoletti, 2001).

## 5. Conclusions

*Calinectes ornatus* has some characteristics that suggest it is an r-strategist species: (1) has the smallest maximum size among all congeners found in the same region (Table 2), as well as the smallest size at sexual maturity (Table 3); (2) invests in continuous production of offspring, independent of the region; (3) is estuary-independent, unlike all other congeners (Buchanan and Stoner, 1988); (4) has a high osmoregulatory capacity (Garçon et al., 2007), which makes it able to inhabit different environments. The results of this study revealed that the population structure, as well as the intensity of recruitment of juveniles of *C. ornatus*, did not change with geographical variations. Thus, this species of crab seems to balance benefits and costs to improve survival and future population fitness.

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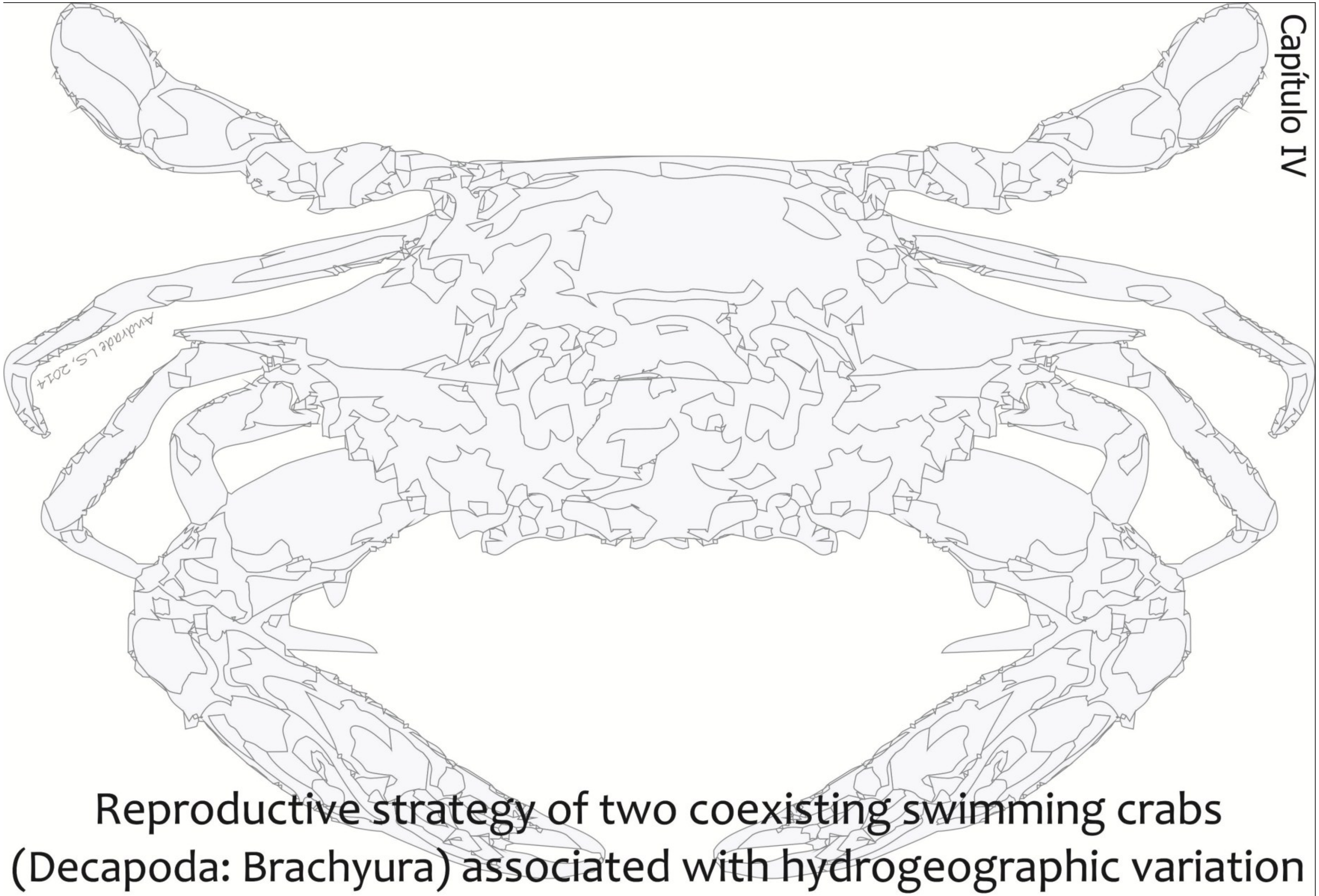
# Capítulo IV



# Reproductive strategy of two coexisting swimming crabs (Decapoda: Brachyura) associated with hydrogeographic variation

## Abstract

This study investigated adults of *Arenaues cribrarius* and *Callinectes ornatus* in three regions along the Brazilian coast characterized by the occurrence of contrasting natural phenomena, such as upwellings and continental input. Our purpose were assess the reproductive periodicity of both species; the relationship of environmental variables with reproductive females and males, and if portunids that coexist follow a pattern in their reproductive strategy. Samples were collected monthly during one year in Macaé, state of Rio de Janeiro (MAC, 22º47'S and 41º45'W), Ubatuba, São Paulo (UBA, 23º 27'S and 44°58'W) and São Francisco do Sul, Santa Catarina (SFS, 26º08'S and 48º34'W). The specimens were identified, counted and sexed. Females and males were classified according to the gonadal maturation stage, and were grouped as individuals with reproductive potential (mature gonads or breeding females) or not (rudimentary gonads or in development). Swimming crabs from regions of lower latitude present continuous reproduction with peaks of abundance on preceding periods of high nutrient availability for larvae. In the region of higher latitude the reproduction was seasonal. The periodicities of externalization of eggs as well as the temporal variation in the abundance of suitable breeding individuals are directed not only by physical characteristics of water and sediment, but also by the availability of food for the larvae and selective fishing pressure.

**Key-words** Coastal inlets · Coastal upwelling · Latitudinal variations · Portunid · Reproduction patterns

## 1. Introduction

Representatives of the family Portunidae (Rafinesque, 1815) are ecologically important because they present omnivorous feeding behavior and they are voracious predators, being considered modelers of the benthic habitat (Reigada and Negreiros-Fransozo 2001). Also constitute a group with economic importance for the extraction of their meat and by-products derived from their industrial processing (Haefner 1985; Rasheed and Mustaquim 2010), activities that are being conducted successfully in different countries since 1990 (Fao–Globefish 2007).

The reproductive strategy of a population is the main mechanism in ensuring the continuity of the species, making this knowledge extremely important for the maintenance of natural stocks (Andrade et al 2013a). Thus, understanding the reproductive patterns, as well as the knowledge of the factors that govern them, are valuable information for protecting these stocks, since that they support the administration of a controlled and sustainable fisheries, generating income to the population dependent on fishing and conserving the marine communities (Fransozo et al. 2012, Andrade et al 2013a).

Several studies on reproductive periodicity of portunids were conducted on the Brazilian coast (Branco and Masunari 2000; Pinheiro and Fransozo 2002; Pardal-Souza and Pinheiro 2013; Andrade et al. 2013a, b). Although most have reported continuous patterns of reproduction, it is possible to note that variations in natural or anthropogenic source environment can model these standards so that the population remains in balance (Hines 1989).

Changes in environmental parameters such as water temperature, salinity, photoperiod and food availability may be critical factors that contribute to changes in population patterns. In addition to environmental stimuli, selective pressures originated from different latitudes and upwelling zones have been widely used to generate hypotheses about changes in the population characteristics of crustaceans (Lonsdale and Levinton 1985; Connolly et al. 2001; Defeo and Cardoso 2004; Costa and Fransozo 2004; Castilho et al. 2007; Mantelatto et al. 2010). Our question was whether performance of geographical and hydrological characteristics of the environment would be supported by the results of a study of two species of swimming crabs in places characterized by the occurrence of contrasting natural phenomena.

Thus, this study investigated adults of *Arenaues cribrarius* (Lamarck, 1818) and *Callinectes ornatus* Ordway, 1863 in three regions of the Brazilian coast, in order to assess: a) the reproductive periodicity of both species; b) the relationship of environmental variables with reproductive females and males; c) if portunids that coexist follow a pattern in their reproductive strategy, regardless of the species.

## 2. Materials and Methods

### 2.1 Study areas

We analyzed three localities of the Brazilian coast (Fig. 1): two in the southeast region (Macaé, state of Rio de Janeiro, 22º47'S and 41º45'W; Ubatuba, state of São Paulo, 23º 27'S and 44°58'W) and one in the southern region (São Francisco do Sul, state of Santa Catarina, 26º08'S and 48º34'W). Macaé (MAC) is near Cabo Frio, where coastal upwelling occurs due to atmospheric circulation associated with the center of the South Atlantic High Pressure. This occurs intensively during the summer months, when prevailing winds blow from the E–NE quadrant and the South Atlantic Central Water (SACW) rises from 300 m depth and reaches the surface in a coastal current 5 km wide, bringing large amounts of nutrients up to the euphotic zone (Valentin et al. 1987). Three main water masses are present in the area. North of MAC, the warm (T > 20 °C) and saline (S > 36) Tropical Water (TW) covers the entire shelf, constituting the main stream of the Brazilian Current (BC). To the south, a mixture of TW and SACW, a relatively cold (< 20 °C) and less saline (< 36) water mass, is predominant. The third type is the Coastal Water, a mixture of continental runoff and the Shelf Water (SW) (Castro-Filho and Miranda 1998). During summer, the TW lay on the surface and the SACW on the bottom, creating a thermal front 15 km long that lasted for several days. In the winter, the SACW thermal front retreats to the outer shelf; and in the spring, due to favorable wind conditions, it is possible to observe the beginning of the progressive intrusion of the SACW (De Léo and Pires-Vanin 2006).

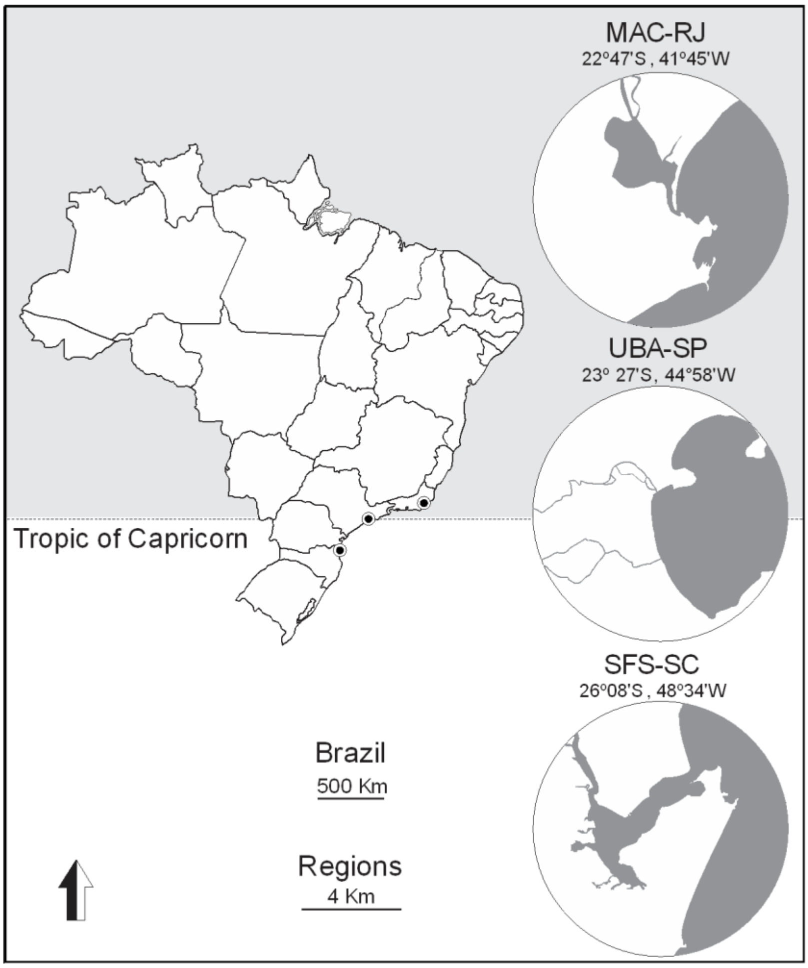


**Fig. 1.** Locations of three Brazilian regions where swimming crabs were collected. MAC-RJ = Macaé, Rio de Janeiro, UBA-SP = Ubatuba, São Paulo, SFS-SC = São Francisco do Sul, Santa Catarina. Scale applies to maps of regions

In the region of Ubatuba (UBA), along the northern coast of São Paulo state, the Serra do Mar mountain range extends into the sea to form a jagged coastline with several semi-confined coves. The water-mass dynamics in UBA differs from MAC because the SACW thermal front, observed during the summer months, remains at subsurface depths, so that upwelling is rarely observed (Castro-Filho and Miranda 1998). Drainages in this area are small and local, with limited exchange of water and sediment between the coastal region and the adjacent shelf (Mahiques 1995). The UBA oceanographic system forms a transition between coastal waters and the continental shelf (Mahiques 1995). The distribution of water masses has distinct patterns (Castro-Filho et al. 1987), since the dynamics of the local water masses depend mainly on the wind, currents and sea-floor relief. Thus, during winter when the SACW thermal front retreats to the outer shelf, warm bottom temperatures (20-22 °C) and low salinities (34-35) indicate the presence of the Coastal Water in the coastal zone. With the approach of spring, different water masses are observed, with lower salinity and higher temperatures. In the summer, the thermal front is located on the inner shelf, with bottom temperatures of 18°C (De Léo and Pires-Vanin 2006).

The coast of São Francisco do Sul (SFS) is generally linear and houses the largest estuarine complex in the state of Santa Catarina, with an area of 1567 km² (see Fig. 1). In this region are four distinct water masses: Coastal Water, Shelf Water, Tropical Water and South Atlantic Central Water. The Coastal Water is closest to the coastal region and covers the study area; this water mass has low salinity (< 34) and temperatures varying seasonally between 19 and 28 ºC in winter and summer, respectively (Schettini et al. 1998). The occurrence of the Coastal Water and its salinity depend on the continental contribution, extending tens of kilometers toward the ocean during periods of maximum rainfall (Emílsson 1961). The Shelf Water occurs farther from the coast and is formed by mixing of Coastal Water, SACW and TW, as well as through heating by solar radiation, with salinity > 35 and temperature between 20 and 23 ºC (Emílsson 1961). In this region, SACW is observed only in greater depths and during the spring and summer months (Schettini et al. 1998).

### 2.2 Data collection

The samples were collected systematically from July 2010 through June 2011, covering 5-20 m depths. For each study region, one-hour hauls were conducted in three different areas for a total of three hours monthly. The swimming crabs were collected from a shrimp-fishing boat equipped with double-rig nets, with the following net specifications: length 10 m, mouth 4.5 m, body mesh diameter 20 mm, cod-end mesh diameter 18 mm. At the end of each trawl, the material was screened on the boat, packed in labeled plastic bags, and kept in a freezer until the specimens were examined.

## 2.3 Environmental variables

For each 1-h haul, the bottom- and surface-water temperatures were recorded using a thermometer attached to a Nansen bottle. Sediment samples were collected in each season with a Van Veen grab, sampling a bottom area of 0.06 m2 in order to measure the organic-matter content (%) and grain size distribution of the sediments. All procedures with sediment samples followed those used by Mantelatto and Fransozo (1999), and sediment grain-size composition was analyzed according to Bertini and Fransozo (2004).

## 2.4 Laboratory procedures

The specimens of *A. cribrarius* and *C. ornatus* were identified according to Melo (1996). The swimming crabs were counted and sexed. Juveniles were checked by the adherence of the abdomen to the thoracic sternites and were not used in this study. Three developmental stages were defined in adult females (F) and males (M) (rudimentary = RU, developing = ED and developed = DE), following the procedures adopted by Andrade et al. (2013a, b). Females carrying fertilized eggs were termed breeding females (BF) and were grouped with FDE when used the term reproductive females. Reproductive males are those which have developed gonads (MDE).

## 2.5 Data analyses

To test the hypotheses that the abundance of reproductive females and males vary temporally differently in MAC, UBA and SFS, were conducted four nonmetric multidimensional scaling ordination – NMS (one by specie and sex), based on Euclidean distances, such that each month and site appeared in the ordination. The abundance data were tested for variation in the reproductive females (DE+BF) and males (MDE) of each site and season (Winter = July to September; Spring = October to December; Summer =

January to March; Autumn = April to June) using a Multiple Response Permutation Procedure (MRPP). The differentiation of reproductive individuals in this statistical analysis is represented by the variable *A*, which expresses the similarity of the samples of each season and region corrected by the similarity observed in randomly distributed samples (A = 0 indicates groups no more different than expected by chance; A = 1 indicates that all sites were identical within groups) (McCune and Grace 2002). Then, the pairwise comparison was used to determine differences between groups (*P*-value) (Hardman and McCune 2010).

A Principal Components Analysis (PCA) was used to identify the relationship between environmental variables and regions using a correlation matrix. Coordination scores were calculated using LC (linear combination), and the relative contribution of environmental variables on each region (axis) was determined from intra-set operations (McCune and Grace, 2002). The statistical significance of eigenvalues of the PCA axis was evaluated by randomization (Monte Carlo) tests, using 9999 randomized runs for each analysis. For determine which principal components would be utilized was used the hypothesis of randomness obtained from the Broken Stick model (Peres-Neto et al. 2005). Environmental variables with load component ≥ ±0.5 (given load for the axes) were retained in the description of the main components (Maliao et al. 2008).

Environmental factors extracted by PCA were used in a Canonical Correspondence Analysis (CCA) (Peck 2010). This test was used to order reproductive and non-reproductive males and females of *A. cribrarius* and *C. ornatus* based on linear relationships (Pearson correlation) between the patterns of redundant co-occurrence and environmental variables. Randomization tests (Monte Carlo test, 9999 permutations), which provided *P*-values, were performed to check the linear relationship between the response and explanatory matrices and the association between the first and second set of sample unit ordination scores in CCA analyses (ter Braak 1986). The p-values from these randomization tests indicate the confidence level associated with the predictions (Peck 2010). All multivariate analyses and group comparisons were performed using PC-ORD 6.0 software (Mccune and Mefford 2011).

## 3 Results

Were collected 3278 swimming crabs, with 761 *A. cribrarius* distributed in Macaé (423), Ubatuba (236) and São Francisco do Sul (102). Of the 2517 *C. ornatus*, 529 were collected in MAC, 1130 in UBA, and 858 in SFS (Table 1).

### 3.1 Spatio-temporal variation of reproductive females of *A. cribrarius*

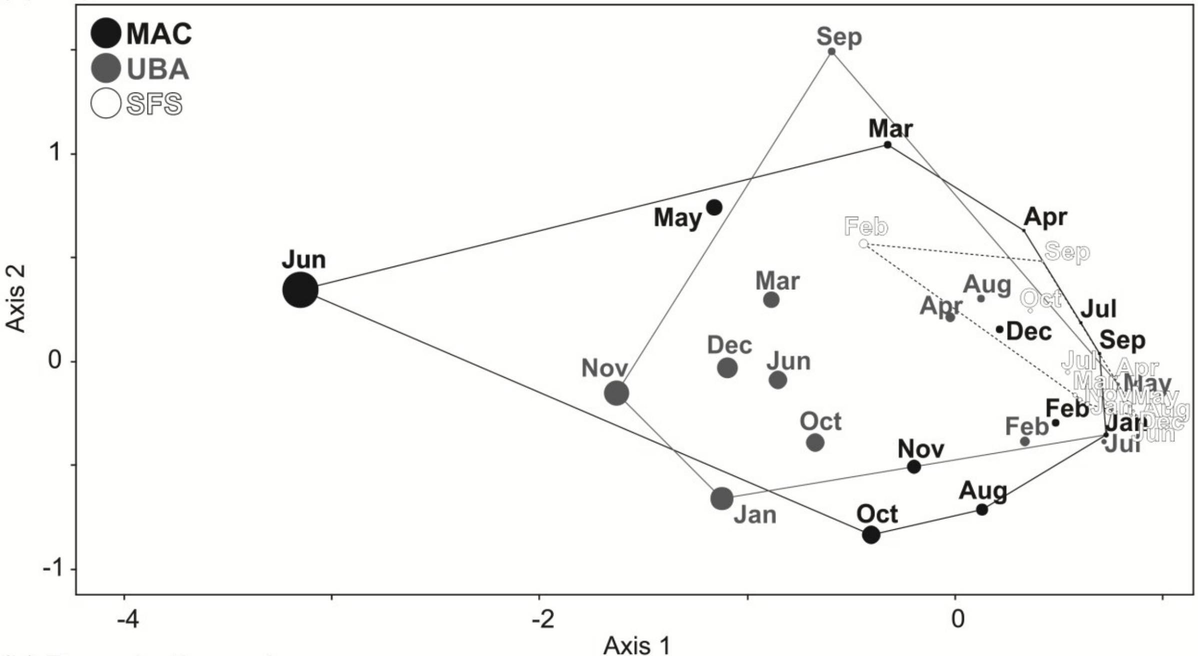
A two-dimensional solution best fit the data, with a final stress of 0.00194 and instability of 0.00000 after 80 iterations was found to *A. cribrarius*. The stress was less than expected by chance (Axis 1, $P$ = 0.004; Axis 2, $P$ = 0.019). The groups provided by NMS (Fig 2a) indicated a spatial variation on abundance of reproductive females of this specie, confirmed by MRPP, which showed significant differences in the abundance of reproductive females of *A. cribrarius* between MAC and SFS ($A$ = 0.098, $P$ < 0.023), and UBA and SFS ($A$ = 0.224, $P$ < 0.001). The groups from MAC and UBA showed greater similarity ($A$ = -0.005, $P$ > 0.440). The dispersion of months on the axes resulting from NMDS also showed that there was temporal variation of reproductive females in the regions (Fig 2a), but the MRPP identified significant variations only in UBA and SFS (Table 2).

Table 1. Abundance of *Arenaeus cribrarius* and *Callinectes ornatus*, according gonadal development, in three sites of Brazilian coast: Macaé (MAC), Ubatuba (UBA) and São Francisco do Sul (SFS)

| | Gonadal development | *A. cribrarius* | | | *C. ornatus* | | |
|---|---|---|---|---|---|---|---|
| | | MAC | UBA | SFS | MAC | UBA | SFS |
| Females | Rudimentary (FRU) | 31 | 26 | 28 | 28 | 23 | 77 |
| | Developing (FED) | 36 | 48 | 7 | 61 | 176 | 106 |
| | Developed (FDE) | 30 | 37 | 7 | 18 | 98 | 62 |
| | Breeding (BF) | 21 | 29 | 2 | 10 | 162 | 95 |
| Males | Rudimentary (MRU) | 69 | 16 | 33 | 77 | 68 | 122 |
| | Developing (MED) | 154 | 46 | 7 | 246 | 437 | 188 |
| | Developed (MDE) | 82 | 34 | 18 | 89 | 166 | 208 |

Evaluating only account the abundance by month of BF+DE, the population from MAC showed continuous reproduction, with abundance of reproductive females similar between months. In UBA the pattern of reproduction is also continuous, however gave peaks during the spring and summer. The population of SFS revealed seasonal reproduction (Fig. 3a).

(a) Reproductive females



(b) Reproductive males

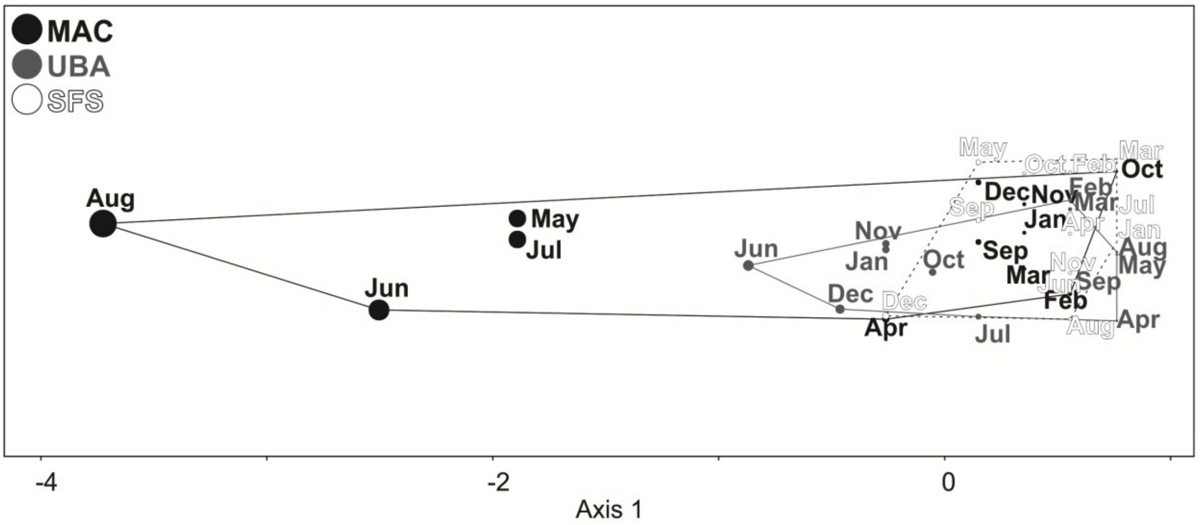


**Fig. 2.** Nonmetric multidimensional scaling of temporal (by month) and spatial variation on abundance of *Arenaeus cribrarius* from three sites of Brazilian coast. (a) Two-dimensional solution best fit the data found to reproductive females. (b) One-dimensional solution best fit the data found to reproductive males. MAC = Macaé; UBA = Ubatuba; SFS = São Francisco do Sul

### 3.2 Spatio-temporal variation of reproductive males of *A. cribrarius*

A one-dimensional solution best fit the data, with a final stress of 0.00006 and instability of 0.000001 after 29 iterations was found. The stress was less than expected by chance

(Axis 1, *P* < 0.004). The groups provided by NMS (Fig 2b) indicated a spatial variation on abundance of reproductive males of this specie, confirmed by MRPP, which showed significant differences between MAC and SFS (*A* = 0.056, *P* < 0.037). The groups from MAC and UBA showed greater similarity (*A* = 0.024, *P* > 0.154), as well as UBA and SFS (*A* = 0.009, *P* > 0.278). The dispersion of months on the axes resulting from NMS (Fig 2b) also showed that there was a greater temporal variation in MAC. The MRPP identified significant variations in MAC and UBA (Table 2).

Table 2. Multiple Response Permutation Procedure for abundance variation of reproductive females and males of *Arenaeus cribrarius* from Brazilian coast. *A* = within-group distance analyses. Win = winter, Spr = Spring, Sum = Summer, Aut = Autumn. UV = unable to verify. Bold values indicate significant difference

| Region | Seasons | Females | | Males | |
|---|---|---|---|---|---|
| | | *A* | *P* | *A* | *P* |
| Macaé | Win vs Spr | 0.184 | 0.152 | 0.116 | 0.159 |
| | Win vs Sum | 0.231 | 0.121 | 0.252 | **0.035** |
| | Win vs Aut | -0.012 | 0.357 | -0.156 | 0.860 |
| | Spr vs Sum | 0.167 | 0.153 | -0.061 | 0.660 |
| | Spr vs Aut | -0.040 | 0.666 | 0.254 | **0.034** |
| | Sum vs Aut | 0.150 | 0.064 | 0.354 | **0.026** |
| Ubatuba | Win vs Spr | 0.490 | **0.022** | 0.309 | **0.029** |
| | Win vs Sum | 0.252 | **0.041** | -0.101 | 0.783 |
| | Win vs Aut | 0.065 | 0.232 | -0.071 | 0.655 |
| | Spr vs Sum | -0.032 | 0.597 | 0.148 | 0.208 |
| | Spr vs Aut | 0.074 | 0.187 | 0.175 | 0.156 |
| | Sum vs Aut | -0.088 | 0.785 | 0.048 | 0.381 |
| São Francisco do Sul | Win vs Spr | -0.111 | 0.475 | -0.105 | 0.884 |
| | Win vs Sum | 0.177 | 0.165 | -0.093 | 0.635 |
| | Win vs Aut | UV | UV | -0.180 | 0.784 |
| | Spr vs Sum | -0.058 | 0.787 | 0.130 | 0.135 |
| | Spr vs Aut | 0.375 | 0.115 | -0.101 | 0.745 |
| | Sum vs Aut | 0.610 | **0.0217** | 0.112 | 0.206 |

### 3.3 Spatio-temporal variation of reproductive females of *C. ornatus*

When evaluating the spatio-temporal variation on abundance of reproductive females of *C. ornatus*, the NMS resulted in a one-dimensional solution, with a final stress of 0.00011 ($P = 0.004$) and instability of 0.000001 after 37 iterations. A spatial variation on abundance of reproductive females (Fig. 4a), was confirmed by MRPP, which showed significant differences between the regions (MAC vs UBA, $A = 0.115$, $P < 0.003$; UBA vs SFS, $A = 0.068$, $P < 0.02$), with greater similarity in groups from MAC and SFS ($A = -0.021$, $P > 0.716$). The dispersion of months on the axes resulting from NMS also showed that there was temporal variation of reproductive females in the regions (Fig 4a), but the MRPP identified significant variations only in MAC and UBA (Table 2).

Take into account the abundance by month of BF+DE, the population from MAC showed continuous reproduction, with greater abundance of reproductive females during spring. In UBA the pattern of reproduction is also continuous, with peaks during the summer and autumn. The population of SFS revealed seasonal reproduction with presence of breeding females since November to February (Fig. 3b).

### 3.4 Spatio-temporal variation of reproductive males of *C. ornatus*

When evaluating the spatio-temporal variation on abundance of reproductive males of *C. ornatus*, the NMS resulted in a one-dimensional solution, with a final stress of 0.00086 ($P = 0.004$) and instability of 0.000001 after 34 iterations. A spatial variation on abundance by region (Fig. 4b), was confirmed by MRPP, which showed significant differences between MAC and SFS ($A = 0.129$, $P < 0.007$), with greater similarity in groups from MAC vs UBA ($A = 0.032$, $P > 0.124$) and UBA vs SFS ($A = 0.016$, $P > 0.222$). The dispersion of months on the axes resulting from NMS (Fig. 4b) also showed that there was temporal variation of reproductive males in the regions, but the MRPP identified significant variations only in MAC (Table 3).

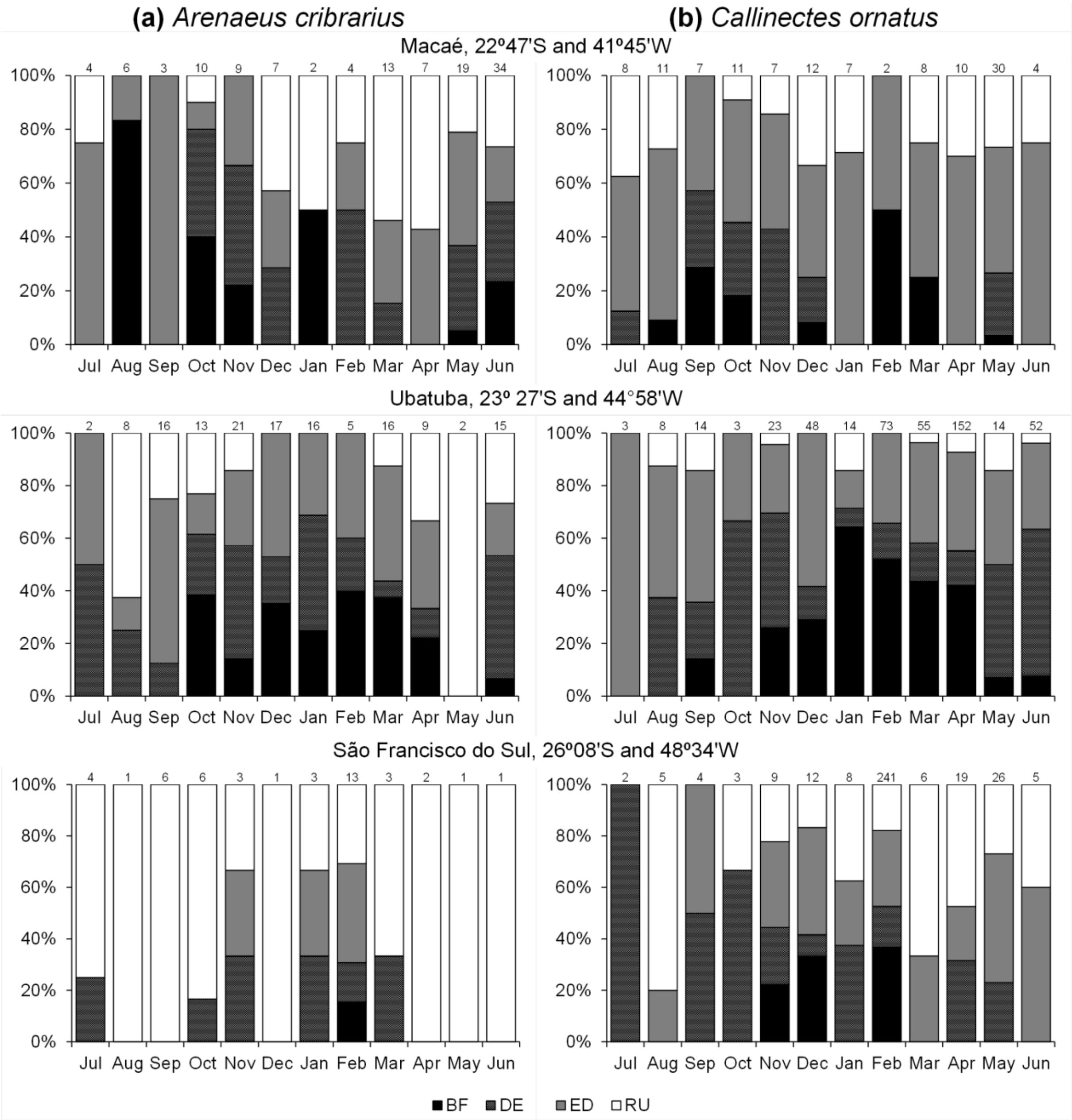
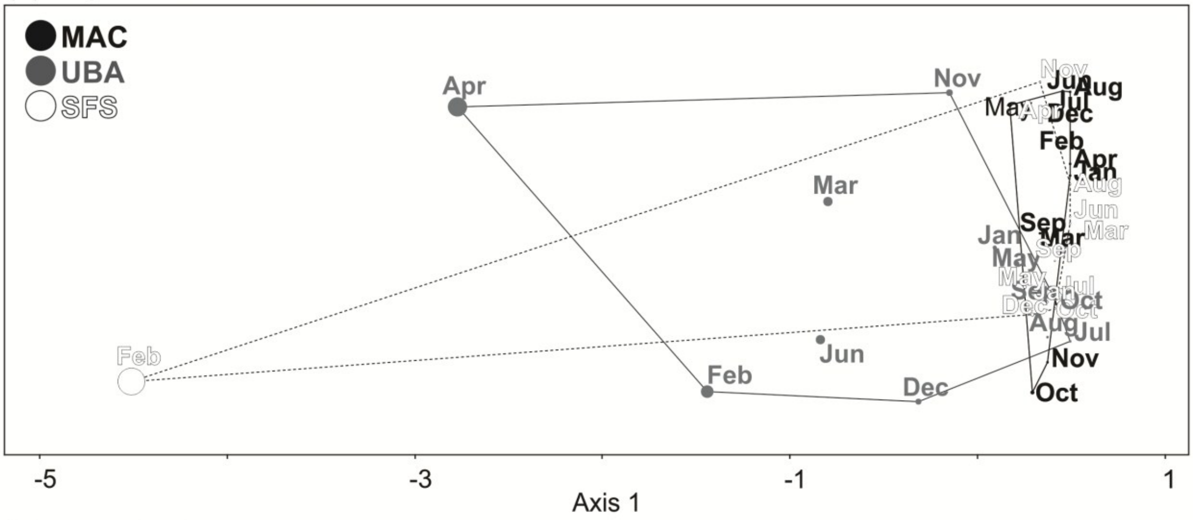


**Fig. 3.** Monthly variation in the proportion of adult females swimming crabs from three sites of Brazilian coast. (a) *Arenaeus cribrarius*; (b) *Callinectes ornatus*. Number above the bars = total of individuals. BF = breeding females; DE = developed gonads; ED = developing gonads; RU = rudimentary gonads

## 3.5 Sites, seasons and environmental variables

The environmental variables were reduced into two principal components (PC), explaining 75.65% of the total variation in the data set (Table 4). The Monte Carlo test indicated that the variation captured by regressions and PCA axes was significant (Table 4). PC1 was referred as temperature (negative correlation) and salinity (positive correlation), while PC2 was referred as organic matter and mean grain size, both correlating positively (Table 4). Thus, temperature and salinity appeared to be the main components driving MAC negative, and driving positively UBA and SFS from late spring to early autumn (Table 4).

(a) Reproductive females



(b) Reproductive males

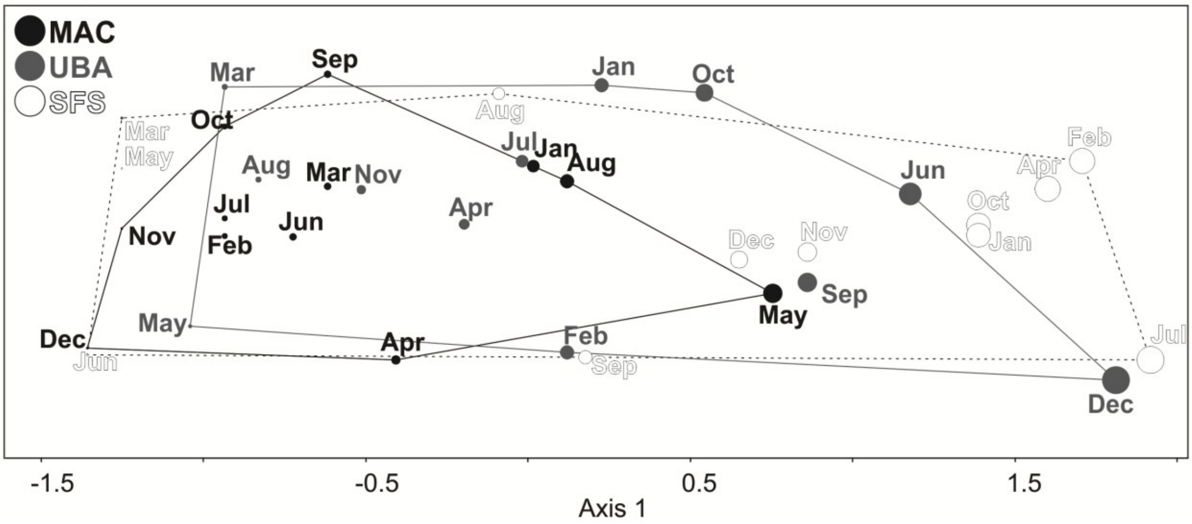


**Fig. 4.** Nonmetric multidimensional scaling of temporal (by month) and spatial variation on abundance of *Callinectes ornatus* from three sites of Brazilian coast. (a) One-dimensional solution best fit the data found to reproductive females. (b) One-dimensional solution best fit the data found to reproductive males. MAC = Macaé; UBA = Ubatuba; SFS = São Francisco do Sul

Table 3. Multiple Response Permutation Procedure for abundance variation of reproductive females and males of *Callinectes ornatus* from Brazilian coast. *A* = within-group distance analyses. Win = winter, Spr = Spring, Sum = Summer, Aut = Autumn. UV = unable to verify. Bold values indicate significant difference

| Region | Seasons | Females | | Males | |
|---|---|---|---|---|---|
| | | *A* | *P* | *A* | *P* |
| Macaé | Win vs Spr | 0.194 | 0.161 | 0.090 | 0.174 |
| | Win vs Sum | -0.101 | 0.891 | -0.209 | 0.873 |
| | Win vs Aut | 0.121 | 0.254 | -0.111 | 0.894 |
| | Spr vs Sum | 0.201 | **0.032** | 0.107 | 0.150 |
| | Spr vs Aut | 0.231 | 0.115 | 0.190 | **0.029** |
| | Sum vs Aut | -0.04 | 0.471 | -0.095 | 0.899 |
| Ubatuba | Win vs Spr | 0.071 | 0.262 | -0.095 | 0.770 |
| | Win vs Sum | 0.254 | **0.039** | -0.119 | 0.810 |
| | Win vs Aut | 0.159 | **0.050** | -0.127 | 0.819 |
| | Spr vs Sum | -0.016 | 0.511 | -0.016 | 0.542 |
| | Spr vs Aut | -0.016 | 0.539 | -0.143 | 0.922 |
| | Sum vs Aut | -0.127 | 0.845 | -0.103 | 0.795 |
| São Francisco do Sul | Win vs Spr | 0.048 | 0.258 | 0.079 | 0.254 |
| | Win vs Sum | -0.016 | 0.529 | -0.095 | 0.719 |
| | Win vs Aut | 0.008 | 0.477 | -0.016 | 0.509 |
| | Spr vs Sum | -0.000 | 0.461 | -0.003 | 0.381 |
| | Spr vs Aut | 0.014 | 0.370 | 0.095 | 0.241 |
| | Sum vs Aut | -0.053 | 0.599 | -0.105 | 0.675 |

### 3.6 Swimming crabs and environmental variables

The CCA revealed two axes of influence of environmental factors on the distribution of reproductive and non-reproductive groups of *A. cribrarius*, with a total of variance explained of 23.3%. The correlation between reproductive groups (FDE+BF and MDE) and the first canonical axis was statistically significant (Monte–Carlo test, $P < 0.007$), indicating a strong correspondence between these groups and the predictor variables. This axis explained 19.5% of the variance among groups according to environmental variables. Bottom temperature, bottom salinity and phi were the variables best correlated with axis 1, as well as FDE+BF and MDE (Table 5). Organic matter and non-reproductive males and females showed best correlation with axis 2 (Table 5). Reproductive females had a positive correlation with bottom temperature and organic matter, and a negative correlation with bottom salinity and phi. Reproductive males showed a greater abundance under the opposite conditions.

Table 4. Summary statistics of the axes generated by the Principal Components Analysis (PCA) and scores for correlation between environmental variables and three sites of Brazilian Coast. Coefficients greater than or equal to +0.4 or less than or equal to –0.4 are considered ecologically important (see Rakocinski et al.1996).

PCA of environmental variables

| | Axis 1 | Axis 2 |
|---|---|---|
| Bottom temperature (BT) | -0.797 | 0.469 |
| Surface temperature (ST) | -0.681 | 0.592 |
| Bottom salinity (BS) | 0.838 | 0.044 |
| Surface salinity (SS) | 0.857 | 0.043 |
| Organic matter (OM) | 0.572 | 0.720 |
| Mean grain size (PHI) | 0.568 | 0.513 |
| Eigenvalue | 3.182 | 53.041 |
| % of variance | 1.356 | 22.605 |

Scores for seasons of sites

| Season | MAC | | UBA | | SFS | |
|---|---|---|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Winter | 1.834 | -0.943 | -0.600 | -0.230 | 0.851 | -2.067 |
| | 1.730 | -0.798 | -0.390 | -1.626 | 0.912 | -2.422 |
| | 1.948 | -0.753 | -0.431 | -2.312 | 0.359 | -0.540 |
| Spring | 1.478 | 1.482 | -0.292 | 0.185 | 0.494 | 0.018 |
| | 2.470 | 1.126 | -1.785 | 1.433 | -0.707 | 0.371 |
| | 1.646 | 1.049 | -3.249 | -0.427 | -1.090 | 1.351 |
| Summer | 2.100 | 0.205 | -3.756 | 1.085 | -1.774 | 0.652 |
| | 2.143 | 0.658 | -2.644 | 1.757 | -3.024 | 0.454 |
| | 1.618 | 1.446 | -1.593 | -2.002 | -1.780 | -0.278 |
| Autumn | 2.087 | 1.363 | -2.820 | -0.258 | -0.511 | -0.018 |
| | 1.532 | 1.388 | -0.719 | -0.208 | 0.474 | -0.226 |
| | 2.098 | 0.908 | 0.265 | -1.167 | 1.121 | -0.655 |

For groups of *C. ornatus*, the CCA also revealed two axes of influence of environmental factors on the distribution of reproductive and non-reproductive individuals, with a total of variance explained of 23.2%. The correlation between reproductive males/females and the first canonical axis (18.0% of explanation) was statistically significant (Monte–Carlo test, P <

0.01), indicating a strong correspondence between these groups and the predictor variables. All environmental variables were best correlated with axis 1, as well as FDE+BF and MDE (Table 5). Reproductive females had a positive correlation with bottom temperature, and a negative correlation with bottom salinity, organic matter and phi. Reproductive males showed a greater abundance under the opposite conditions.

Table 5. Summary of results of Canonical Correspondence Analysis (CCA) for abundance of reproductive groups of *Arenaeus cribrarius* and *Callinectes ornatus* in three sites of Brazilian Coast. Coefficients greater than or equal to +0.4 or less than or equal to –0.4 are considered ecologically important (see Rakocinski et al.1996). Refer to table 1 for codes of each demographic group and to table 4 for environmental variables

| | *Arenaeus cribrarius* | | *Callinectes ornatus* | |
|---|---|---|---|---|
| Axis summary statistics | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Eigenvalue | 0.035 | 0.007 | 0.022 | 0.006 |
| % of variance explained | 19.5 | 3.7 | 18 | 5.2 |
| Final scores | | | | |
| BF+FDE | -1.810 | -0.776 | -2.082 | 0.091 |
| FED+FRU | -0.309 | 1.526 | 0.040 | -1.430 |
| MDE | 0.438 | -1.123 | 0.248 | 1.467 |
| MED+MRU | 1.016 | -0.120 | 0.840 | -0.147 |
| Intra-set correlations | | | | |
| BT | -0.791 | 0.021 | -0.806 | -0.432 |
| BS | 0.598 | -0.573 | 0.836 | -0.407 |
| OM | 0.255 | -0.896 | 0.526 | 0.168 |
| Phi | 0.593 | -0.522 | 0.618 | 0.108 |

Surface temperature and surface salinity were removed from the environmental matrix of CCA because it highly correlated with bottom temperature and bottom salinity, respectively, in the results of PCA (McCune and Grace 2002).

## 4. Discussion

The swimming crab *C. ornatus* was more abundant than *A. cribrarius* in the three regions studied. This difference indicates that, in relation to *A. cribrarius*, the species *C. ornatus* is less demanding on environmental conditions that govern their reproduction. However, both species suffered interference in the abundance of breeding individuals and their reproductive periodicity, when taken into consideration the geographical and hydrological characteristics on the collection environment. Apparently, low latitude sites, affected by upwelling or cold inlet of water during the summer, offer better conditions for the continuous reproduction of the studied species. This statement can be supported by the fact that in these regions, the food supply for larval recruitment is so high during the summer that ensures nutritive reserves in the sediment throughout the year (Mahiques et al. 2002; De Léo and Pires-Vanin 2006), whereas on the larger latitude site this amount may be reduced during colder months (Andrade et al, in press). According to Andrade et al (2013a), females of *A. cribrarius* adjusted their reproductive periodicity according to the quantity and quality of food for the larvae, this statement can be extended to other Portunoidea.

The higher abundance of *A. cribrarius* occurred in regions of higher latitude, with the presence of embryonated females and/or with gonads developed throughout the year. However, we observed a significant monthly variation in the number of reproductive females and males, showing peaks of reproduction. This variation can be explained by the fact that, usually, the South Atlantic Central Water penetrates these regions during a season, bringing loads of nutrients to the photic zone (Schettini et al 1998; Borzone et al 1999), which favors an increase in the abundance of embryoneted females due to good conditions for larval development. In São Francisco do Sul, the abundance of this species was reduced compared to the other locations, which may have contributed to a lower monthly variation of reproductive individuals. Andrade et al (in press) evaluated the juvenile recruitment of *A. cribrarius* in SFS and revealed that the percentage of young exceeded the adults by more than 80%. Considering the environmental preferences for reproductive females and males, detected by CCA, are characteristic of SACW, it becomes possible to suggest that adults of this species occupy more distant areas of the coast in the south of Brazil. According to Schettini et al (1998) this water mass reaches the Brazilian south coast only at great depths, not sampled in this study.

Consolidating this hypothesis, studies using acoustic telemetry stated that the species *A. cribrarius* is highly mobile (Guerra-Castro et al 2007). The authors of this study above also stated that some individuals prefer to move to more nutritious areas, though highly competitive, because the energy invested in displacement may be less than the cost of agonistic encounters. This migratory behavior was described by Andrade et al (2013b) for reproductive females of the species *C. ornatus*, which migrated to the most remote areas from the coast in order to enhance larval dispersion and the offspring survival rate. These implications help in the justification for the reproductive seasonality in the lower latitude region, since gonadal development is associated with the organic and minerals reserves that will contribute to improve the litter quality (Johnson 1980; Zara et al 2013). The juveniles of *A. cribrarius* from São Francisco do Sul were studied by Andrade et al (in press) and recruited only during the summer, reaching significantly smaller sizes than juveniles crabs from Macaé and Ubatuba. Thus, the coastal region of SFS seems not to be an area with great hydrological conditions for the establishment of *A. cribrarius*.

On the other hand, *C. ornatus* revealed to be better adapted to the hydrological and geographical variations, since it was collected with significant abundance in three distinct regions. However, the patterns of reproductive periodicity and variations in the percentage of males and females able to reproduce suffered changes over the sampled points. The greater abundance of reproductive females occurred in Ubatuba cove. This region belongs to an extremely cropped area with bays little disturbed by anthropic action, which favors the establishment of adults that intended to ensure the quality of the offspring in large numbers (Pires 1992). The environmental factors that act in this type of environment may interfere in many aspects of the reproductive biology of the local fauna, since they are under the strong influence of water masses, fluctuations in temperature, salinity and primary production (Andrade et al 2013c). Such fluctuations, which also occur extensively in Macaé, may be responsible for the greater variation in the abundance of reproductive individuals in these regions. In SFS the peak of reproductive females in February may be due to the pressure of fishing activity on the stocks of crabs in the region, which induces migration of females to sheltered areas (Branco and Fracasso 2004).

It is noteworthy that females and males of *C. ornatus* are governed by different environmental characteristics, as can be seen in the results of the CCA. In this species, the environmental requirements of breeding females induces a migration to deeper regions, whereas males are restricted to the coastal region, especially near estuaries (Andrade et al 2013c), which explains the greater abundance of males in SFS, which has great continental intake. Anyway, also as previously stated for *A. cribrarius*, the reproductive periodicity in the region of higher latitude is seasonal, while in MAC and UBA the reproduction proved to be continuous with peaks, due to the mass of water regimes.

The environmental stimulus and selective pressures from different latitudes and upwelling zones have been widely used as answers to the causes of differences in life history of the population of crustaceans, including reproductive periodicity. Terossi et al (2010) also observed greater seasonality in reproduction of *Pagurus exilis* (Benedict, 1892) captured in higher latitudes. Bauer and Rivera Vega (1992) studied the reproductive patterns of *Sicyonia parri* (Burkenroad, 1934) and *S. laevigata* Stimpson, 1871 and suggested continuous reproduction, on the population level, in tropical sicyoniids and increasing restriction and seasonality of breeding periods in Sicyonia species from higher latitudes. In all cases, the temperature was decisive in defining the reproductive pattern; however a number of factors expressed by hydrological variations in each region should be decisive in the reproductive characterization of populations.

## 6. Conclusion

The reproductive aspects of species of swimming crabs may be governed by hydrological and geographic phenomena. The periodicity of externalization of eggs as well as the temporal variation in the abundance of suitable breeding individuals, are directed not only by physical characteristics of water and sediment, but also by the availability of food for the larvae and selective fishing pressure. Thus, studies focusing on tracing conservationist strategies must take into account the environmental preferences of the species and environmental characteristics that set the biological patterns of the population.

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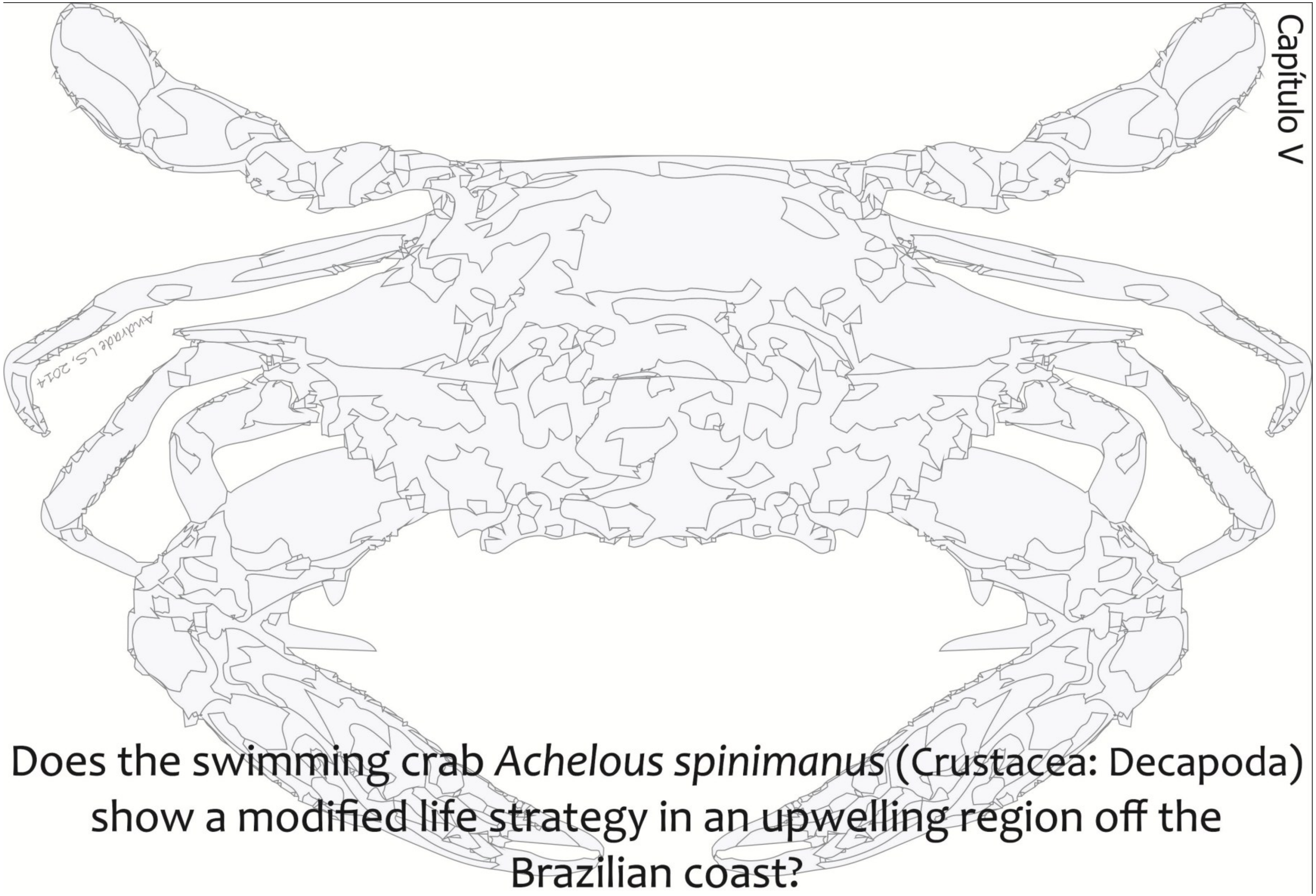
# Capítulo V



# Does the swimming crab *Achelous spinimanus* (Crustacea: Decapoda) show a modified life strategy in an upwelling region off the Brazilian coast?

## Abstract

Regions affected by upwelling show environmental characteristics that may change the population characteristics of species. This study investigated the temporal abundance, periods of reproduction and recruitment, sexual maturity, sex ratio and size of individuals of *A. spinimanus* in a region of the Brazilian coast affected by upwelling events. For this, the samples were collected monthly, during one year. The crabs were counted, sexed, measured for maximum carapace width (MCW), and four developmental stages were defined in males and females. Environmental variables including temperature, salinity, organic matter, mean grain size and chlorophyll a (µg.L$^{-1}$) were measured monthly. The Principal Components Analysis indicated that the environmental variables were strongly correlated with seasons, directly affecting the abundance of this species, which was high during summer and autumn. This same fact seems to have governed the periods of reproduction and recruitment assessed as seasonal in this study. Males and females did not differ in carapace width or in size at sexual maturity, estimated at 39.9 and 42.9 mm MCW, respectively. The present study revealed that the environmental conditions in this upwelling region may have induced the population of *A. spinimanus* to show distinct characteristics and behaviors in relation to populations from other parts of the Brazilian coast, since alterations linked to the periods of reproduction and recruitment, as well as the population structure and distribution, may reveal differentiated survival strategies of the species.

**Keywords** Geographic variations · Management plans · Migratory behavior · Portunidae · *Portunus* sp

## 1. Introduction

Portunid crabs are key elements of the trophic chain, and strongly influence the dynamics and organization of these environments (Bertini and Fransozo 2004). The crab *Achelous spinimanus* (Latreille, 1819), is widely distributed in the western Atlantic, occurring from the states of New Jersey (USA) to Rio Grande do Sul (Brazil), and is found at depths down to 90 m (Melo 1996). In Brazil, the species is often part of the bycatch of the fishery for shrimps such as *Farfantepenaeus brasiliensis* (Latreille, 1817), *F. paulensis* (Pérez Farfante, 1967), *Litopenaeus schmitti* (Burkenroad, 1936), and *Xiphopenaeus kroyeri* (Heller, 1862) (Vasconcellos and Gasalla 2001). This increases interest in the extraction of meat and byproducts for economic use, activities that have been successfully applied in different countries since the 1990s (Fao–Globefish 2007).

To reach a balance between shrimp fishing exploration and recovery of fishing stock, knowing the dynamics of the populations that are captured by the fishing gear used in different regions is a priority for the development of a proper management plan. Regions with unusual features such as upwelling may provide substantial enrichment for the marine communities, which show distribution patterns closely related to the dynamics of the water masses (De Léo and Pires-Vanin 2006). Species found in these regions may show different population characteristics (i. e., periods of reproduction and recruitment, size at which sexual maturity is reached, proportion of males and females, size of individuals, and others) in relation to other parts of the Brazilian coast.

In view of the marked oceanographic and biological differences found in regions affected by upwelling, such as low temperatures, high sedimentation rate and increased primary productivity (Mahiques et al. 2002; De Leo and Pires-Vanin 2006), the present study investigated the population characteristics of *A. spinimanus*, including temporal abundance, periods of reproduction and recruitment, sexual maturity estimation, and the proportion of sexes and sizes of individuals.

## 2. Material and Methods

The samples were collected systematically from July 2010 through June 2011, over depths of 5-20 m, in Macaé (22º47'S and 41º45'W) on the southeastern Brazilian coast (Fig. 1). Macaé is near Cabo Frio, where coastal upwelling occurs due to atmospheric circulation associated with the center of the South Atlantic High Pressure. Three main water masses are present in the region. North of Macaé, the warm (T > 20 °C) saline (S > 36) Tropical Water (TW) covers the entire shelf, constituting the main stream of the Brazilian Current (BC). To the south, a mixture of TW and the South Atlantic Central Water (SACW), a relatively cold (< 20 °C) and less saline (< 36) water mass, is predominant. The third type is the Coastal Water (CW), a mixture of continental runoff and the Shelf Water (SW) (Castro-Filho and Miranda 1998).

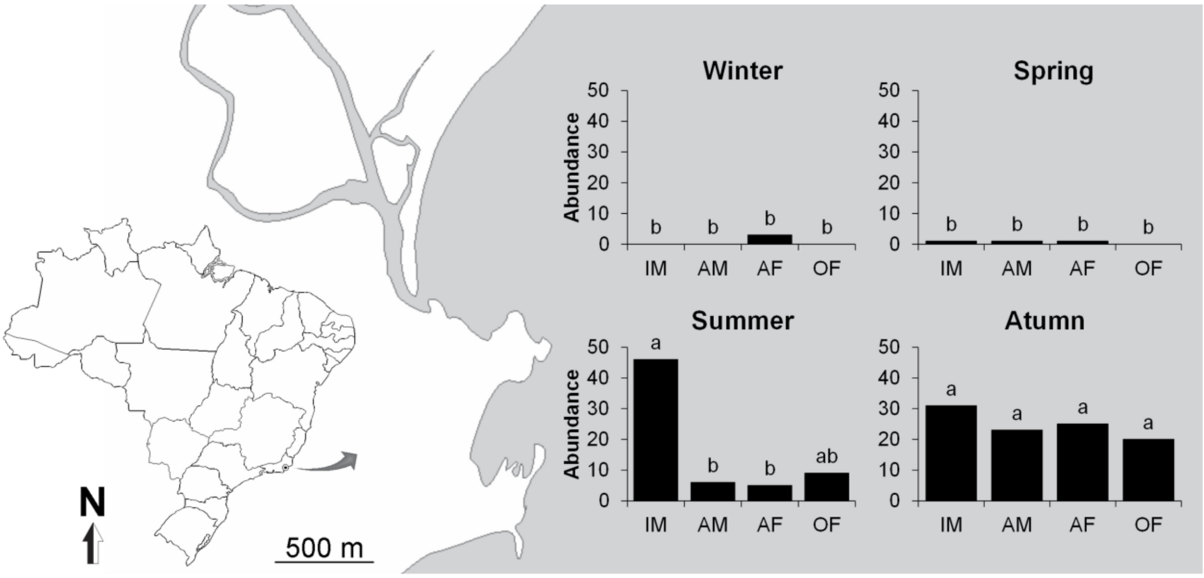


Fig. 1. Map of Macaé, an upwelling region off southeastern Brazil, showing the seasonal abundance of demographic groups of the swimming crab *Achelous spinimanus*. IM = immatures, AM = adult males, AF = adult females, OF = ovigerous females

### 2.1 Data collection

One-hour hauls were conducted for 3 h monthly, totaling 9 h and about 324,000 m$^2$ of catch per season. The crabs were collected from a shrimp-fishing boat equipped with double-rig nets, with the following net specifications: length 10 m, mouth 4.5 m, body mesh diameter 20 mm, cod-end mesh diameter 18 mm. At the end of each trawl, the material was screened on the boat, packed in labeled plastic bags, and kept in a freezer until the specimens were examined.

### 2.2 Laboratory procedures

The specimens of *A. spinimanus* were identified according to Melo (1996). The crabs were counted, sexed, and measured for maximum carapace width (MCW), disregarding the lateral teeth, using a caliper (0.01 mm). All individuals obtained were grouped in the following demographic categories: adult males, adult females, ovigerous females, and juveniles (checked by the adherence of the abdomen to the thoracic sternites and the stage of the gonads, which are thin and translucent in juveniles). Four developmental stages were defined in males and females (immature – IM, rudimentary – RU, developing – ED, and developed – DE). All procedures were adapted from Pinheiro and Fransozo (1998); Mantelatto and Fransozo (1999a).

### 2.3 Environmental variables

For each 1-h haul, the bottom- and surface-water temperatures were recorded using a thermometer attached to a Nansen bottle. Sediment samples were collected in each season with a Van Veen grab, sampling a bottom area of 0.06 $m^2$ in order to measure the organic-matter content (%) and grain size distribution of the sediments. In the laboratory, the sediment was dried at 70 °C for 72 h in an oven. The sediment organic-matter content (%) was obtained by ash-weighing: 3 aliquots of 10 g each per station were placed in porcelain crucibles and incinerated for 3 h at 500 °C. The samples were then re-weighed to calculate the organic-matter content. All these procedures followed those used by Mantelatto and Fransozo (1999b). Sediment grain-size composition was analyzed according to Bertini and Fransozo (2004). The sediment remaining after analysis of the organic matter was re-dried and passed through a series of sieves with graduated mesh sizes, following the Wentworth (1922) scale.

The concentration of chlorophyll a in the water (µg.L$^{-1}$) was determined according to Golterman et al. (1978). A volume of 2 L of water was filtered on a Millipore filter (AP40). The filter containing the material was preserved in the laboratory at a temperature of -20°C, until later determination through extraction. Chlorophyll a was extracted in a volume of 10 mL of cold acetone (90%), by grinding. The extracts in 10 mL were transferred to test tubes and placed in a refrigerator for approximately 12 h, protected from light. After this period, the samples were centrifuged for 10 min at 4900 rpm. Then, the absorbancies were measured at 663 and 750 nm, using a spectrophotometer.

### 2.4 Data analyses

Prerequisites of normality and homoscedasticity were tested and accepted by the routines of Kolmogorov-Smirnov ($P < 0.2$) and Levene ($P > 0.05$) tests. A Principal Components Analysis (PCA) was used to identify the relationship between environmental variables (bottom and surface temperature, bottom and surface salinity, organic matter, phi, and chlorophyll a) and seasons (Winter = July to September, Spring = October to December, Summer = January to March, Autumn = April to June). For determine which principal components would be utilized, the hypothesis of randomness obtained from the Broken Stick model (Jackson 1993) was used. Environmental variables with a component load ≥ ± 0.5 were retained in the description of the principal components (Maliao et al. 2008; McCune and Grace 2002).

The values for abundance of each demographic group were log-transformed, and a one-way analysis of variance (One-Way ANOVA) was carried out to assess differences among seasons ($\alpha = 0.05$) (Zar 1996). To determine the relationships between environmental variables and abundance of demographic groups, a redundancy analysis (RDA), a constrained ordination method, was used. For this, the data were normalized ($\log_{x+1}$), and the RDA constrained the ordination to a space defined by a linear combination of the measured environmental variables (Jongman et al. 1995). RDA allowed the selection of the variables that best described the distribution of the selected species. Randomization tests

(Monte Carlo test, 999 permutations), which provided p-values, were performed to check the validity axis of multivariate analysis (ter Braak 1986). P-values from these randomization tests indicate the level of confidence in the predictions (Peck 2010).

The Binomial test (Wilson and Hardy 2002) was applied to evaluate the proportion between males (M) and females (F) in each season. To represent the size of the population structure, from the maximum and minimum size of the crabs, size classes were defined following the method suggested by Sturges (1926). To evaluate sexual dimorphism by size, the Mann-Whitney test was used to compare sizes of adults. To estimate sexual maturity in each bay, the relative frequency (%) of adult size classes was plotted on graphs, which were fitted by the method of least squares to a sigmoid curve resulting from the logarithmic equation: $Y = 1/\left[1 + e^{r(MCW-MCW50)}\right]$, where *MCW50* is the carapace width at which 50% of individuals attain sexual maturity, and *r* is the curve slope (Vazzoler 1996). The matrices for frequency of immature and adult crabs by size classes, of males and females, were compared using the Mantel test (distance measure by Sørensen index). This test allows a comparison of the patterns of response redundancy in two structurally related matrices, and an evaluation of the similarity between them. In this test, a low p value indicated that the observed association between the matrices was statistically unusually high, leading us to reject the null hypothesis of no relationship between matrices (Legendre et al. 2005), indicating that there is some association in the patterns of redundancy within these two datasets. The randomization was evaluated by Monte Carlo test (999 permutations) (Peck 2010). All multivariate analyses were performed using PC-ORD (version 6, McCune and Mefford 2011).

The reproductive period was determined by the presence of females with developed gonads and ovigerous females (Rasheed and Mustaquim 2010). The presence of immatures in each season was used to estimate the recruitment period.

## 3. Results

The environmental factors analyzed varied widely. During the summer months, concentrations of chlorophyll a were high, and the widest differences between bottom and surface temperatures were measured (Table 1). The PCA indicated that the environmental variables were strongly correlated with seasons (Monte Carlo test, $P < 0.00$). The seven environmental variables were reduced to four principal components (PC), which explained 80.07% of the total variation in the data set. Organic matter was the only variable that correlated with PC1, which explained 36.46% of the variation. The variable with the highest correlation with the axis was bottom salinity (Spearman rank correlation = 0.69) (Table 2).

Table 1. Descriptive values (mean ± standard deviation) of the environmental variables recorded from July 2010 through June 2011 off Macaé, southeastern Brazilian coast. Winter = July to September; Spring = October to December; Summer = January to March; Autumn = April to June. OM = organic matter; PHI = mean grain size; ST = surface temperature; BT = bottom temperature; SS = surface salinity; BS = bottom salinity; Clo = chlorophyll a

| Environmental variables | Winter | Spring | Summer | Autumn |
|---|---|---|---|---|
| OM (%) | 4.51 ± 2.04 | 11.78 ± 1.05 | 9.33 ± 1.80 | 10.53 ± 2.90 |
| PHI | 3.47 ± 0.98 | 4.55 ± 0.60 | 4.18 ± 0.73 | 4.69 ± 0.14 |
| ST (°C) | 20.50 ± 0.54 | 23.75 ± 1.06 | 22.25 ± 0.89 | 23.75 ± 0.35 |
| BT (°C) | 19.58 ± 0.12 | 22.92 ± 0.47 | 19.50 ± 0.35 | 21.67 ± 0.12 |
| SS | 35.83 ± 0.23 | 36.33 ± 1.03 | 35.67 ± 1.54 | 36.92 ± 0.65 |
| BS | 37.00 ± 0.14 | 36.17 ± 0.85 | 36.50 ± 0.41 | 38.00 ± 0.41 |
| Clo ($\mu g.L^{-1}$) | 2.22 ± 0.66 | 1.42 ± 0.25 | 6.84 ± 5.71 | 0.66 ± 0.42 |

We analyzed a total of 171 specimens, including 30 adult males, 63 adult females (29 ovigerous) and 78 immature individuals. The highest abundance of individuals was found during summer and autumn, differing significantly from winter and spring (One-Way ANOVA: $F = 52.07$, $P < 0.00$) (Fig. 1). Among demographic groups, adult males ($F = 9.97$, $P < 0.00$) and females ($F = 18.82$, $P < 0.00$) were most abundant in autumn. Ovigerous females ($F = 53.96$, $P < 0.00$) and immatures ($F = 32.61$, $P < 0.00$) were most abundant in summer and autumn (Fig. 1).

Table 2. Summary statistics of the axes (PC) generated by the Principal Components Analysis for seven environmental variables measured during one year off Macaé, southeastern Brazilian coast.

| Environmental variables | Component | | | |
|---|---|---|---|---|
| | PC1 | PC2 | PC3 | PC4 |
| Organic matter (OM) | **-0.53** | -0.09 | -0.18 | 0.20 |
| Bottom salinity (BS) | -0.02 | **0.69** | -0.06 | -0.33 |
| Surface salinity (SS) | 0.14 | **0.54** | **-0.58** | 0.36 |
| Chlorophyll a (Clo) | 0.33 | -0.39 | **-0.58** | -0.15 |
| Mean grain size (PHI) | -0.44 | -0.18 | **-0.52** | -0.35 |
| Surface temperature (ST) | -0.46 | 0.00 | 0.01 | **0.57** |
| Bottom temperature (BT) | -0.42 | 0.15 | 0.10 | **-0.50** |
| Percent variance explained (Total = 80.07) | 36.46 | 20.19 | 12.96 | 10.46 |

Table 3. Summary of Results of Redundancy Analysis (RDA) for demographic groups of *Achelous spinimanus* in an upwelling region off southeastern Brazil. Bold values denote those variables that were considered to be biologically meaningful for that RDA axis. (i.e. ≥ 0.4; Rakocinski et al. 1996)

| | Axis | | Permutation test |
|---|---|---|---|
| | RDA1 | RDA2 | |
| Eigenvalue (total inertia = 0.26) | 0.15 | 0.10 | 0.02 |
| Cumulative % variation explained | 28.6 | 48.0 | |
| Species-predictor correlation | 0.70 | 0.81 | 0.03 |
| Immatures (IM) | **0.78** | **0.44** | |
| Adult males (AM) | 0.21 | -0.39 | |
| Adult Females (AF) | 0.28 | **-0.44** | |
| Ovigerous Females (OF) | **0.46** | -0.29 | |
| Organic matter (OM) | -0.32 | 0.24 | |
| Mean grain size (Phi) | 0.27 | -0.29 | |
| Surface Temperature (ST) | 0.28 | **0.50** | |
| Bottom Temperature (BT) | **0.43** | -0.32 | |
| Surface Salinity (SS) | **0.59** | -0.00 | |
| Bottom Salinity (BS) | 0.21 | 0.14 | |
| Chlorophyll a (Clo) | **0.42** | 0.28 | |

The permutation test of RDA showed that the eigenvalue observed for the first axis (RDA1) was significant, indicating that the patterns of association were identified (Table 3). This permutation also revealed that the variation observed between the embedded scores and the scores in the space of the response variable was significant, suggesting that the environmental variables explain part of the variation (Table 2). The first two RDA axes represented 48% of the variation in the abundance of the demographic groups of *A. spinimanus* (Fig. 2). The correlation between the environmental variables and the ordination axis showed that the surface and bottom temperature, surface salinity and chlorophyll a all showed positive relationships to the distribution of the demographic groups. According to the resulting correlation, these variables were the most important to explain the temporal distribution of the demographic groups of *A. spinimanus*. Immature individuals was the demographic group that showed the best correlation with the variables (Table 2), and similarly to the ovigerous females, were positively associated with the variables that affected axis 1 (Fig. 2).

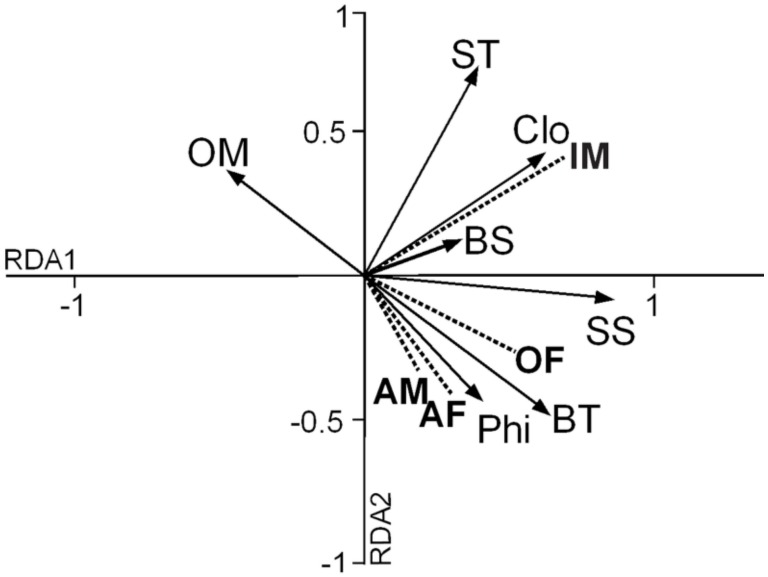


Fig. 2. Biplot of the redundancy analysis (RDA) of variations in environmental variables (indicated by solid arrows) of demographic groups of the swimming crab *Achelous spinimanus* (indicated by dashed arrows). Refer to Table 2 for codes of each demographic group and environmental variables

The reproductive period was clearly revealed as seasonal, with a peak of females with developed gonads and ovigerous females during autumn (Fig. 3a). Males with developed gonads were present in summer, but were more abundant during autumn (Fig. 3b). Immature individuals were rarely found in spring, and peaked in abundance in summer and autumn, also indicating seasonal recruitment (Fig. 4).

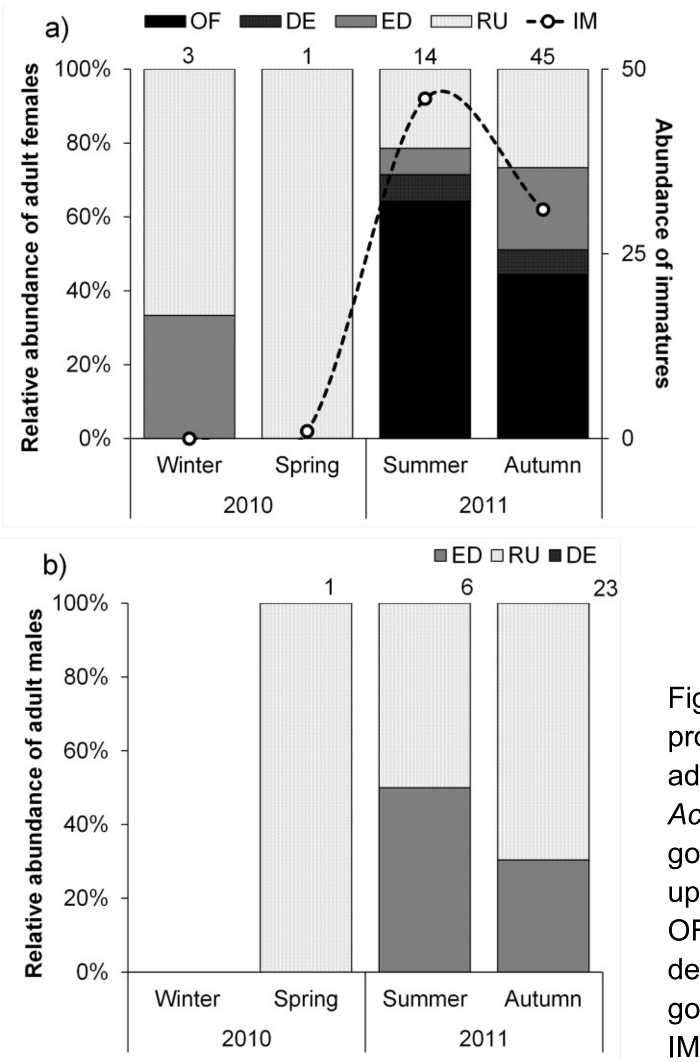


Fig. 3. Seasonal variation in the proportion of **(a)** adult females and **(b)** adult males of the swimming crab *Achelous spinimanus* in different gonadal stages from Macaé, an upwelling region off southeastern Brazil. OF = ovigerous females, DE = developed gonads, ED = developing gonads, RU = rudimentary gonads, and IM = immatures

The sex ratio favored females during the period of study (0.7M:1.0F, $P < 0.00$). This difference was apparent in each season, but was significant only during summer (1M: 2.7F, $P < 0.01$). The swimming crabs were separated in 10 size classes with an interval of 10 mm. The smallest individual caught was a male, in autumn, measuring 16.4 mm MCW. The largest was an ovigerous female, in summer, measuring 98.6 mm MCW (Fig. 4). The MCW showed no sexual dimorphism, i.e., there was no significant difference between the sizes of males and females (Mann-Whitney: $Z = 0.34$, $P > 0.74$). The sizes at which males and females reached sexual maturity (39.9 mm MCW and 42.9 mm MCW, respectively) also did not differ between the sexes (Fig. 5); the matrices of males and females, with frequency of juveniles and adults by size class, were strongly associated (Mantel: $r = 0.84$, $P < 0.00$). The smallest ovigerous female measured 52.8 mm MCW.

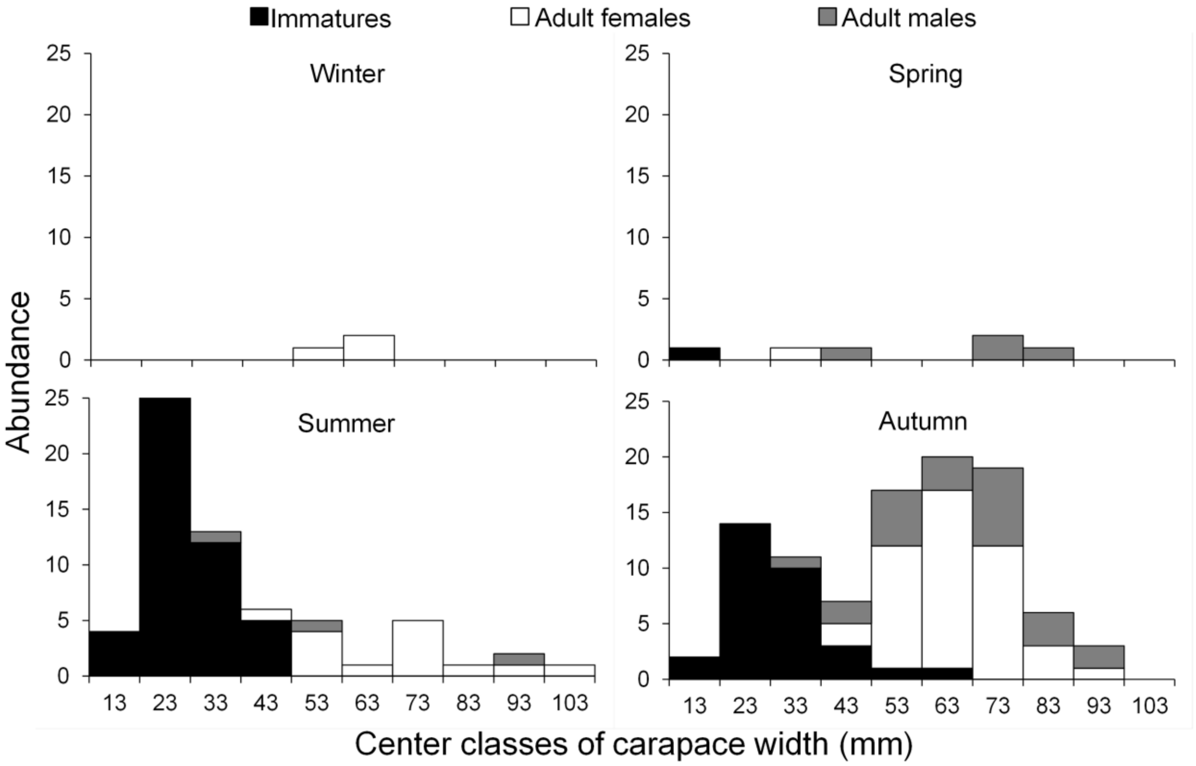


Fig. 4. Size-frequency distribution for demographic groups and recruitment period of the swimming crab *Achelous spinimanus* collected off Macaé, an upwelling region on the southeastern Brazilian coast. Intervals of 10 mm size class were used, ranging from 8 |— 18 mm (class 1) to 98 |— 108 mm (class 10)

## 4. Discussion

The oscillation of the environmental variables along the seasons of the year seemed to directly influence the abundance of *A. spinimanus*, which was high in summer and autumn. Surface and bottom temperature, surface salinity and chlorophyll a were determinant factors for the increase in the species' abundance, dictating the seasonality of the reproduction and recruitment periods. In contrast to many other portunoid species (see Mantelatto and Fransozo 1999a; Andrade et al. 2013b), sexual dimorphism was not apparent when considering carapace width; the estimated sizes at which males and females reach sexual maturity were similar.

The variations of temperature, salinity and chlorophyll a concentration are characteristic of the water masses present in the region. According to Valentin et al. (1987), during winter, the SACW remains farther off the coast, while the Tropical Water (TW) remains at the subsurface, indicating subsidence, i.e., the opposite of upwelling. During summer, the SACW remains at the subsurface, resulting in a typical seasonal thermocline; the intrusion of this water mass with the temperature increase at the surface is a characteristic of coastal upwelling (Valentin et al. 1987). Thus, the exchange between the upwelling and the subsidence, and the inconstant entry of inorganic nutrients influence the structure of the biological communities in the area (De Léo and Pires-Vanin 2006). In addition to these variables, the organic matter may also vary significantly among seasons; however, this factor is not necessarily a precursor of *A. spinimanus* abundance*,* as ordinated by RDA.

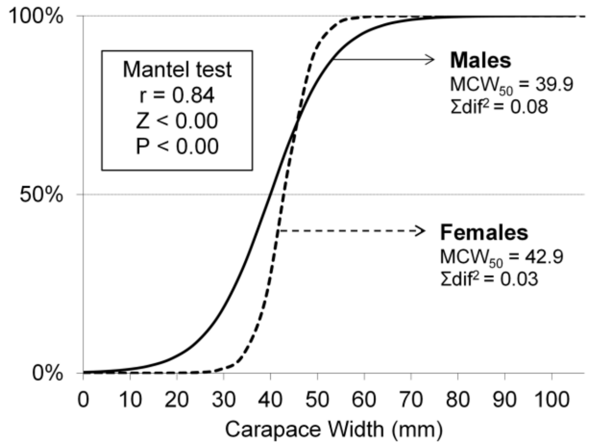


Fig. 5. Adjustment of the logistic equation indicating the maximum carapace width (MCW) for males and females of the swimming crab *Achelous spinimanus*, in which 50% of the crabs are mature according to the analyses of gonadal development. The result of the Mantel test refers to the comparative matrices (frequency per size class of adult and immature females vs. adult and immature males) and the similarity between them

Our results revealed that the crabs showed a marked tendency to move out of the system at the beginning of winter and spring. Their return seems to begin with the upwelling, when there is an increase in productivity and consequently the availability of food sources (De Leo and Pires Vanin 2006) for juveniles of *A. spinimanus*. This suggestion of a migratory process is based on the correlation of the demographic groups with temperature, salinity and chlorophyll a, the last being mainly associated with the abundance of juveniles. These variables are most influenced by the dynamics of water masses present in these regions (Valentin et al. 1987; Gonzalez-Rodriguez et al. 1992; Moser and Gianesella-Galvão 1997; Carbonel and Valentin 1999; Sumida 2005; De Leo and Pires Vanin 2006).

When assessing the composition and abundance of brachyurans off the Ubatuba coast, which is located approximately 500 Km from Macaé, Bertini and Fransozo (2004) recorded opposite abundance patterns to those found in the present study. During winter and spring, when the abundance of *A. spinimanus* at Macaé was very low, the abundances of this species in Ubatuba were highest, up to ten times more than during summer and autumn in the same region. These results suggest that the species migrates in order to find ideal conditions for reproduction and the development of juveniles. Therefore, during the period of upwelling (summer and the following autumn), the Macaé region may provide more food (see De Leo and Pires-Vanin 2006) for maintenance of the population of *A. spinimanus* that is found in Ubatuba during winter and spring.

The migration of other species of *Portunus* Weber, 1795, which includes species now identified as *Achelous* De Haan, 1833 (see Mantelatto et al. 2007) was reported in Western Australia by Potter et al. (1983), for the blue manna crab *P. pelagicus* (Linnaeus, 1758); and Edgar (1990), who studied the interaction of *P. pelagicus* with seagrass beds. Liu et al. (2009), in a study of the genetic differentiation between populations of *P. trituberculatus* (Miers, 1876) in the East China Sea, also reported migratory behavior. De Leo and Pires Vanin (2006) also suggested the occurrence of a migratory process for *A. spinicarpus* (Stimpson, 1971), stating that the species is cold-water related. The same authors also indicated *A. spinimanus* as a warm water-related species. According to Liu et al. (2009), *P. trituberculatus* is a long-distance migrator and a repeat spawner. These authors stated that in the spring, *P. trituberculatus* migrates to spawning grounds to reproduce, and after spawning, the adults migrate gradually from coastal water to deep water to feed, and then move to the southeast to overwinter in the late autumn and winter (Liu et al. 2009).

The reproductive pattern found in this study suggests, in concordance with a possible migratory behavior, a seasonal reproduction period during summer and autumn. Less than 500 Km to the south, Santos and Negreiros-Fransozo (1999) established the presence of ovigerous females of *A. spinimanus* in all months of their study, during two years of collection. A continuous presence of ovigerous females was also reported by Branco et al. (2002) in southern Brazil. The results presented in this study, however, are more similar to those in the northern hemisphere. In the southeastern United States, ovigerous females of this species were caught during the warmest months of the year (Dudley and Judy 1971; Camp et al. 1977; Olsen 1978).

The reproductive period of species with a broad geographic distribution may vary along a latitudinal gradient, and is affected by many environmental factors (Sastry 1983). The reproductive pattern observed here represents a physiological adjustment of reproduction to the local upwelling conditions. The reproduction of marine invertebrates must be highly synchronized with the environmental conditions to assure success. For *Arenaeus cribrarius* (Lamarck, 1818), Andrade et al. (2013b) observed a reproductive adjustment of the population to the new conditions imposed by the environment. Our results indicate that synchronization of the reproduction occurs in the months of higher availability of food for the larvae, i.e. during summer and autumn. Therefore, the juvenile recruitment is also seasonal, occurring in this same period.

The migration to coastal waters during larval dispersal, suggested for *A. spinimanus*, seem to be the opposite of what occurs in species of the genus *Callinectes*. Andrade et al. (2013a) reported that the adult females of *Callinectes ornatus* Ordway 1863 migrate to areas farther from the coast to disperse their larvae, and few males with developed gonads follow them, remaining near the coast. In the present study, males with developed gonads were not caught, probably because they copulated in deeper waters and remained there. Males with rudimentary gonads and gonads under development were found in low numbers, perhaps waiting to copulate with migratory females. Individuals of this species have been found in depths from 6 (Branco et al. 2002) to 40 m (Bertini and Fransozo 2004; De Leo and

Pires Vanin 2006). The areas sampled in this study included depths from 5 to 20 m, so males with developed gonads might not have been caught because they were in deeper water.

The sex ratio favorable to females during the entire study period might also be explained by migration of *A. spinimanus* to coastal waters during reproduction. As mentioned above, the males may remain in deeper areas, whereas only females migrate for larval dispersal. Another result found in this study, which might be a consequence of migratory behavior, is the absence of sexual dimorphism in carapace width. In this case, we believe that only the smallest males, those that could not copulate in areas farthest from the coast and migrated with the females, were caught.

The estimated size at which *A. spinimanus* reaches sexual maturity did not differ between males and females, in agreement with the findings of Santos and Negreiros-Fransozo (1996). Other congeners also show a similar maturation size between sexes, including *A. sanguinolentus* (Herbst, 1783) (Rasheed and Mustaquim 2010) and *A. spinicarpus* (Pardal-Souza and Pinheiro 2013). Assuming that the mortality rate tends to be higher among adults, and that the sooner an animal reaches sexual maturity the sooner it can produce descendants (Haefner 1990), the elimination of a molting cycle must be yet another adaptation strategy of *A. spinimanus.*

## 6. Conclusions

The present study revealed that the environmental conditions in this upwelling region may have induced the population of *A. spinimanus* to show distinct characteristics and behaviors in relation to populations from other parts of the Brazilian coast. Alterations linked to the periods of reproduction and recruitment, as well as the population structure and distribution, may reveal differentiated survival strategies of the species. The results of this study also raise the question of whether the patterns shown by other species with broad geographic distributions may also be altered by local geographic variations. Answers to these questions would improve understanding of local effects on the dynamics and distribution of populations, which is essential for the development of differentiated management plans.

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# Considerações finais

As características ambientais de Macaé e São Francisco do Sul divergem, em sua maioria, das características ambientais de Ubatuba, fato que reforça os relatos de que este local é uma região de transição geográfica e, consequentemente, transição faunística. Apesar das alterações em padrões populacionais ocorrerem conforme a variação da latitude, esse padrão não pode ser considerado uma tendência universal, uma vez que diferentes latitudes podem ser interrompidas por regiões que recebem interferência de fenômenos naturais, como o verificado neste estudo. Áreas afetadas por fenômenos distintos, independente da latitude, promovem mudanças abruptas na composição e abundância de espécies-chave da taxocenose de Portunoidea, sendo que as exigências ambientais de cada espécie governarão padrões em sua dinâmica populacional.

Ao avaliar a abundância e composição das espécies ao longo dos pontos amostrados, foi verificado que não havia possibilidade de se comparar as populações de todas as espécies das regiões, devido à inexpressividade de indivíduos em determinadas áreas. Foi o que ocorreu com *Achelous spinimanus* e *Callinectes danae*, por exemplo. O primeiro foi abundante em Macaé, todavia indivíduos dessa espécie foram raramente encontrados em Ubatuba e São Francisco do Sul. Com *C. danae* ocorreu o contrário, encontrada com abundância em São Francisco do Sul, a espécie foi coletada ocasionalmente em Macaé e Ubatuba. Já as espécies *Arenaeus cribrarius* e *Callinectes ornatus* foram abundantes, nas três regiões, com poucas variações, que refletiram em variações dos padrões populacionais. Acontecimentos como este estruturam comunidades locais de forma diferenciada, refletindo em modificações dos índices ecológicos da assembleia em questão.

Assim, o conceito de que o sucesso de determinada população depende das exigências peculiares de cada uma e das condições oferecidas pelo ambiente é confirmado. A espécie *A. cribrarius*, encontrada com expressivo número em toda área de estudo, mas não semelhante, é exemplo disso. As populações de *A. cribrarius* do sudeste e sul do Brasil apresentaram características diferentes em termos de largura da carapaça, proporção sexual e período de recrutamento (sazonal em maior latitude). Os indivíduos maiores foram encontrados em locais com águas mais frias, como encontrado em Macaé e Ubatuba, apontando que para essa espécie, locais de menor latitude, afetados por massa de águas frias, possuem melhores condições para o estabelecimento contínuo de juvenis.

Ao avaliar a estrutura da população e o recrutamento juvenil de *C. ornatus* verificou-se que a abundância total de espécimes foi muito semelhante entre as áreas estudadas, e o recrutamento de jovens ocorreu de forma contínua ao longo do ano nas três localidades. Tais resultados revelaram grande capacidade de adaptação dessa espécie em habitats com características ambientais muito distintas, mas as variações locais ainda podem influenciar no tamanho dos indivíduos, que foram significativamente maiores em São Francisco do Sul. Tal variação de tamanhos pode ser justificada pelo paradigma latitudinal, que prevê maiores indivíduos em maiores latitudes, e é intensamente relatado para diversas espécies de crustáceos.

Comparando a biologia reprodutiva dessas duas espécies, ambas sofreram interferência na abundância de indivíduos reprodutores e na sua periodicidade reprodutiva, quando levado em consideração as características geográficas e hidrológicas do ambiente. Aparentemente, locais de menor latitude, afetados pela ressurgência ou com entrada de massa de água rica em nutrientes, oferecem melhores condições para a reprodução contínua das espécies estudadas, uma vez que o suprimento alimentar para as larvas são mais elevados. A sazonalidade reprodutiva foi evidente em São Francisco do Sul, onde as condições ambientais da região parecem não ser favoráveis à permanência de indivíduos reprodutores durante o ano todo.

Além dos indivíduos reprodutores, a espécie *A. spinimanus* também parece optar por águas frias, uma vez que foi encontrado com abundância apenas em Macaé, durante os meses que compreenderam o verão e o outono. Neste período, a Água Central do Atlântico Sul ocasiona uma termoclina sazonal típica com afloramento junto à superfície, assinalando a ressurgência costeira, que traz condições ideais para eventos reprodutivos da espécie, que neste caso é sazonal.

Os resultados encontrados nesta tese permitem afirmar que as alterações vinculadas a períodos de reprodução e recrutamento, bem como à estrutura e distribuição das populações, podem revelar estratégias diferenciadas para permanência da espécie no ambiente. Estes ajustes podem modificar, ou não, a composição e estruturação de assembleias ao longo de um gradiente latitudinal interrompido por áreas distintas quanto às características hidrológicas e geográficas.