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

DISSERTAÇÃO DE MESTRADO

Crescimento e dinâmica reprodutiva do camarão-ferrinho *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea) no litoral norte do estado de São Paulo: síntese de cinco anos de estudo

Ana Elisa Bielert Lopes
Orientador: Prof. Dr. Antonio Leão Castilho
Coorientadora: Prof^{a}. Dra. Kátia Aparecida Nunes Hiroki

Botucatu, São Paulo
2017

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

Crescimento e dinâmica reprodutiva do camarão-ferrinho *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea) no litoral norte do estado de São Paulo: síntese de cinco anos de estudo

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

Aluna: Ana Elisa Bielert Lopes
Orientador: Prof. Dr. Antonio Leão Castilho
Coorientadora: Profª. Dra. Kátia Aparecida Nunes Hiroki

Botucatu, São Paulo
2017

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

Lopes, Ana Elisa Bielert.
Crescimento e dinâmica reprodutiva do camarão-ferrinho Rimapenaeus constrictus (Stimpson, 1874) (Penaeoidea) no litoral norte do estado de São Paulo : síntese de cinco anos de estudo / Ana Elisa Bielert Lopes. - Botucatu, 2017

Dissertação (mestrado) - Universidade Estadual Paulista "Júlio de Mesquita Filho", Instituto de Biociências de Botucatu
Orientador: Antonio Leão Castilho
Coorientador: Kátia Aparecida Nunes Hiroki
Capes: 20400004

1. Camarão - Reprodução. 2. Dinâmica populacional. 3. Copulação. 4. Estudos de coortes.

Palavras-chave: Conservação dos estoques; Coortes de recrutamento; Cópula; Razão sexual; Variação latitudinal.

Dedico esta dissertação aos meus pais, Kátia e Cleito, e ao meu irmão, Augusto, pelo apoio e amor incondicional durante toda a minha vida.

Agradecimentos

A Deus, pela oportunidade incrivelmente mágica da vida.

Ao meu orientador, Prof. Dr. Antonio Leão Castilho, por ter me recebido em seu laboratório e, ao acreditar na minha capacidade, me dar a valiosa oportunidade de cursar o mestrado, mesmo quando não havia mais vaga para nenhum aluno. Pelas horas de discussões, pelo enorme conhecimento compartilhado, pela paciência, conselhos e todo o tempo dedicado a mim nestes mais de dois anos para que eu realizasse um bom trabalho. Espero que venham mais alguns anos para que eu possa aprender muito mais com você. Muito obrigada Tony, acima de tudo, pela oportunidade e pela confiança em mim depositada!

À Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP – pela concessão da bolsa de estudos (processo nº 2015/13639-5) durante o período de mestrado.

Ao Programa BIOTA/FAPESP (processo nº 2010/50188-8), pelo financiamento do Projeto Temático "Crustáceos Decápodes: multidisciplinaridade na caracterização da biodiversidade marinha do Estado de São Paulo (taxonomia, espermiotaxonomia, biologia molecular e dinâmica populacional)" (e professores vinculados: Dr. Rogério Caetano da Costa, Dr. Fernando José Zara e Dr. Fernando Luis Medina Mantelatto), ao qual a presente dissertação está vinculada.

Às agências de fomento que apoiaram financeiramente as coletas das quais os dados aqui apresentados são provenientes: FAPESP (Biota, processo nº 98/07090-3; bolsas de estudo, processos nº: 97/12106-8 e 07/56733-5), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES / Ciências do Mar) (processo nº 23038.004310/2014-85) e Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (bolsas de pesquisa, processos nº PQ305919/2014-8 e PQ308653/2014-9).

Aos pescadores pela dedicação, responsabilidade e todo o conhecimento que tornou possível a realização das coletas e, consequentemente, deste estudo.

Aos alunos e ex-alunos do Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos (NEBECC), que participaram ativamente, se dedicaram e se esforçaram em cada coleta. Vocês foram imprescindíveis para a coleta dos dados analisados neste trabalho e, portanto, para a construção desta dissertação.

Ao Prof. Dr. Adilson Fransozo e à Prof.ª Dra. Maria Lúcia Negreiros Fransozo, por estarem sempre disponíveis a ajudar e compartilhar o seu amplo conhecimento. Pelos ensinamentos, conselhos e conversas, sempre muito agradáveis.

À minha querida orientadora de iniciação científica, atual coorientadora de mestrado e amiga, Profª. Dra. Kátia Hiroki, por ter me apresentado ao mundo da ciência e dos crustáceos. Por ter sido uma "mãe científica" e me orientado a sempre seguir e buscar o seu exemplo de profissionalismo e caráter. Por ter me guiado ao melhor caminho durante e após a iniciação científica, me apresentando ao meu atual orientador (Tony), que compartilha das mesmas características que você. Muito obrigada por tudo que você faz por mim, você é muito especial Kátia!

Aos colegas do NEBECC: Aline, Camila e Thiago (Cabelo), pelas discussões científicas (ou não), pelos momentos tão prazerosos no café e por estarem sempre à disposição para ajudar, vocês são muito especiais. Em especial à minha grande amiga de longa data, Aline, que tanto me apoiou, incentivou e auxiliou não só na realização das minhas principais etapas acadêmicas, como fora delas também. Obrigada por ter me acolhido tão bem no tempo em que nos divertimos muito dividindo o mesmo quarto, e pelos conselhos tão valiosos que foram imprescindíveis para que eu crescesse e amadurecesse, tanto profissionalmente quanto emocionalmente.

Aos colegas do "Laborantônio": Alexandre (Dino), Geslaine, Gilson (Nerso), Isabela, João, Joyce, Mariana (Magrela), Milena, Raphael, Renan (Greg) e Thiago (Chuck), pelos inúmeros bons momentos de descontração no laboratório, no café, conversas e discussões úteis (ou não). Por toda a parceria em congressos, disciplinas e coletas ao longo do meu tempo aqui. Cada um de vocês me marcou de alguma forma e me fez crescer muito. Muito obrigada!

À minha querida amiga Joyce por ser muito mais que uma colega de sala, sendo uma verdadeira amiga. Por ter me acolhido tão bem no laboratório desde o princípio, quando eu ainda estava perdida. Pela sua maneira única de ensinar, com paciência e amor, pelas inúmeras discussões diárias sobre a minha dissertação (e não), e ideias mirabolantes que me deixavam intrigadas e com vontade de aprender cada vez mais. Por não só me ajudar com as dúvidas científicas (que eram muitas), mas por diariamente me ensinar a viver a vida de uma maneira muito mais calma, tranquila e positiva. Quantas coisas eu aprendi com você, Jó! Muito obrigada, por tudo, de coração.

À minha família de coração, Ermeia, Luiz, Ju, Nando, Dani, tios e primos, por me acolherem tão bem em sua família. Pela torcida, apoio, carinho, conselhos, e por todos os ótimos momentos que passamos juntos. Vocês são muito especiais. Muito obrigada!

À toda a minha família (Fer, Gio, avós, tios, primos, etc), especialmente às pessoas mais especiais do mundo, que são diariamente a minha fonte de inspiração para lutar e seguir em frente, meus pais Kátia e Cleito, e meu irmão Augusto. Por todo apoio e incentivo, que fazem das dificuldades apenas um pequeno obstáculo a ser superado. Pelo amor incondicional e pelo exemplo de vida tão bonito que sempre serão para mim. Quanto privilégio eu tive por ter pais como vocês, e ainda um irmão que cuidou de mim da mesma forma! Eu me orgulho muito de vocês e espero que um dia eu possa ser tão boa quanto vocês sempre foram e são para mim. Me faltam palavras para descrever o quão grata eu sou. Muito obrigada!!!

Em especial aos meus tão amados avós, Léia e Francisco, que fazem parte do que eu sou hoje. Por cuidarem de mim tão bem quanto os meus pais, pelo amor incondicional e incomparável de avós, e por tornarem real e cheia de amor a expressão “casa de vô e vó”. Por fazerem tudo e qualquer coisa por mim, não só durante a infância. Por compreenderem a minha ausência e me receberem com tanto carinho a cada reencontro. Que sorte grande a minha em ter vocês comigo. Vocês são maravilhosos, muito obrigada!

Ao meu namorado Raphael, pelo enorme carinho, companheirismo, apoio e incentivo durante todo este tempo. Por me impulsionar e me fazer crescer a cada dia, superando as dificuldades. Pela paciência em me ajudar quando eu te deixava quase louco com tantas perguntas ao mesmo tempo, e até mesmo quando você perdia um pouco a paciência por ter que me explicar a mesma coisa 15 vezes até eu entender (eu juro que não era zoeira!). Por todos os momentos de descontração, risadas, especialmente quando o motivo era mais uma das histórias que só você protagonizaria (você precisa escrever um livro sobre). Por toda a sua contribuição na minha vida acadêmica e pessoal, me ensinando de tudo um pouco, a cada dia. Você foi fundamental, e é a minha base e apoio. Muito obrigada por tudo!

A todas as pessoas (amigas (os), etc) que participaram de alguma forma e colaboraram para o meu crescimento profissional e para a elaboração desta dissertação. Muito obrigada!

Sumário

Capítulo 1:

Population dynamics of *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea) on the southeastern Brazilian coast: implications for shrimp fishing management from a 5-year study on a bycatch species

Capítulo 2:

A five-year study on the reproduction and recruitment pattern of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) on the southeastern Brazilian coast

Considerações iniciais

Caracterização da área de estudo

O relevo da região litorânea do Estado de São Paulo é caracterizado por uma conformação topográfica que se reflete em um litoral intensamente recortado, com praias de pequena extensão e a formação de diversas enseadas (Ab'Sáber 1955). Estas representam ambientes favoráveis ao estabelecimento e desenvolvimento de inúmeras formas de vida marinha, desde que as características e necessidades ecológicas sejam propícias às particularidades de cada espécie (Negreiros-Fransozo et al. 1991; Mantelatto et al. 1995).

A principal característica oceanográfica estruturadora dos ecossistemas da plataforma continental sudeste e sul do Brasil é a presença sazonal da Água Central do Atlântico Sul, massa de água caracterizada por baixa temperatura e salinidade (ACAS; T < 18º C; S < 36). Além da ACAS, a costa norte do Estado de São Paulo sofre forte influência de outras duas massas de água, com características específicas e modelos distintos de distribuição entre o verão e inverno: Água Costeira, com alta temperatura e baixa salinidade (T > 20º C; S < 36), e Água Tropical, que apresenta temperatura e salinidade altas (T > 20º C; S > 36) (Castro-Filho et al. 1987).

A ACAS alcança a região costeira junto ao fundo, ao longo da plataforma continental, sendo responsável pelas baixas temperaturas da água durante o fim da primavera e o início do verão. Esta massa de água pode apresentar temperatura mínima de 15º C, ocasionando uma termoclina localizada em profundidades de 10 a 15 m, devido à presença de água fria junto ao fundo e de água aquecida no restante da coluna. Os processos físicos da coluna d'água influenciam consideravelmente os processos biológicos e, assim, propõe-se uma tendência de enriquecimento da água na plataforma durante os meses de verão, ocasionada pela penetração da ACAS, até aproximadamente a região costeira (Castro-Filho et al. 1987).

As características particulares da região de Ubatuba (23º29′06″S, 45º05′00″W), litoral norte do Estado de São Paulo, a tornam uma importante área de abrigo para inúmeros crustáceos decápodes (Mantelatto e Fransozo 2000), bem como inúmeros organismos marinhos provenientes de diferentes regiões, representando, portanto, uma região de transição faunística (Sumida e Pires-Vanin 1997). Por este motivo, estudos foram conduzidos na região de Ubatuba, correlacionando a influência de características ambientais à distribuição, reprodução, estrutura populacional e outros aspectos da dinâmica populacional de crustáceos. Dentre estes, Castilho et al. (2007; 2008ab; 2012;

2015ab), Pantaleão et al. (2016), Stanski e Castilho (2016), Grabowski et al. (2016), Pinheiro e Pardal-Souza (2016) e Pinheiro et al. (2017).

Ainda assim, o camarão *Rimapenaeus constrictus* (Stimpson, 1874) permanece pouco estudado na região. Esta espécie reserva informações relevantes considerando sua história de vida, especialmente tratando-se de estudos de ampla escala temporal que busquem padrões mais específicos e mais evidentes, facilitando a compreensão da biologia da espécie.

A espécie estudada

O filo Arthropoda (no qual insere-se o subfilo Crustacea) é caracterizado, principalmente, pela presença de um exoesqueleto rígido, constituído majoritariamente por quitina e proteínas. Os crustáceos representam mundialmente o grupo com maior abundância nos oceanos, sendo encontrados em ambientes que vão desde os marinhos, salobros e dulcícolas até o ambiente terrestre, a exemplo dos tatuzinhos-de-jardim (isópodes). Além de sua ampla distribuição e diversificação, estão entre os invertebrados mais populares, visto que os camarões, caranguejos e lagostas são itens alimentares muito apreciados na gastronomia mundial, exibindo ainda uma grande diversidade morfológica e de hábitos (Brusca e Brusca 2007; Fransozo e Negreiros-Fransozo 2016).

Os Crustacea subdividem-se em seis classes: Remipedia, Cephalocarida, Branchiopoda, Malacostraca, Maxillopoda e Ostracoda. Destas, Malacostraca representa a de maior abundância, com aproximadamente 40.000 espécies descritas (Brusca e Brusca 2007; Fransozo e Negreiros-Fransozo 2016). Dentro dela, a ordem Decapoda se destaca como principal enfoque nas pesquisas realizadas, em vista da sua ampla diversidade e importância econômica (Martin e Davis 2001). Os Decapoda compõem aproximadamente um terço de todos os crustáceos descritos, sendo representados por aproximadamente 17.000 espécies (De Grave et al. 2009). O caractere diagnóstico do grupo é a presença de cinco pares de apêndices birremes que podem encontrar-se modificados, sendo utilizados para sua locomoção, bem como outras funções, como alimentação e natação (Fransozo e Negreiros-Fransozo 2016).

A ordem Decapoda subdivide-se em duas subordens: Pleocyemata (representada dentre outros, por camarões carídeos, lagostas e caranguejos) e Dendrobranchiata (representada, basicamente, por camarões peneídeos e sergestídeos). Dentre as diferenças que separam os dois grupos, estão o tipo de brânquia (filobrânquias ou tricobrânquias em

Pleocyemata; dendrobrânquias em Dendrobranchiata) e o tipo de desenvolvimento embrionário (pleopodial apenas em Pleocyemata; espécies inseridas em Dendrobranchiata não apresentam ovos aderidos aos pleópodes) (Fransozo e Negreiros-Fransozo 2016). Dentre as aproximadamente 500 espécies inseridas em Dendrobranchiata (Tavares e Martin 2010), uma grande quantidade apresenta interesse econômico na pesca mundial de camarões, sendo a maioria explorada muito além dos seus níveis de sustentabilidade (Brusca e Brusca 2007).

Os camarões peneídeos são um importante alvo da exploração de camarões no Brasil, estando incluídos entre os camarões mais capturados e de maior valor comercial (Tavares e Martin 2010), sendo assim um dos mais importantes recursos pesqueiros (D'Incao et al. 2002). A pesca camaroeira nas regiões Sudeste e Sul do Brasil é direcionada principalmente aos camarões sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862), branco *Litopenaeus schmitti* (Burkenroad, 1936), rosa *Farfantepenaeus paulensis* (Perez-Farfante, 1967) e *F. brasiliensis* (Latreille, 1817), barba-ruça *Artemesia longinaris* Spence Bate, 1888 e santana *Pleoticus muelleri* (Spence Bate, 1888) (D'Incao et al. 2002).

Porém, a não seletividade da pesca camaroeira (redes de arrasto) captura acidentalmente inúmeros outros organismos marinhos que compartilham do mesmo hábitat (fauna acompanhante ou *bycatch*), sendo a atividade pesqueira mais prejudicial em termos de biomassa de *bycatch* (Vianna e Almeida 2005). Dados disponibilizados pela Organização das Nações Unidas para Agricultura e Alimentação (FAO) (2015), indicam que a biomassa de organismos capturados acidentalmente na pesca camaroeira pode ser de 3 a 15 vezes maior que as espécies de interesse comercial. Portanto, é evidente a necessidade de estudos e políticas de manejo que priorizem e forneçam subsídio à conservação e proteção não apenas das espécies-alvo, mas também dos estoques de *bycatch*, assim evitando o desequilíbrio da cadeia trófica marinha.

Dentre os camarões peneídeos capturados pela atividade pesqueira, *R. constrictus* não é comercialmente explorado em vista do seu tamanho reduzido em comparação aos demais peneídeos (Costa e Fransozo 2004a). Entretanto, este torna-se suscetível à exploração predatória, uma vez que representa uma das principais espécies amplamente capturadas acidentalmente na pesca de arrasto (Mantelatto et al. 2016).

Rimapenaeus constrictus apresenta ampla distribuição no Atlântico Ocidental, sendo encontrado desde a Nova Escócia (Canadá) até Santa Catarina (Brasil) (Pérez-Farfante e Kensley 1997) (Fig. 1). Embora não possua interesse comercial, a espécie desempenha um importante papel ecológico como parte da cadeia trófica marinha (Costa e Fransozo 2004a), o que justifica os estudos anteriormente desenvolvidos com a mesma. Atualmente, dentre os estudos disponíveis realizados com a espécie, pode-se citar o de Bauer e Lin (1994), desenvolvido no hemisfério norte, especificamente em Mississipi (EUA), abordando os padrões de reprodução e recrutamento. No litoral norte do Estado de São Paulo, as pesquisas foram conduzidas por Costa e Fransozo (2004a) destacando a abundância e distribuição da espécies, e Costa e Fransozo (2004b), abordando os seus aspectos reprodutivos. Além disso, na mesma região, Hiroki et al. (2011) descreveram sua distribuição batimétrica, enquanto que no litoral sul paulista, Garcia et al. (2016) forneceram informações sobre seus parâmetros de crescimento, reprodutivos e da estrutura populacional.

Figura 1. *Rimapenaeus constrictus* (Stimpson, 1874), vista lateral. Imagem: Castilho AL, 2010.

Plano de estudo

A presente dissertação de mestrado esteve plenamente vinculada ao Programa Biota/FAPESP (Processo: 2010/50188-8) e contou com a participação dos pesquisadores Dr. Fernando Luis Medina Mantelatto (coordenador do temático - USP), Dr. Antonio Leão Castilho (UNESP), Dr. Fernando José Zara (UNESP) e Dr. Rogério Caetano da Costa (UNESP). Vale salientar que, a presente proposta teve como objetivo agregar e comparar informações de campo obtidas por projetos anteriormente aprovados pela FAPESP em um cenário de cinco anos de estudo, com a participação dos pesquisadores Dr. Adilson Fransozo (UNESP 94/4878-8, 98/07090-3) e o orientador Dr. Antonio Leão Castilho (UNESP - 07/56733-5 pós-doutorado). Além disso, a dissertação foi desenvolvida com o auxílio de bolsa FAPESP (#2015/13639-5).

Espera-se que este estudo apresente informações relevantes para demais pesquisas realizadas com *R. constrictus* e forneça subsídios para o desenvolvimento de estudos e políticas de manejo, conservação e proteção, evitando assim a exploração predatória da espécie e, consequentemente, eventuais distúrbios e desequilíbrio na cadeia trófica marinha.

A dissertação foi dividida em dois capítulos, redigidos sob a forma de artigo científico, considerando que o primeiro capítulo já se encontra publicado na revista "Anais da Academia Brasileira de Ciências", volume 89(2), páginas 1013-10125. (anexo). O primeiro capítulo aborda a dinâmica populacional da espécie, com destaque para os parâmetros de crescimento e razão sexual, incluindo algumas considerações sobre as implicações para o gerenciamento da pesca de camarões sobre uma espécie que compõe o *bycatch*.

O segundo capítulo descreve os padrões de reprodução e de recrutamento encontrados para *R. constrictus* na região de Ubatuba, de janeiro de 1998 a junho de 2003.

Referências

Ab'Sáber AN, 1955. Contribuição à geomorfologia do litoral paulista. Revista Brasileira de Geografia, 17(1): 3-37.

Bauer RT e Lin J, 1994. Temporal patterns of reproduction and recruitment in populations of the penaeid shrimps *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson) (Crustacea: Decapoda) from the Northcentral Gulf of Mexico. Journal of Experimental Marine Biology and Ecology, 182(2): 205-222.

Brusca RC e Brusca GJ, 2007. Invertebrados. Segunda edição. Editora Guanabara-Koogan, Rio de Janeiro, Brasil, 968p.

Castilho AL, Costa RC, Fransozo A, Boschi EE, 2007. Reproductive pattern of the South American shrimp *Artemesia longinaris* (Decapoda: Penaeoidea), off São Paulo State, Brazil. Revista de Biologia Tropical, 55(1): 39-48.

Castilho AL, Costa RC, Fransozo A, Negreiros-Fransozo ML, 2008a. Reproduction and recruitment of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. Marine Biology Research, 4: 361-368.

Castilho AL, Furlan M, Costa RC, Fransozo V, 2008b. Reproductive biology of the rock shrimp *Sicyonia dorsalis* (Decapoda: Penaeoidea) from the southeastern coast of Brazil. Invertebrate Reproduction and Development, 52 (1-2): 59-68.

Castilho AL, Wolf MR, Simões SM, Bochini GL, Fransozo V, Costa RC, 2012. Growth and reproductive dynamics of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. Journal of Marine Systems, 105: 135-144.

Castilho AL, Bauer RT, Freire FAM, Fransozo V, Costa RC, Grabowski RC, Fransozo A, 2015a. Lifespan and reproductive dynamics of the commercially important sea bob shrimp *Xiphopenaeus kroyeri* (Penaeoidea): synthesis of a 5-year study. Journal of Crustacean Biology, 35: 30-40.

Castilho AL, Grabowski RC, Simões SM, Santos APF, Costa RC, Fransozo A, 2015b. Lifespan and population dynamics of the endemic South American shrimp *Artemesia longinaris* (Crustacea: Penaeidae) in southeastern Brazil. Anais da Academia Brasileira de Ciências, 87(4): 2123-2138.

Castro-Filho BM, Miranda LB, Miyao SY, 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. Boletim do Instituto Oceanográfico 35: 135-151.

Costa RC e Fransozo A, 2004a. Abundance and ecologic distribution of the shrimp *Rimapenaeus constrictus* (Crustacea: Penaeidae) on the northern coast of São Paulo State, Brazil. Journal of Natural History, 38(7): 901-912.

Costa RC e Fransozo A, 2004b. Reproductive biology of the shrimp *Rimapenaeus constrictus* (Decapoda, Penaeidae) in the Ubatuba region of Brazil. Journal of Crustacean Biology, 24(2): 274-281.

De Grave S, Pentcheff ND, Ahyong ST, Chan TY, Crandall KA, Dworschak PC, Felder DL, Feldmann RM, Fransen CHJM, Goulding LYD, Lemaitre R, Low MEY, Martin JW, Ng PKL, Schweitzer CE, Tan SH, Tshudy D, Wetzer R, 2009. A classification of living and fossil genera of Decapod Crustaceans. Raffles Bulletin of Zoology, 21: 1-109.

D’Incao F, Valentini H, Rodrigues LF, 2002. Avaliação da pesca de camarões nas regiões sudeste e sul do Brasil. Atlântica, 24(2): 103-116.

Food and agriculture organization of the United Nations (FAO), 2015. Transforming wasted resources for a sustainable future. The sustainable management of bycatch in

Latin America and Caribbean trawl fisheries. Fisheries and Aquaculture Department, 8p.

Fransozo A e Negreiros-Fransozo ML, 2016. Zoologia dos Invertebrados, primeira edição. Roca, Rio de Janeiro, Brasil, 661p.

Garcia JR, Wolf MR, Costa RC, Castilho AL, 2016. Growth and reproduction of the shrimp *Rimapenaeus constrictus* (Decapoda: Penaeidae) from the southeastern coast of Brazil. Regional Studies in Marine Science, 6: 1-9.

Grabowski RC, Negreiros-Fransozo ML, Castilho AL, 2016. Reproductive ecology of the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) in a coastal area of Southern Brazil. Chinese Journal of Oceanology and Limnology, 34(1): 125-135.

Hiroki KAN, Fransozo A, Costa RC, Castilho AL, Shimizu RM, Almeida AC, Furlan M, 2011. Bathymetric distribution of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) (Decapoda, Penaeidae) in two locations off the southeastern Brazilian coast. Marine Biology Research, 7(2): 176-185.

Mantelatto FLM, Fransozo A, Negreiros-Fransozo ML, 1995. Distribuição do caranguejo *Hepatus pudibundus* (Herbst, 1785) (Crustacea, Decapoda, Brachyura) na Enseada da Fortaleza, Ubatuba (SP), Brasil. Boletim do Instituto Oceanográfico, 43(1): 51-61.

Mantelatto FLM e Fransozo A, 2000. Brachyuran community in Ubatuba Bay, Northern Coast of São Paulo State, Brazil. Journal of Shellfish Research, 19(2): 701-709.

Mantelatto FL, Bernardo CH, Silva TE, Bernardes VP, Cobo VJ, Fransozo A, 2016. Composição e distribuição de crustáceos decápodes associados à pesca do camarão-sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862) no litoral norte do estado de São Paulo. Boletim do Instituto de Pesca, 42(2): 307-326.

Martin JW e Davis GE, 2001. An updated classification of the recent Crustacea. Natural History Museum of Los Angeles County, Science Series, 39: 123p.

Negreiros-Fransozo ML, Fransozo A, Pinheiro MAA, Mantelatto FL, Santos S, 1991. Caracterização física e química da Enseada de Fortaleza, Ubatuba, SP. Revista Brasileira de Geociências, 21(2): 114-120.

Pantaleão JAF, Carvalho-Batista A, Fransozo A, Costa RC, 2016. The influence of upwelling on the diversity and distribution of marine shrimp (Penaeoidea and Caridea) in two tropical coastal areas of southeastern Brazil. Hydrobiologia, 763: 381-395.

Pérez-Farfante I e Kensley B, 1997. Penaeoid and Segestoid shrimps and prawns of the World. Keys and diagnoses for the families and genera. Paris, Éditions du Muséum national d'Histoire naturelle, 233p.

Pinheiro MAA e Pardal-Souza AL, 2016. Historical background of the population biology of the swimming crab *Arenaeus cribrarius* (Crustacea: Portunidae) in the Ubatuba coast, Southeastern Brazil. Boletim do Instituto de Pesca, 42(2): 419-429.

Pinheiro MAA, João MCA, Leme MHA, Matsunaga AKM, Rio JPP, Hernáez P, 2017. Insights of the life history in the porcellanid crab *Petrolisthes armatus* (Gibbes, 1850) (Crustacea: Anomura: Porcellanidae) from the Southwestern Atlantic coast. Invertebrate Reproduction and Development: 1-12.

Stanski G e Castilho AL, 2016. Reproductive biology of the South American endemic hermit crab *Isocheles sawayai* (Crustacea, Anomura) from the Southern coast of Brazil. Invertebrate Reproduction and Development, 60(2): 103-111.

Sumida PYG e Pires-Vanin AMS, 1997. Benthic Associations of the Shelfbreak and Upper Slope off Ubatuba-SP, South-eastern Brazil. Estuarine, Coastal and Shelf Science, 44: 779-784.

Tavares C e Martin JW, 2010. Suborder Dendrobranchiata Bate, 1888. In: Schram FR, von Vaupel Klein JC, Forest J, Charmantier-Daures M (eds). Treatise on Zoology – Anatomy, Taxonomy, Biology: The Crustacea. Leiden, Boston: Brill, 2010, 9A(63): 99-164.

Vianna M e Almeida T, 2005. Bony fish bycatch in the southern Brazil pink shrimp (*Farfantepenaeus brasiliensis* and *F. paulensis*) fishery. Brazilian Archives of Biology and Technology, 48(4):611-623.

Capítulo 1

Population dynamics of *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea) on the southeastern Brazilian coast: implications for shrimp fishing management from a 5-year study on a bycatch species

Population dynamics of *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea) on the southeastern Brazilian coast: implications for shrimp fishing management from a 5-year study on a bycatch species

Abstract

This is the first study to evaluate in broad spatiotemporal scales the growth parameters and population structure of *Rimapenaeus constrictus*, a barely damaged species composing the bycatch from shrimp fishing in the Western Atlantic. The abundance and size-class frequency distribution, growth, longevity and sex ratio were evaluated from monthly samples obtained in the northern littoral of São Paulo state from Jan/1998 to Jun/2003. We measured 5,812 individuals in which the sex ratio was skewed toward females; this was more evident in size classes greater than 10 mm in CL (carapace length) (binomial test, $p<0.05$). We selected 16 growth cohorts of females, and 8 of males, the majority consisting of younger individual cohorts excluded from the fisheries closure period. Growth estimates resulted in a CL_∞ of 17.42 mm, a growth coefficient of 0.008 and a longevity of 579 days (1.60 year) for females, as well as a CL_∞ of 16.3 mm, a growth coefficient of 0.01 and a longevity of 425 days (1.17 year) for males. Our results provide information of incontestable relevance to our knowledge of fishing management. We therefore strongly recommend that the fisheries closure period be changed to protect this species' recruitment period and consequently its adult individuals.

Keywords: Fisheries biology; latitudinal variation; recruitment cohorts; roughneck shrimp; stock conservation.

Introduction

Crustacean fisheries production has been declining throughout the southeastern Brazilian Coast, mainly in the Ubatuba region, which within a 10-year period (2005-2015) has shown a 64% of reduction in biomass landings (Instituto de Pesca, São Paulo: www.pesca.sp.gov.br). Commercial fishery trawling in the Brazilian Southeastern region targets species such as *Farfantepenaeus brasiliensis* (Latreille, 1817), *F. paulensis* (Pérez-Farfante 1967), *Litopenaeus schmitti* (Burkenroad, 1938), *Xiphopenaeus kroyeri* (Heller, 1862), *Artemesia longinaris* Spence Bate, 1888 and *Pleoticus muelleri* (Spence Bate, 1888) (D'Incao et al. 2002). In Brazilian Southeastern coast, the use of motor boats for shrimp trawling from March 1st to May 31st is forbidden by the Brazilian Institute of

Environment and Natural Renewable Resources (IBAMA). During this season (the fisheries closure period), fishermen are prohibited from using such gear to capture economically marketable shrimp species or to transport, stock or commercialize these animals. This measure aims to protect their regular population structure, reproduction and recruitment period (normative instruction available at: www.ibama.gov.br).

Trawling activity uses non-selective fishing gear, i.e., along with the target species, many non-target organisms (bycatch fauna) are incidentally caught. According to Dias Neto (2011), a minority of the bycatch fauna is landed and is locally commercialized (often at very low prices), on the other hand, most is discarded back to the sea already dead due to their negligible commercial value. On average, in a trawl to obtain tropical shrimp, the captured bycatch is 3 to 15 times larger than the captured target species (FAO 2015). The ecological impacts resulting from shrimp fishing are still poorly understood, but are known to be considerable. One of the main effects of the bycatch capture on the ecosystem is the alteration in the species composition and/or in the stock size of the bycatch species (Dias Neto 2011). Theoretically, species with no economic value (bycatch), such as *Rimapenaeus constrictus* (Stimpson, 1874), are protected by the fisheries closure period as well, since the bycatch and economically important species are not being captured during this period.

Rimapenaeus constrictus exhibits a broad geographical distribution ranging from Nova Scotia (Canada) to Santa Catarina (Brazil). This species is among those most often accidentally caught during fishery activities, and due to its small size, it is not commercially exploited. However, it plays an important ecological role as part of the trophic web chain within its habitat range (Pérez-Farfante and Kensley 1997; Costa and Fransozo 2004b).

The biological knowledge about species and estimates of their population parameters (size class distributions, growth rates, sex ratios, etc.) are highly relevant to provide essential information about the management of fishing resources (Gab-Alla et al. 1990; Bauer and Rivera Vega 1992; Castilho et al. 2015a). With regard to shrimp growth studies, the most accepted (and consequently most utilized) methodology is the von Bertalanffy (1938) growth model, which estimates the age of an individual of a given body size according to a mathematical equation. This methodology is necessary due to the impossibility of periodic tissue tagging, since crustaceans do not have permanent skeletal structures (Hartnoll 2001; Fonseca and D’Incao 2003; Campos et al. 2011; Castilho et al. 2015b).

However, only a few studies have been undertaken to guide and clarify the basic biology of the population dynamics and life history of this species. In the northern littoral of São Paulo state, Costa and Fransozo (2004ab) studied its reproductive biology and its abundance and ecological distribution, respectively, and Hiroki et al. (2011) investigated its bathymetric distribution. In the southern littoral of São Paulo, only the study addressing its growth and lifespan carried out by Garcia et al. (2016) is available in a different region. In addition to the studies conducted on the Brazilian coast, Bauer and Lin (1994) evaluated the reproductive and recruitment periods of the congeneric species, *Rimapenaeus similis* (Smith, 1885) and *R. constrictus*, in the Gulf of Mexico.

It is important to point out that to date, no studies have been done concerning growth and longevity of *R. constrictus* in the Ubatuba region or on the northern coast of São Paulo state; thus, this is a pioneer study for this approach. It is therefore necessary to strengthen our biological knowledge about the bycatch by obtaining appropriate data. These findings are essential to substantiate the implementation of management and sustainable use measures for marine shrimp fishing along the Brazilian coast, especially since current knowledge is insufficient to make scientifically based decisions (Dias Neto 2011).

On the basis of this scenario, we here describe the population structure and sex ratio and estimate the growth parameters for *R. constrictus* across a wide temporal scale, for 5 years, in Ubatuba in the northern littoral of São Paulo state. Additionally, we tested the hypothesis that such parameters undergo alterations induced by environmental features related to the latitude and compared our results to the studies on *R. constrictus* available to date. For the first time, a growth analysis covers the whole bathymetric distribution of this species on the Brazilian coast, and distinct results can therefore be observed. Thus, we could determine whether the commonly referred to “latitudinal effect paradigm” proposed by Bauer (1992) and Castilho et al. (2007b) is applicable to the growth parameters of the species concerned here, as it was already reported to apply to its reproductive aspects (Costa and Fransozo 2004a). We also verified the applicability of the current fisheries closure period to this species with regard to its functionality for the recruitment observed during the study period.

Material and methods

Study area

The Ubatuba region presents an extremely indented coastline, resulting in the creation of many bays with particular environmental conditions exhibiting very irregular internal limits that are favorable to the establishment of the local fauna. It is a result of the peculiar characteristics and ecological needs of each species and the consequent development of particular marine faunas (Negreiros-Fransozo et al. 1991).

The main oceanographic feature structuring ecosystems on the southeastern and southern Brazilian continental shelf is the presence of the South Atlantic Central Waters, a water mass characterized by low temperature and salinity (SACW: T<18º C; S<36) (Pires-Vanin 2001; Soares-Gomes and Pires-Vanin 2003). In addition, the northern coast of São Paulo state is strongly influenced by two other water masses, each showing specific characteristics and distinct models of distribution between summer and winter: Coastal Water (AC: high temperature (>20º C) and low salinity [<36]) and Tropical Water (TW: high temperature (>20º C) and high salinity [>36]) (Castro-Filho et al. 1987).

The SACW approaches from the continental shelf in the bottom water layers, reaching the coastal zone and causing the low water temperatures recorded during spring and early summer (minimum values of 15º C). This process creates a thermocline at depths of 10 to 15 m due to the presence of cold water in the bottom layers of the water column and warm water in the remaining layers (Castro-Filho et al. 1987).

Biological sampling

Samplings were carried out monthly from Jan/1998 to Jun/2003, with a gap between January 2001 to June 2001, along the northern coast of São Paulo state in the Ubatuba region. Samples were obtained during the day using a shrimp-fishing boat outfitted with double-rig nets (mesh size: 20 mm knot-to-knot in the body and 15 mm in the cod end). Trawls were extended for two kilometers for 30 minutes each, sampling a total area of 18,000 m².

Carapace length (CL) was adopted as a standard measurement in this study, corresponding to the linear distance from the post-orbital angle and the posterior margin of the carapace, which has been widely used in investigations concerning penaeid shrimps (Castilho et al. 2015ab). CL size frequencies were distributed in 1-mm classes to each sex, separately. Both were compared by a Kolmogorov-Smirnov two-sample test in which the null hypothesis adopted was that size distribution among sexes did not differ (Castilho et al. 2008a). Recruitment was estimated as the percentage of the population sampled in the lower 25% of all possible size classes (males+females). Thus, for the purposes of measuring recruitment, all individuals with a CL less than 9.4 mm were considered recruits (Bauer and Rivera Vega 1992; Castilho et al. 2008a).

Sex ratio

Individuals were classified to sex according to the presence of a petasma (males) or a thelycum (females) (Pérez-Farfante 1988). The sex ratio was estimated as the quotient between the number of males and the total number of individuals in the monthly samples. Differences in the expected ratio of 1:1 (males:females) were tested with the binomial test (α=0.05) (Wilson and Hardy 2002; Grabowski et al. 2014).

Growth and longevity

Growth and longevity were analyzed separately for each sex according to the von Bertalanffy (1938) growth model and using the methodology purposed by Simões et al. (2013). Modal values were determined for each CL frequency using the software Peakfit 4.0 (Automatic Peak Fitting Detection and Fitting, Method I-Residual, no Data Smoothing) in size classes of 1.0 mm. The models were plotted on a scatter graph vs. age to verify the growth rhythm of the cohorts. Growth parameters (CL_∞: asymptotic carapace length; k: growth coefficient (day-1); t_0: theoretical age at size 0) were estimated using the SOLVER supplement in Microsoft Excel, which applies the von Bertalanffy growth model: $CL_t=CL_\infty[1-exp-k^{(t-t0)}]$ (CL_t: carapace length at age t). The cohort data were pooled, and the growth parameters estimated. The estimated growth curves for each sex were compared by an F test (p=0.05) (Cerrato 1990). Longevity was calculated using the inverse von Bertalanffy growth model with a modification suggested by D'Incao and Fonseca (1999) given by $longevity = 0-(1/k)ln[1-(CL_t/CL_\infty)]$ (considering t_0 = 0, and CL_t/CL_∞ = 0.99). Cohorts including the modal peaks of recruitment size (<9.4 mm CL) were identified as recruitment cohorts, and the age at which individuals become adult was estimated by the equation purposed by King (1995): $t = t_0-(1/k).ln(1-(CL_t/CL_\infty)$.

Results

Population structure

During this study 5,812 individuals were sampled, including 1,458 males and 4,354 females. Carapace length varied from 4.2 to 17.9 mm in males (mean: 9.21 mm ± 1.31 SD [standard deviation]) and from 3.4 to 19.2 mm in females (mean: 12.1 mm ± 2.31 SD). Males were more abundant in the 5 to 9 mm size classes and females, from 10 to 19 mm, with a peak abundance observed at 12 mm (Figure 1). The size class distributions for males and females showed a statistically significant difference (Kolmogorov-Smirnov, d_{max}= 0.61; p= 0.04).

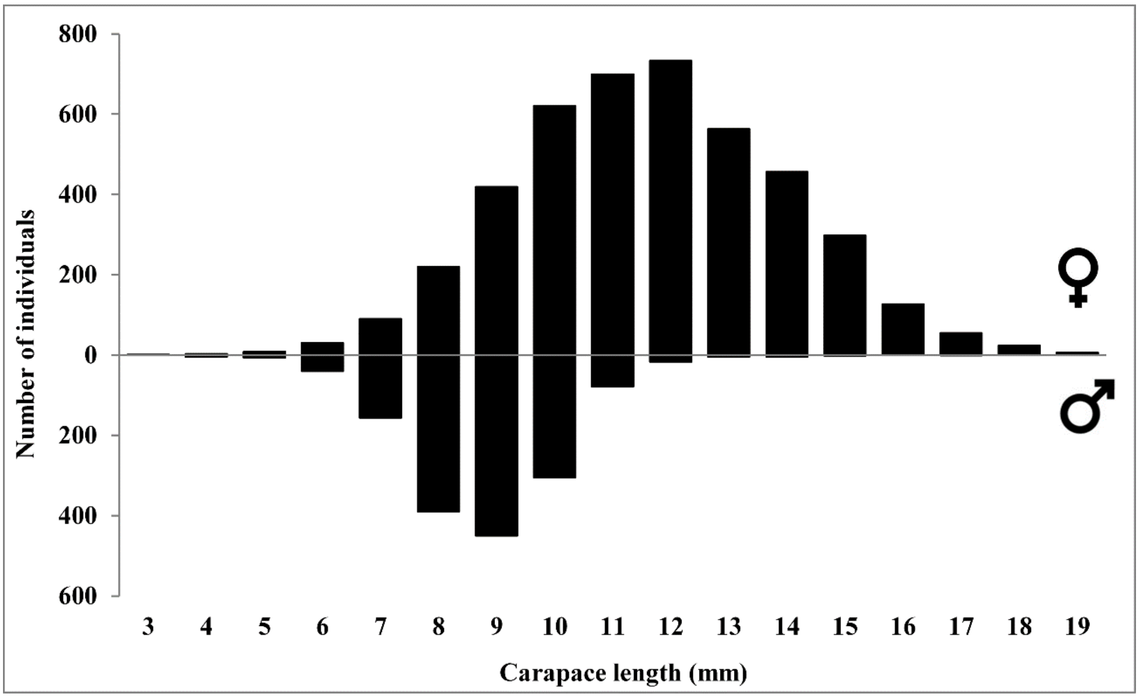

Figure 1. *Rimapenaeus constrictus* (Stimpson, 1874). Size class distributions of males and females for samples obtained from January 1998 to June 2003 at the northern littoral of São Paulo state.

Sex ratio

Throughout the sampling period, we observed a female-biased sex ratio (binomial test, p<0.05), as they were more abundant compared to the number of males (Figure 2).

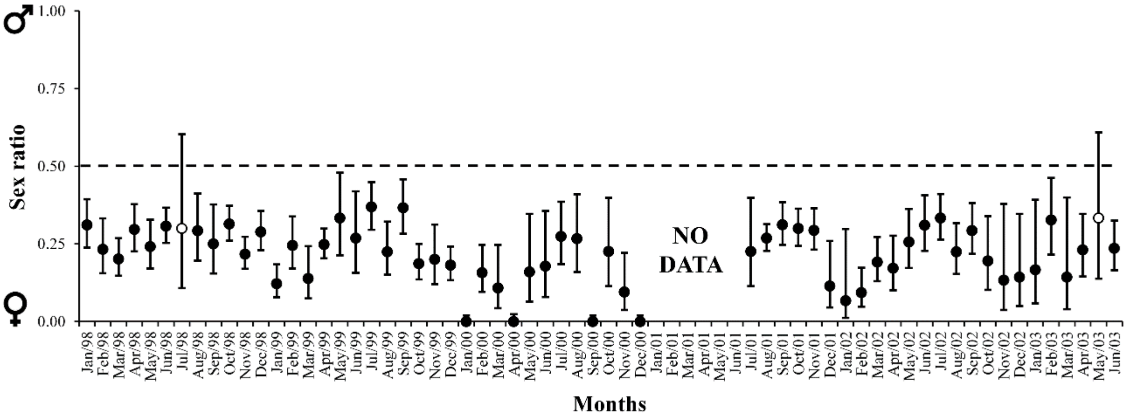

Figure 2. *Rimapenaeus constrictus* (Stimpson, 1874). Monthly sex ratio (estimate ± standard error) for samples from January 1998 to June 2003 from the northern littoral of São Paulo state. Black circles indicate a significant deviation from a 1:1 (M:F) sex ratio (binomial test, p<0.05).

From the size class distribution for adult individuals, it was possible to observe a male-biased sex ratio in the smaller size classes (5-9 mm). From 10 mm on, the sex ratio was exclusively female biased (Figure 3).

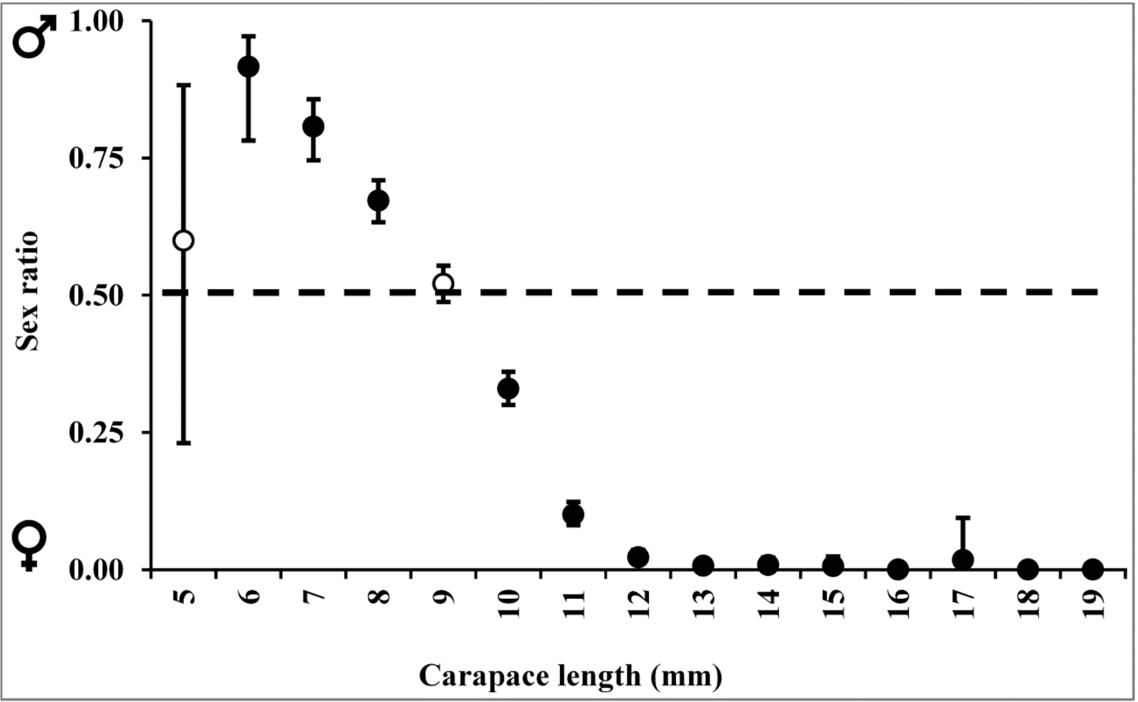

Figure 3. *Rimapenaeus constrictus* (Stimpson, 1874). Sex ratio observed among the size classes (estimate ± standard error) for individuals sampled from January 1998 to June 2003 from the northern littoral of São Paulo state. Black circles

indicate a significant deviation from a 1:1 (M:F) sex ratio (binomial test, $p<0.05$).

Growth and longevity

We identified 16 female and 8 male cohorts (Figures 4 and 5). For males, only 2 recruitment cohorts (< 9.4mm CL) (cohorts 3 and 7) were set in the fisheries closure periods from the time of their emergence until reaching adult size. This condition is even more critical for females because only 3 recruitment cohorts (cohorts 5, 15 and 16) were set in the fisheries closure periods from their emergence until reaching adult size. Moreover, the majority of the remaining cohorts including recruitment sizes were identified in December and February (females: cohorts 2, 6 and 10; males: cohorts 1, 4 and 8). Estimates of the growth parameters resulted in CL_{∞}: 17.42 mm, k: 0.008 and t_0: -1.50 days for females, and CL_{∞}: 16.3 mm, k: 0.01 and t_0: -0.60 days for males (Figure 6 and 7). From the growth curves, longevity was estimated as 579 days (1.60 year) for females and 425 days (1.17 year) for males. Growth curves for males and females showed a significant difference through an F test ($F_{critical}= 2.688 < F_{calculated}= 4.124$; p= 0.008). The time necessary for recruits to reach the adult size here proposed (9.4 mm CL) was estimated as 85 and 95 days for males and females, respectively.

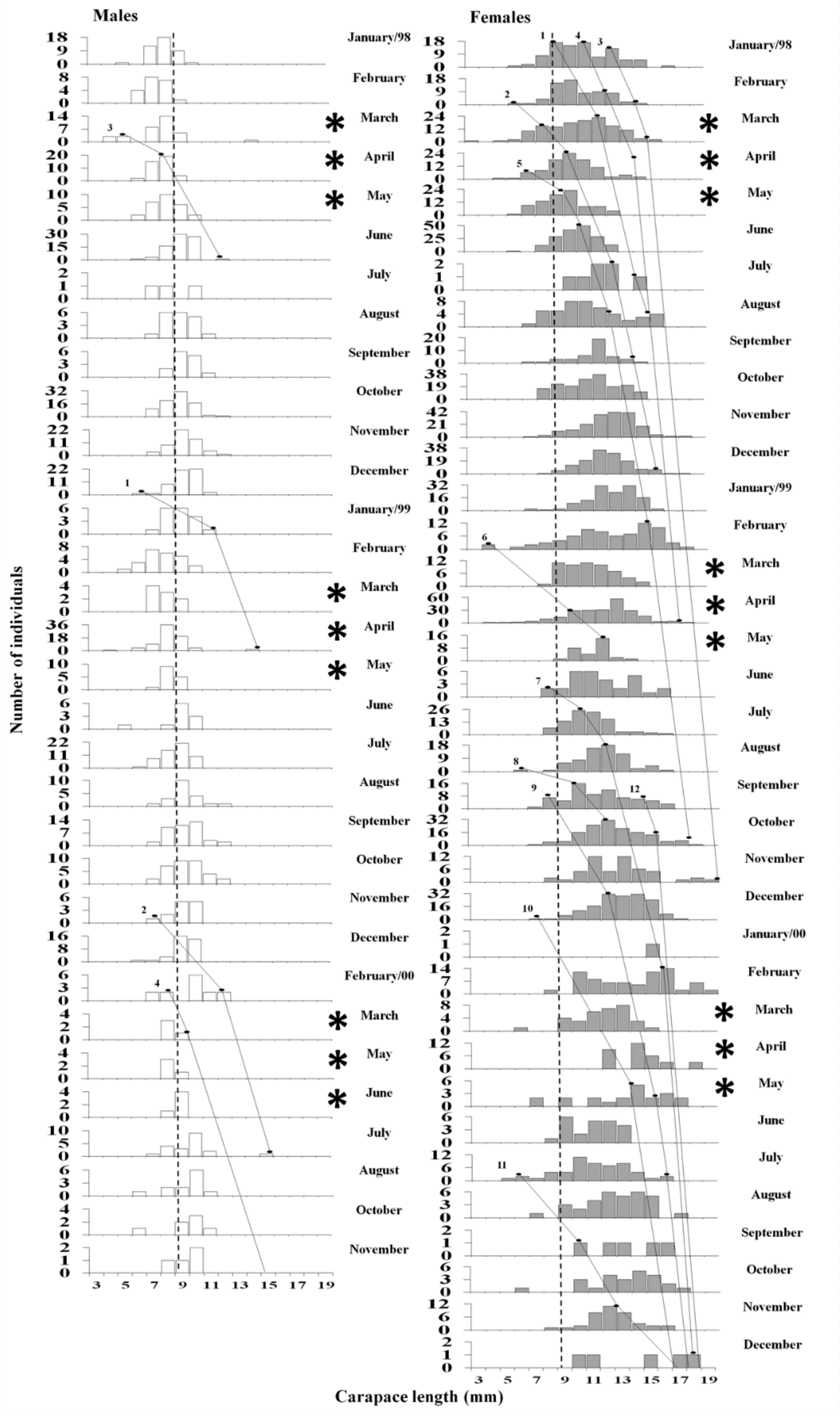

Figure 4. *Rimapenaeus constrictus* (Stimpson, 1874). Selected cohorts (lines) for growth analyses performed on data sampled from January 1998 to December 2000 at the Northern littoral of São Paulo state. Dotted lines: recruitment size (9.4 mm CL); *: periods in which shrimp-fishing activities are prohibited by the responsible federal environmental agency.

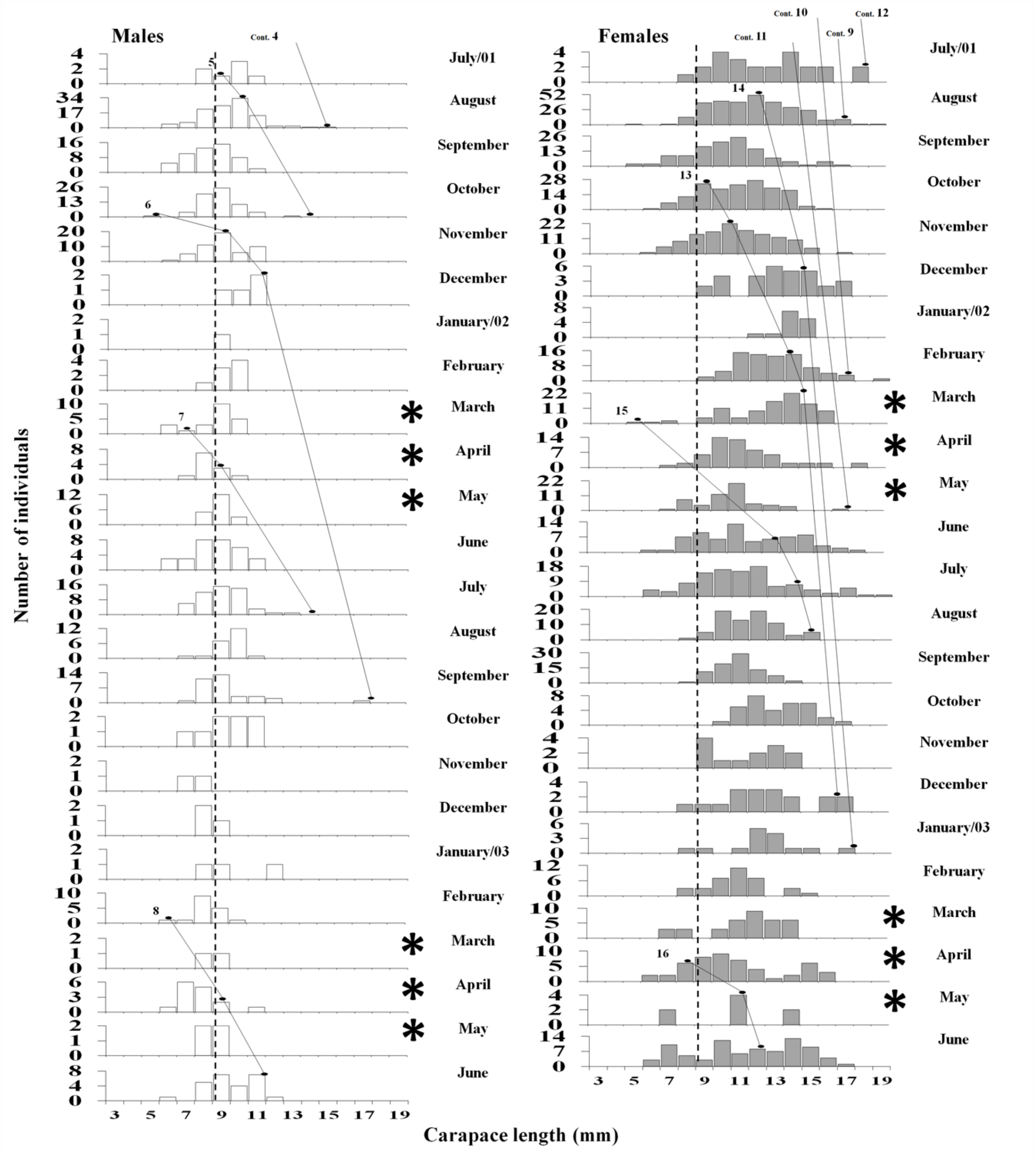

Figure 5. *Rimapenaeus constrictus* (Stimpson, 1874). Selected cohorts (lines) for growth analyses performed on data sampled from July 2001 to June 2003 at the Northern littoral of São Paulo state. Dotted lines: recruitment size (9.4 mm CL); *: periods in which shrimp-fishing activities are prohibited by the responsible federal environmental agency.

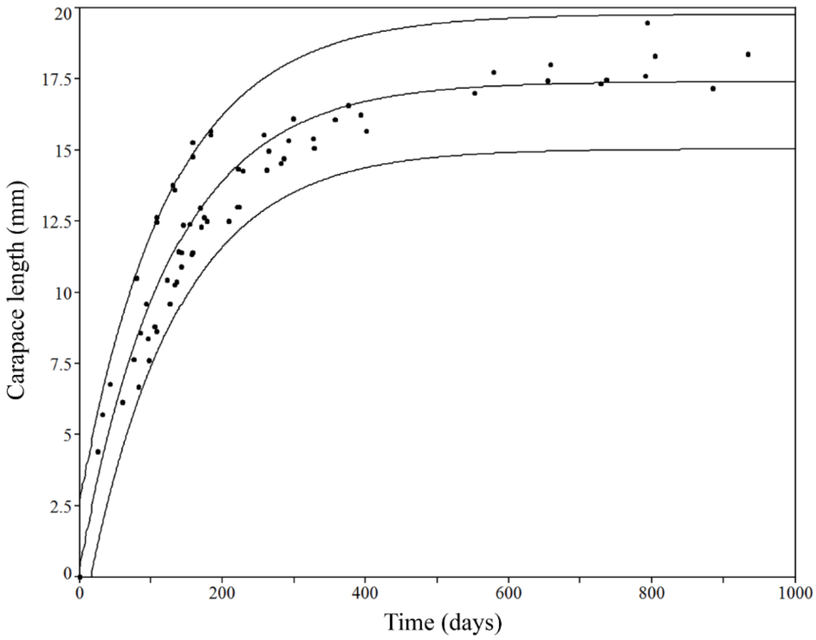

Figure 6. *Rimapenaeus constrictus* (Stimpson, 1874). Mean estimated growth curve based on the von Bertalanffy growth model for females sampled from July 1998 to June 2003 in the Ubatuba region, northern São Paulo state. Outer lines: 95% prediction intervals.

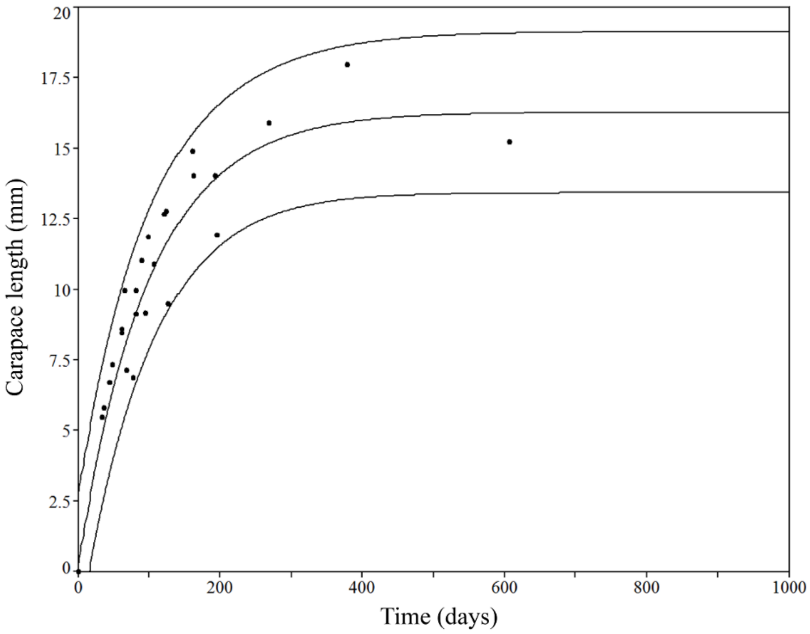

Figure 7. *Rimapenaeus constrictus* (Stimpson, 1874). Mean estimated growth curve based on the von Bertalanffy growth model for males sampled from July 1998 to June 2003 in the Ubatuba region, northern São Paulo state. Outer lines: 95% prediction intervals.

Discussion

In our study, we observed that females reached larger sizes than males, which was previously observed for the same species by Costa and Fransozo (2004a) in the Ubatuba region and by Garcia et al. (2016) in the Cananéia region, as well as in studies of other penaeoid shrimps (Semensato and Di Beneditto 2008; Castilho et al. 2008ab; 2015b; Grabowski et al. 2014; 2016). Such sexual dimorphism is considered a general rule among penaeids (Boschi 1989), indicating a likely adaptation to increase egg production (Gab-Alla et al. 1990; Yamada et al. 2007). In addition, Simões et al. (2013), studying *Acetes americanus* Ortmann, 1893, also found such differential growth between the sexes. Such growth differences thus occur in both superfamilies included in the Dendrobranchiata (Penaeoidea and Sergestoidea).

The theory purposed by Fisher (1930) states that gonochoristic species present equal abundances between the sexes, which runs counter to the results of Wenner (1972) in which several crustacean species show exceptions to this pattern. Recent studies carried out along the Brazilian coast also run counter to Fisher (1930)'s theory, including *Sicyonia dorsalis* Kingsley 1878 (Castilho et al. 2008a), *A. longinaris* (Castilho et al. 2007a; 2015b), *P. muelleri* (Castilho et al. 2008b) and *X. kroyeri* (Castilho et al. 2015a; Grabowski et al. 2014; 2016). In this study, *R. constrictus* constitutes an exception to Fisher's (1930) theory and also agrees with previous studies carried out on the species (Costa and Fransozo 2004a; Garcia et al. 2016).

Deviations from a 1:1 sex ratio can be a result of the interaction of countless factors, such as differential growth rates, migration patterns and mortality rates between the sexes (Wenner 1972). In addition, certain growth parameters (higher growth coefficient and lower asymptotic length in males) can induce female-biased sex ratios (Simões et al. 2013). Garcia et al. (2016) also observed female-biased sex ratios for *R. constrictus*, as in our study. According to the authors, the female-biased sex ratios in higher size classes can also be a consequence of the lower longevity observed for males.

The longevity observed in wild animals is highly variable and may be equal for both sexes of certain species or even differ between them (Vogt 2012). However, it is quite common to observe penaeoid males showing a lower longevity than females, as previously described in the literature (Simões et al. 2013; Grabowski et al. 2014; Castilho et al. 2015ab) and as observed in our results. Vogt (2012) pointed out some factors that can influence the discrepancy observed in this parameter, such as geographical latitude, habitat, differences in mortality rates, energy costs of reproduction, and hormonal issues. Additionally, penaeoid males generally present a higher growth coefficient (*k*) and consequently a lower asymptotic length (CL_∞) (Boschi 1969; García and Le Reste 1986; Petriella and Boschi 1997), as well as lower longevity (Castilho et al. 2012).

Garcia et al. (2016) propose that the lower longevity (and consequent lower asymptotic length) of males is due to their higher metabolic rate, which leads to a cellular senescence induced by the higher investment in the growth rate (a higher *k* than for the females). This could also explain the tendency for males to show higher mortality rates compared to females (Gab-Alla et al. 1990). We therefore propose that the lower longevity of males is the main reason for the female-biased sex ratio, even though we do not discard the possible influence of other factors. Among them, are the higher susceptibility of females to sampling gear as a function of their search for food during the period of ovary maturation (Kevrekidis and Thessalou-Legaki 2006), migratory activities, and differential habitat occupation (Wenner 1972), among others.

Many studies have observed that some marine crustaceans can experience differential environmental influences at latitudinal scales that can impact their life history parameters (Castilho et al. 2015a; Garcia et al. 2016). Bauer (1992) and Castilho et al. (2007b) state that penaeoid life history aspects such as longevity and size at the onset of sexual maturity can vary according to the environmental conditions related to latitude, such as water temperature and nutrient availability. According to this “latitudinal effect paradigm”, in subtropical and temperate regions, individuals tend to exhibit a slower growth rhythm and a higher longevity, likely influenced by the lower water temperatures found in these areas (Bauer 1992).

To date, Garcia et al. (2016) have provided the only available data on *R. constrictus* growth estimates carried out on the Brazilian Coast. This study, carried out in the Cananéia region at higher latitudes values (25°S) than Ubatuba, reports lower asymptotic lengths (females: 16.40 mm; males: 11.74 mm), longevities (females: 415 days [1.14 year]; male: 267 days [0.73 year]) and growth coefficients (females: 0.011; males: 0.017) compared to our results, suggesting that the latitudinal effect paradigm is not applicable to this species’ population dynamics between these two regions.

To comprehend this scenario, it is necessary to keep in mind that physical processes influence the biological ones (Castro-Filho et al. 1987). Cananéia (southern littoral) and Ubatuba (northern littoral) show distinct physical features and thus have distinct biological processes. We propose, therefore, that uncountable factors related to the peculiar features of the Ubatuba region (different from Cananéia) influenced the biological processes in different ways and intensities, resulting in such exceptions to the latitudinal pattern. We propose three possible factors that can be held responsible for such a situation, which are listed below.

The first of these, typical of Ubatuba, is the water temperature, which is strongly molded by water masses such as the SACW which approaches the coastal zone during late spring and early summer, causing a decrease in bottom water temperature (<18º C) and salinity (<36) (Castro-Filho et al. 1987). According to Mantelatto and Fransozo (1999), the approaching SACW exerts a strong influence on the water temperature close to the bottom and causes considerable changes in the local communities. The SACW-induced low water temperatures possibly influence the environmental patterns so that Ubatuba presents subtropical rather than tropical environmental features (since shrimp seem to grow more slowly, reach larger sizes, and live longer).

Bauer (1992) points out that some taxa may have planktotrophic larvae, which are affected by very different pressures in the plankton (oscillations in the food supply and predators, for instance) that may influence larval success and recruitment in a variety of ways. Thus, the second factor is based on the statement by Vega-Pérez (1993) asserting that during the approaching SACW the chlorophyll values are higher due to an increase in phytoplankton production, confirming the tendency for water enrichment along the continental shelf during summer (Castro-Filho et al. 1987). Therefore, we propose here that the amount of nutrients in the water column might also have influenced the life history parameters observed in this study. Because the SACW may provide an important source of nutrients and allow a greater larval success, it also makes sense that individuals would be able to reach greater sizes and longevities.

The third and last proposed influencing factor is the type of sediment found in this region, which was characterized by Mantelatto and Fransozo (1999) and shown to be composed mainly of very coarse, coarse, and medium sand. This type of sediment favors not only a higher retention of organic matter content (a possible food resource) but also favors this species' common burrowing behavior. Such behavior may play a fundamental role in the defense of these organisms against predators (Dall et al. 1990), which could also correspond to a higher longevity. According to Negreiros-Fransozo et al. (1991), the distribution of different types of sediment is controlled by water currents. The sinuous littoral observed in Ubatuba (Ab'Sáber 1955) provides great barriers to the entry of seawater, possibly decreasing the intensity with which currents approach this region, which would stir the sediment, forcing animals to emerge and making them more susceptible to capture and predation.

Castilho et al. (2015b) observed that the geographical proximity between regions could establish migratory connections between groups that are part of the same population. However, despite the latitudinal proximity between Cananéia (23ºS) and Ubatuba (25ºS), we strongly suggest that the peculiar oceanographic conditions from Ubatuba (particularly, the above-mentioned effects of the SACW) produced the factors that most likely led to the exceptions.

Several studies carried out with different penaeoidean species suggest the necessity for adaptations to the fisheries closure period. Studies on *P. muelleri*, *X. kroyeri* and *A. longinaris* (Castilho et al. 2012; 2015ab, respectively) show only 1, 11 and 2 growth curves protected in the fisheries closure seasons, from 15, 37 and 14 curves, respectively. We also observed that most of the recruitment cohorts do not arise during the months included in the closed fishery period (see figs. 5 and 6), thus strengthening this idea. Thus, it is reasonable to infer that the highest efficiency for protecting the species would be realized with an adaptation to the fisheries closure period in the months in which we can observe recruitment cohorts. Therefore, we propose here that the shrimp fishing closed season include late spring and early summer (from December to February) in addition to the already established closed months (March to May).

On the other hand, it is comprehensible that increasing the number of months covered by the fisheries closure period could induce social and economic issues (Castilho et al. 2015a). It is important to remember that the fishery activity is an essential source of income, employment and livelihood for millions of families, which are partially or totally dependent on it. Therefore, Castilho et al. (2015a) suggest further migration studies concerning the locations of the main stocks of reproductive and recruitment individuals in different areas. These data could be crucial for determining the zones and periods of total fishery prohibition, protecting not only the economically important species, but also the bycatch taxa. Additionally, Silva et al. (2013) attest that the management effectiveness of the shrimp fishery is not only achieved by closed fishing seasons, but also by the number of fishing licenses issued, the engine size and dimensions of fishing vessels, minimum mesh sizes and other characteristics as well.

We can infer that *R. constrictus* completes its ontogeny in the studied region since we sampled individuals in a wide range of size classes from juveniles to adults. We strongly believe that the growth coefficient was directly related to the longevity of the individuals and that the growth parameters ran counter to the expected latitudinal effect paradigm, likely in response to the environmental conditions observed in Ubatuba. The present study provides information of undoubted relevance to the field of fishing management, since we present a basis for the establishment of sustainable capture policies. On the basis of such results, therefore, we strongly recommend that the fisheries closure period be changed to protect this species' recruitment period and, consequently, also its adult individuals. It is important to keep in mind that scientifically based knowledge is indispensable for protecting with greater efficiency the ecologically important stocks and avoiding their collapse in the near future. To achieve excellence in such activities, it is crucial to support additional studies at a wide geographical scale in order to understand the influence of latitudinal variations in the growth dynamics of this species.

References

Ab'Sáber AN, 1955. Contribuição à geomorfologia do litoral paulista. Revista Brasileira de Geografia, 17: 3-48.

Bauer RT, 1992. Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. Invertebrate Reproduction and Development, 22: 193-202.

Bauer RT and Lin J, 1994. Temporal patterns of reproduction and recruitment in populations of the penaeid shrimps *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson) (Crustacea: Decapoda) from the Northcentral Gulf of Mexico. Journal of Experimental Marine Biology and Ecology, 182: 205-222.

Bauer RT and Rivera Vega LW, 1992. Pattern of reproduction and recruitment in two sicyoniid shrimp species (Decapoda: Penaeoidea) from a tropical seagrass habitat. Journal of Experimental Marine Biology and Ecology, 161: 223-240.

Boschi EE, 1969. Crecimiento, migración y ecología del camarón comercial *Artemesia longinaris* Bate de Mar del Plata. FAO Fisheries Report, 57: 833-846.

Boschi EE, 1989. Biología pesquera del langostino del litoral patagonico de Argentina (*Pleoticus muelleri*). Instituto Nacional de Investigacion y Desarrollo Pesquero, 646: 5-71.

Campos BR, Branco JO, D'Incao F, 2011. Crescimento do camarão-sete-barbas (*Xiphopenaeus kroyeri* (Heller 1862)), na Baía de Tijucas, Tijucas, SC (Brasil). Atlântica, 33: 201-208.

Castilho AL, Bauer RT, Freire FAM, Fransozo V, Costa RC, Grabowski RC, Fransozo A, 2015a. Lifespan and reproductive dynamics of the commercially important sea bob shrimp *Xiphopenaeus kroyeri* (Penaeoidea): synthesis of a 5-year study. Journal of Crustacean Biology, 35: 30-40.

Castilho AL, Costa RC, Fransozo A, Boschi EE, 2007a. Reproductive pattern of the South American endemic shrimp *Artemesia longinaris* (Decapoda: Penaeoidea), off São Paulo state, Brazil. Revista de Biologia Tropical, 55: 39-48.

Castilho AL, Costa RC, Fransozo A, Negreiros-Fransozo ML, 2008b. Reproduction and recruitment of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the Southeastern coast of Brazil. Marine Biology Research 4: 361-368.

Castilho AL, Furlan M, Costa RC, Fransozo V, 2008a. Reproductive biology of the rock shrimp *Sicyonia dorsalis* (Decapoda: Penaeoidea) from the southeastern coast of Brazil. Invertebrate Reproduction and Development, 52: 59-68.

Castilho AL, Gavio MA, Costa RC, Boschi EE, Bauer RT, Fransozo A, 2007b. Latitudinal variation in population structure and reproductive pattern of the endemic South American shrimp *Artemesia longinaris* (Decapoda: Penaeoidea). Journal of Crustacean Biology, 27: 548-552.

Castilho AL, Grabowski RC, Simões SM, Santos APF, Costa RC, Fransozo A, 2015b. Lifespan and population dynamics of the endemic South American shrimp *Artemesia longinaris* (Crustacea: Penaeidae) in southeastern Brazil. Anais da Academia Brasileira de Ciências, 87: 2123-2138.

Castilho AL, Wolf MR, Simões SM, Bochini GL, Fransozo V, Costa RC, 2012. Growth and reproductive dynamics of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. Journal of Marine Systems, 105-108: 135-144.

Castro-Filho BM, Miranda LB, Miyao SY, 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. Boletim do Instituto Oceanográfico, 35: 135-151.

Cerrato RM, 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Canadian Journal of Fisheries and Aquatic Sciences, 47: 1416-1426.

Costa RC and Fransozo A, 2004a. Reproductive biology of the shrimp *Rimapenaeus constrictus* (Decapoda, Penaeidae) in the Ubatuba Region of Brazil. Journal of Crustacean Biology, 24: 274-281.

Costa RC and Fransozo A, 2004b. Abundance and ecologic distribution of the shrimp *Rimapenaeus constrictus* (Crustacea: Penaeidae) on the northern coast of São Paulo State, Brazil. Journal of Natural History, 38 (7): 901-912.

Dall W, Hill BJ, Rothlisberg PC, Sharples DJ, 1990. The Biology of the Penaeidae. In: Blaxter JHS and Southward AJ (Eds), Advances in Marine Biology. San Diego: Academic Press, 489pp.

Dias Neto J, 2011. Proposta de plano nacional de gestão para o uso sustentável de camarões marinhos do Brasil. Brasília: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis e Ministério do Meio Ambiente. IBAMA, 59 (1): 242pp.

D'Incao F and Fonseca DB, 1999. Performance of the von Bertalanffy growth curve in penaeid shrimps: a critical approach. In: von Vaupel Klein JC and Schram FR (Eds), The Biodiversity Crisis and Crustacea: Proceedings of the Fourth International Crustacean Congress. Amsterdam (The Netherlands), Brill Academic Publishers, Leiden, The Netherlands, pp. 733-737.

D'incao F, Valentini H, Rodrigues LF, 2002. Avaliação da pesca de camarões nas regiões Sudeste e Sul do Brasil. Atlântica 24: 103-116.

Fisher RA. 1930. The genetical theory of natural selection. New York Dover Publications, 318pp.

Fonseca DB and D'Incao F, 2003. Growth and reproductive parameters of *Kalliapseudes schubartii* in the estuarine region of the Lagoa dos Patos (southern Brazil). Journal of the Marine Biological Association of the United Kingdom, 5: 931-935.

Food and agriculture organization of the united nations (FAO), 2015. Transforming wasted resources for a sustainable future. The sustainable management of bycatch in

Latin America and Caribbean trawl fisheries. Fisheries and Aquaculture Department, 8pp.

Gab-alla AAFA, Hartnoll RG, Ghobashy AF, Mohammed SZ, 1990. Biology of penaeid prawns in the Suez Canal lakes. Marine Biology, 107: 417-426.

García S and Le Reste L, 1986. Ciclos vitales, dinámica, explotación y ordenación de las poblaciones de camarones peneidos costeros. FAO Documento Técnico de Pesca, 203: 180.

Garcia JR, Wolf MR, Costa RC, Castilho AL, 2016. Growth and reproduction of the shrimp *Rimapenaeus constrictus* (Decapoda: Penaeidae) from the southeastern coast of Brazil. Regional Studies in Marine Science, 6: 1-9.

Grabowski RC, Negreiros-Fransozo ML, Castilho AL, 2016. Reproductive ecology of the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) in a coastal area of Southern Brazil. Chinese Journal of Oceanology and Limnology, 34: 125-135.

Grabowski RC, Simões SM, Castilho AL, 2014. Population structure, sex ratio and growth of the seabob shrimp *Xiphopenaeus kroyeri* (Decapoda, Penaeidae) from coastal waters of southern Brazil. In: Wehrtmann IS, Bauer RT (Eds) Proceedings of the Summer Meeting of the Crustacean Society and the Latin American Association of Carcinology, Costa Rica. ZooKeys, 457: 253-269.

Hartnoll RG, 2001. Growth in Crustacea - twenty years on. Hydrobiologia, 449: 111-122.

Hiroki KAN, Fransozo A, Costa RC, Castilho AL, Shimizu RM, Almeida AC, Furlan M, 2011. Bathymetric distribution of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) (Decapoda, Penaeidae) in two locations off the southeastern Brazilian coast. Marine Biology Research, 7: 176-185.

Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). <www.ibama.gov.br >. Acesso em Maio de 2016.

Kevrekidis K and Thessalou-Legaki M, 2006. Catch rates, size structure and sex ratio of *Melicertus kerathurus* (Decapoda: Penaeidae) from an Aegean Sea trawl fishery. Fisheries Research, 80: 270-279.

King M, 1995. Fisheries biology, Assessment and Management. Fishing News Books, Oxford, UK, 341pp.

Mantelatto FLM and Fransozo A, 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo state, Brazil. Revista Brasileira de Biologia, 59: 23-31.

Negreiros-Fransozo ML, Fransozo A, Pinheiro MAA, Mantelatto FLM, Santos S, 1991. Caracterização Física e Química da Enseada de Fortaleza, Ubatuba, SP. Revista Brasileira de Geociências, 21: 114-120.

Pérez-Farfante I, 1988. Illustrated key to Penaeoid shrimps of commerce in the Americas. NOAA Technical Report NMFS, 64: 1-32.

Pérez-Farfante I and Kensley B, 1997. Penaeoid and Sergestoid shrimps and prawns of the World. Keys and diagnoses for the families and genera. Paris, Éditions du Muséum National d Histoire Naturalle, 233pp.

Petriella AM and Boschi EE, 1997. Crecimiento en crustáceos decápodos: resultados de investigaciones realizadas en Argentina. Investigaciones Marinas 25: 135-157.

Pires-Vanin AMS, 2001. Identifying the components of ecological variation in a marine benthic megafauna. Revista Brasileira de Oceanografia, 49: 29-38.

Semensato XEG and Di Beneditto APM, 2008. Population dynamic and reproduction of *Artemesia longinaris* (Decapoda, Penaeidae) in Rio de Janeiro State, South-Eastern Brazil. Boletim do Instituto de Pesca, 34: 89-98.

Silva CNS, Broadhurst MK, Medeiros RP, Dias JH, 2013. Resolving environmental issues in the southern Brazilian artisanal penaeid-trawl fishery through adaptive co-management. Marine Policy, 42: 133-141.

Simões SM, D'Incao F, Fransozo A, Castilho AL, Costa RC, 2013. Sex ratio, growth and recruitment of the pelagic shrimp *Acetes americanus* on the southeastern coast of Brazil. Journal of Crustacean Biology, 33: 1-9.

Soares-Gomes A and Pires-Vanin AMS, 2003. Padrões de abundância, riqueza e diversidade de moluscos bivalves na plataforma continental ao largo de Ubatuba, São Paulo, Brasil: uma comparação metodológica. Revista Brasileira de Zoologia, 20: 717-725.

Vega-Pérez LA, 1993. Estudo do zooplâncton da região de Ubatuba, Estado de São Paulo. Publicação Especial do Instituto Oceanográfico, 10: 65-84.

Vogt G, 2012. Ageing and longevity in the Decapoda (Crustacea): A review. Zoologischer Anzeiger, 251: 1-25.

Von Bertalanffy L, 1938. A quantitative theory of organic growth. Human Biology 10: 181-213.

Wenner AM, 1972. Sex ratio as a function of size in marine crustacean. American Naturalist, 106: 321-350.

Wilson K and Hardy ICW, 2002. Statistical analysis of sex ratio: an introduction. In: Hardy ICW (Ed), Sex ratios: concepts and research methods. Cambridge University Press, Cambridge, pp 48-92.

Yamada R, Kodama K, Yamakawa T, Horiguchi T, Aoki I, 2007. Growth and reproductive biology of the small penaeid shrimp *Trachysalambria curvirostris* in Tokyo Bay. Marine Biology, 151: 961-971.

Capítulo 2

A five-year study on the reproduction and recruitment pattern of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) on the southeastern Brazilian coast

A five-year study on the reproduction and recruitment pattern of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) on the southeastern Brazilian coast

Abstract

This is the first study to evaluate in a wide spatiotemporal scale the reproduction and recruitment of *Rimapenaeus constrictus*, a bycatch species strongly affected by the amount of fishing activities. Monthly samples were obtained in the northern littoral of São Paulo state from Jan/1998 to Jun/2003, with a gap from Jan/01 to Jun/01, in order to determine the size at the onset of sexual maturity, the reproductive and recruitment patterns and the copulation period. In our study, 6,456 shrimps were captured among which 5,774 were measured, which 4,322 were females and 1,452 were males. The estimated maturity was 8.3 mm and 11.2 mm, for males and females, respectively. Reproductive females were found over the 5-year study. These results suggests a continuous reproduction pattern, with peaks in summer and in spring. We verified a positive significant relation between reproductive females and temperature (lag +1 and +3), although the decrease in bottom water temperature in some peaks of reproductive activity (spawning), which was probably induced due to SACW intrusion. The recruitment was considered episodic and even though no significant relation was found between immatures and reproductive females, we suggested that the main recruitment peaks observed were a consequence of the major reproductive activities a few months prior to it. The copulation period was continuous in the sampled period, and ISP females (recently copulated) were significant correlated with reproductive males (lag 0). Thus, we propose that during this period the sexual proportion is 1:1, probably due to the migration of reproductive males, attracted to copulate. Our results provide information of incontestable relevance to our wide knowledge of the species' reproductive biology, in order to support an accurate fishing management.

Keywords: Mating, spawning, sex ratio, bimodal reproduction.

Introduction

In the Brazilian coastal area, the artisanal shrimp fishing activities aims to capture mainly the stocks of the pink shrimp (*Farfantepenaeus brasiliensis* (Latreille, 1817) and *F. paulensis* (Pérez-Farfante, 1967)) and of the seabob shrimp (*Xiphopenaeus kroyeri* (Heller, 1862)). Secondarily, the industrial fishing fleet focuses their effort in capturing other Dendrobranchiata species such as the “barba-ruça” shrimp (*Artemesia longinaris* Spence Bate, 1888), the “santana" shrimp (*Pleoticus muelleri* (Spence Bate, 1888)) and the white shrimp (*Litopenaeus schmitti* (Burkenroad, 1936)) (D’Incao et al. 2002). Even though only a small group of species presents a considerable economical interest, fishermen around the globe capture a much larger number of organisms (among them, other crustaceans, mollusks, fishes, jellyfishes, echinoderms, etc.) together to the target species. Such biodiversity (known as the bycatch fauna) is unintentionally captured due to the low selectivity of the used fishing gear (i.e. trawling nets), and in most of the times, such individuals are discarded back to the sea, highly weakened, or even dead (Branco 2005; FAO 2015; Mantelatto et al. 2016).

The species addressed in this study, *Rimapenaeus constrictus* (Stimpson, 1874), presents a wide geographical distribution, with occurrences recorded from Canada (44ºN) to southern Brazil (26ºS) (Costa et al. 2003). Unfortunately, their wide geographical range may result in an equally high influence from the shrimp fishing activities. Therefore, even though *R. constrictus* does not represent an expressive economic resource, it should be considered for fisheries management purposes, since it is a part of the bycatch fauna, and also plays an important ecological role in the trophic web where they inhabit (Costa and Fransozo 2004ab; Keunecke et al. 2007; Robert et al. 2007).

Even presenting such an ecological importance and being captured by the trawling fleet, only a few studies were carried out addressing the reproductive biology of *R. constrictus* along the Brazilian coast. Costa and Fransozo (2004a) described the spatio-temporal variation in their reproductive and recruitment patterns in three different bays along the Ubatuba region, and Garcia et al. (2016) addressed its growth and reproductive dynamics in the Cananéia region. The remaining studies composing the available literature were focused in the species’ ecological distribution (Costa and Fransozo 2004b; Hiroki et al. 2011) and long-term growth analysis (Lopes et al. 2017). However, the reproductive and recruitment patterns were not analyzed under a long-term perspective so far.

In the study of penaeid shrimps’ reproductive biology, an accurate description of the spawning and reproductive stocks, as well as the dynamics acting over their relation, is essential to the better understanding of the variables associated to this process. The spawning and recruitment periodicity are commonly assessed by the variation in the frequency of reproductive females and juveniles, respectively (Crocos and Van Der Velde

1995; Castilho et al. 2007). Dall et al. (1990) considered that the reproductive process may occur seasonally or continuously throughout the year, depending on the variation in environmental conditions observed in each locality and period. Concerning tropical penaeids, the higher homogeneity observed in environmental features (especially water temperature) in this region allows them to reproduce year-round, even though with peaks, while reproductive seasonality becomes the rule for penaeids far from the equator (Sastry 1983; García 1988; Dall et al. 1990).

Temperature might be considered as an important factor determining the reproductive periodicity, acting as an environmental stimulus over the ovarian development in several marine invertebrate species (Orton 1920; Bauer 1992). Furthermore, Thorson (1950) purposes that, in fact, the "real" selective pressure ("ultimate factor") influencing the reproductive dynamics would be the food availability for early larval stages (i.e., phytoplankton and zooplankton), and thus, temperature would be no more than the environmental clue that would trigger this process ("proximate factor"). In other words, variations in temperature levels would increase or decrease the abundance of planktonic food, which in turn, would indeed affect the reproductive success of a given species.

The aim of this study was to describe and characterize the long-term reproductive pattern of *R. constrictus* in the Ubatuba region, off the São Paulo state, southeastern Brazil. The specific objectives were to assess the influence of bottom water temperature over the reproductive parameters, as well as to describe the long-term seasonal variations in sex ratio and recruitment patterns.

Material and methods

Sampling

Sampling were carried out monthly from Jan/1998 through Jun/2003, with a gap from January 2001 through June 2001, along the northern coast of São Paulo State in the Ubatuba region (23º29′06″S, 45º05′00″W). Samples were obtained during the day using a shrimp-fishing boat outfitted with double-rig nets (mesh size: 20 mm knot-to-knot in the body and 15 mm in the cod end). We performed 564 trawls, with each of them extending for two kilometers and 30 minutes, sampling a total area of 18,000 m².

Due to the high number of individuals captured in some trawls, a 100-g subsample was taken at random for the analysis of individuals according to sex, gonadal development and size (using a vernier caliper to assess the carapace length, CL, to the nearest 0.1 mm). The abundance of individuals was extrapolated from this subsample for each defined gonadal stage: immature, spent, developed and mature (females); and immature, lacking spermatophores and mature (males) (more details see topic 2.3, below) (Garcia et al. 2016). Since the annual capture effort has differed in each year of sampling, the catch per unit effort (CPUE) was used in order to standardize the data when subjected to comparative analyses among years.

Bottom water temperature

Since *R. constrictus* is a benthic species (Costa and Fransozo 2004ab), we only analyzed the bottom water temperature. It was assessed in each sampling station, using a Nansen bottle, and measured (º C) with a mercury thermometer attached to it.

Reproduction

Individuals were measured to their carapace length (CL), a standard body measurement that corresponds to the linear distance from the post-orbital angle and the posterior margin of the carapace. Shrimps were then sorted to sex, according to the morphology of the first pleopod (males) or of the sternum (females) (Costa et al. 2003). Their reproductive condition was assessed by the macroscopic observation of the degree of ovarian development in females (color and volume occupied by the gonads), thus considering four stages, as it follows. Immature individuals (IM) displayed ovaries varying from thin and transparent strands to thicker strands; spent (SP) presented white ovaries, much larger and thicker than the ones observed for IM; developed (DE) had light green ovaries; and mature (MA) displayed green to dark green ovaries, much larger than the ones observed for the previous stages (Costa and Fransozo 2004a). Females were defined as recruits if their gonads were in the IM stage; adults if in the SP, DE and MA stages, whereas reproductive if they were in the DE and MA stages (Garcia et al. 2016). The presence of the sperm plug attached to the thelycum was macroscopically observed for adult females, thus referring to them as inseminated females (IN).

In penaeids, sexual maturity of males is indicated by joining of the cincinnuli from the endopods of the first abdominal appendage in adults, while in recruits (IM), the endopods are not joined (Bauer and Rivera Vega 1992). Since spermatophores are visible through the transparent exoskeleton, the maturity of adult males was classified according to their developmental stage, visible through the terminal ampoule (ejaculatory duct) (Chu 1995). Males were thus defined as lacking spermatophores (LS) when this structure was not macroscopically visible in adults; and as spermatophore-bearing males (MA) if the same structure was visible and occupied a portion of or all the terminal ampoules (Castilho et al. 2015a). If individuals were in the LS and MA stages, they were defined as adults; if they were in the IM stage, we considered them as recruits; while MA individuals were considered as reproductive males.

In the present study, the reproductive period (spawning) was estimated by the frequency in the CPUE of reproductive females (DE+MA) along the studied months, while the copulation period was determined by the abundance of inseminated spent (ISP) females. The recruitment was determined based on the frequency in the CPUE of recruits (immatures) of both sexes in the population along the studied months.

Crosscorrelation analyses were performed to evaluate the possible relation between monthly abundance of reproductive females with recruits and with the monthly mean values of water temperature. Furthermore, this analysis was also used to test the association between ISP females and reproductive males, aiming to determine the copulation periods. We also tested the relation between the abundance of reproductive and ISP females, attempting to confirm if there is a time lag between the abundance of females that copulate (ISP) and then develop their ovaries (reproductive). In cross-correlations, two series of data are compared as a function of time lag (n), using the Pearson correlation coefficient to measure relations between values of the first data series with values of the second series either from earlier (in negative lags) or later months (in positive lags). Correlation coefficient values at lag 0 are equivalent to the standard Pearson correlation (Statsoft 2011).

Sexual maturity

To determine the size at the onset of male and female sexual maturity, we analyzed the proportion of immature and adult individuals in size classes of 1.0 mm CL. The procedure was based on fitting the sigmoid logistic curve (Somerton 1980). We used the equation $y = 1/(1 + e^{(-r(CL-CL50))})$, where y is the estimated proportion of adult shrimps, CL_{50} is the carapace size at the onset of sexual maturity, and r is the coefficient for the slope of the logistic curve. The logistic curve was fitted by least squares to the previously mentioned proportions for each size class of all individuals and samples using maximumlikelihood iterations. After adjusting the regression model, sexual maturity (CL_{50}) was estimated as the size in which 50% of both males and females reached maturity.

Results

During this study, 6,456 shrimps were captured, with an average of 11.5 individuals per trawl set (ind/t). From this amount, 5,774 were randomly sorted and measured, among which 4,322 were females and 1,452 were males.

Males and females showed different size distributions, where females reached greater carapace lengths. While most of the males were in the mature stage (especially in the 8-11 mm size classes), most of the females were in the spent stage (especially in the 10-13 mm size classes). The estimated CL_{50} was smaller for males than females, with estimates of 8.3 mm and 11.2 mm, respectively (Fig. 1).

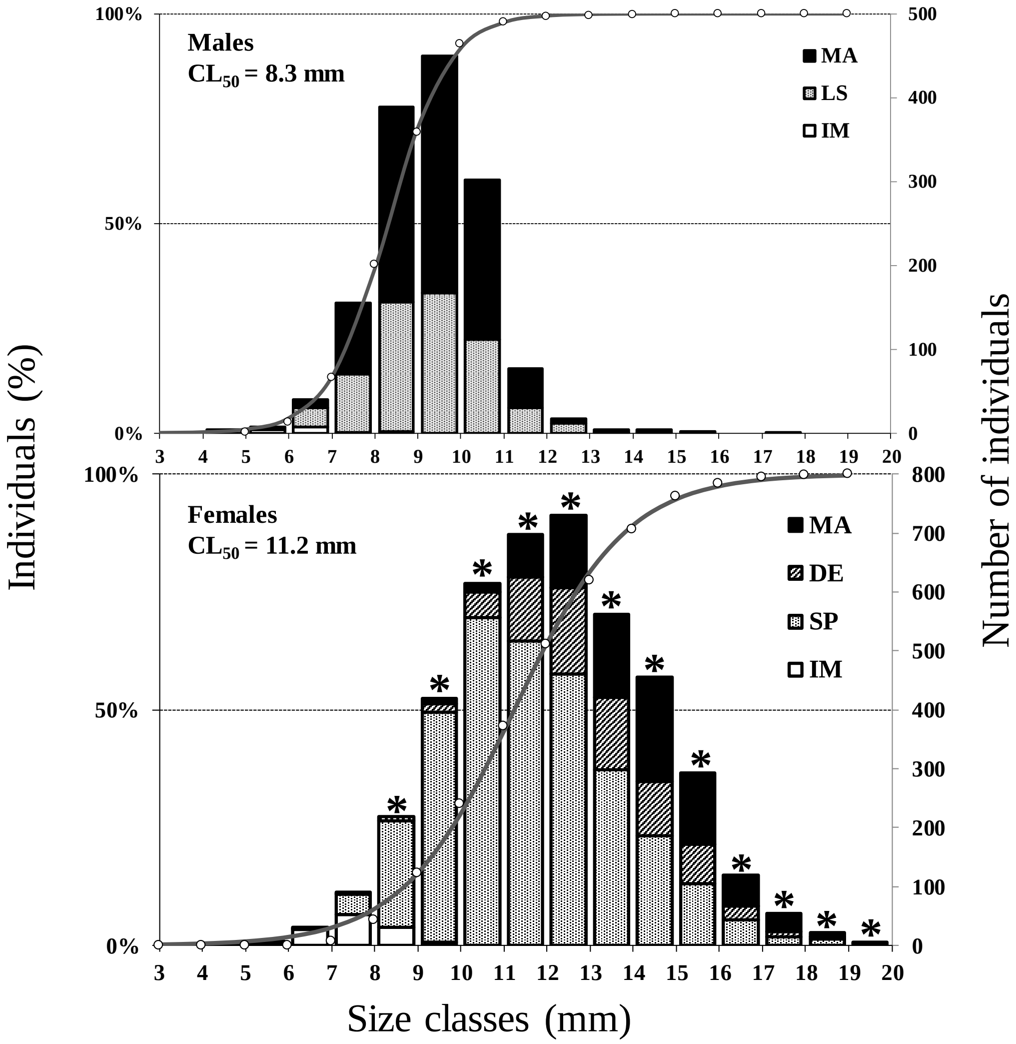

Figure 1. *Rimapenaeus constrictus* (Stimpson, 1874). Distribution of demographic categories for males and females among size classes from January 1998 through June 2003 in the Ubatuba region, southestern Brazil (IM= immature; SP= spent females; LS= lacking spermatophore males; DE= developed females; MA= mature males and females; *= size classes in which inseminated females were observed).

Variation in the CPUE for reproductive females is shown together with bottom water temperature (Fig. 2A). During the whole sample period, we observed reproductive females in most of the months, except for July (winter) 1998, January (summer) and June (autumn) 2000, and May (autumn) 2003. For all the sampled years, higher abundances of reproductive females were recorded mostly from October through March (spring - summer), with two peaks of greater abundance in each year. In most of the years, it was possible to observe a decreasing trend in bottom water temperature (below 20ºC), especially in November 1999, 2000, 2001 and December 2002 (spring). The bottom water temperature was positively correlated with the number of reproductive females in a time lag of +1 and +3 (Crosscorrelation, $p<0.05$).

Immature individuals did not show any clear distribution pattern along the sampling periods (Fig. 2B), even though we identified peaks in April 1999, July 2000, October 2001, and June 2002/2003. Furthermore, they were captured in low monthly abundances (up to a maximum of approximately 3 individuals per trawl), being even absent in some months, or in most of them, as observed in 2000. No significantly statistical relation was observed between immature individuals and reproductive females (Crosscorrelation, $p>0.05$).

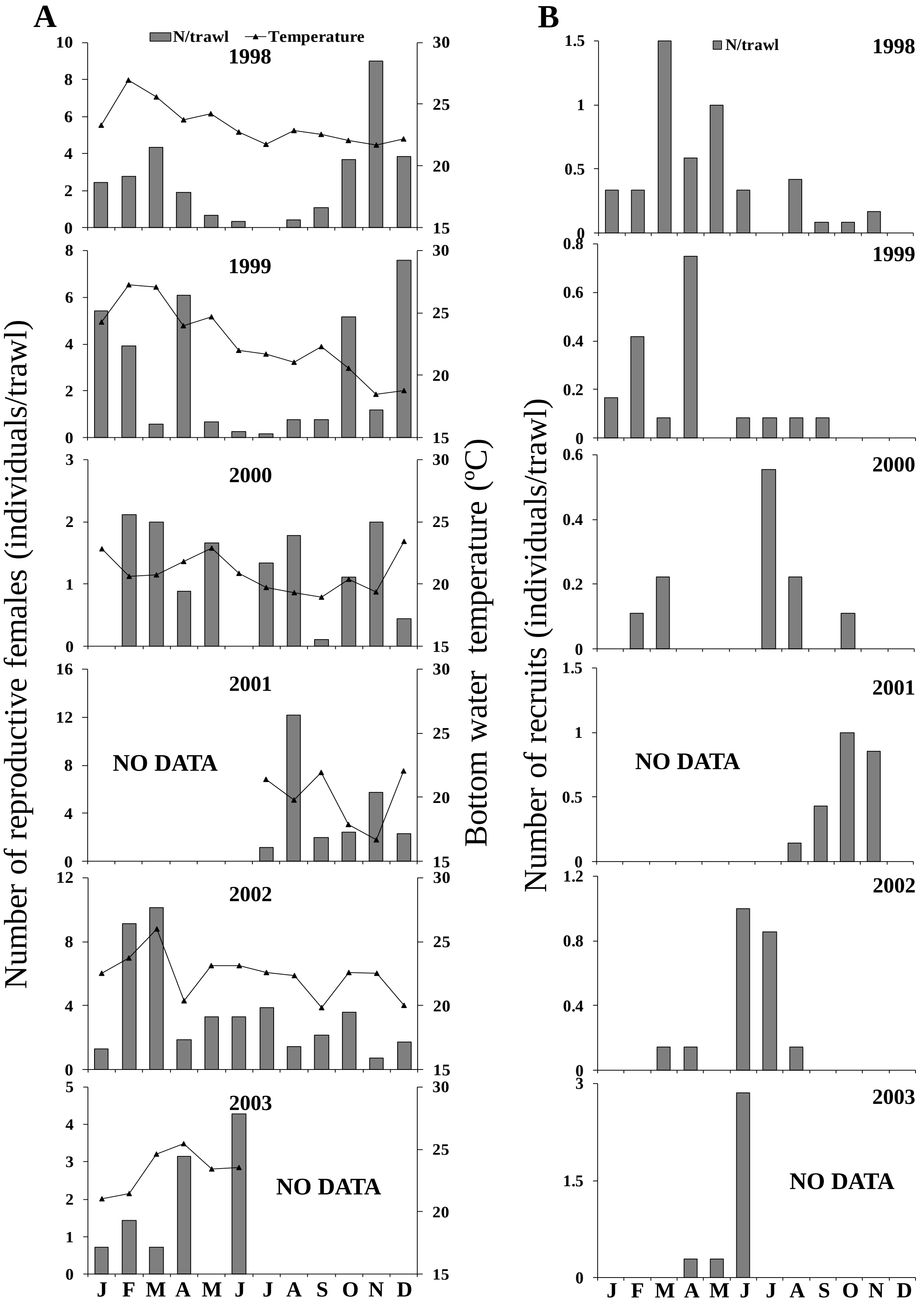

Figure 2. *Rimapenaeus constrictus* (Stimpson, 1874). A: Variation in the CPUE of reproductive females and monthly mean bottom water temperature (° C); B: Variation in the CPUE of immature individuals over the 5-year study period, in the Ubatuba region, southeastern Brazil.

A significant positive relation between the abundance of reproductive and ISP females was observed in a time lag of 0 and -2. The abundance of ISP females was positively correlated with the number of reproductive males with no time lag (0) (Crosscorrelation, $p<0.05$). Except for 2003, when no ISP females were recorded, the abundance of ISP females was observed in all months, with a trend of higher total abundance recorded mainly during spring (October to December) and summer-early autumn (January and April) (Fig. 3).

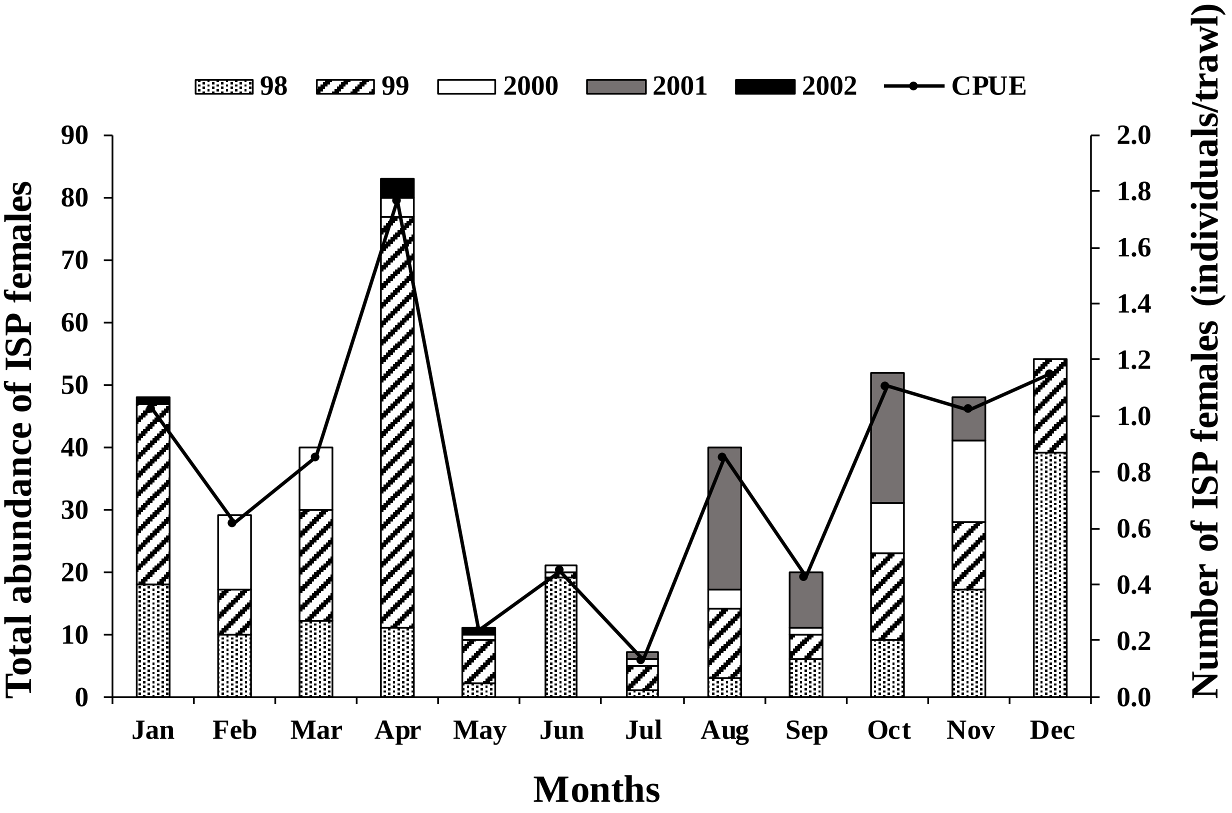

Figure 3. *Rimapenaeus constrictus* (Stimpson, 1874). Monthly variation in the abundance and CPUE of inseminated spent (ISP) females. Samples taken from January 1998 through June 2003 in the Ubatuba region, southeastern Brazil.

Discussion

In this study, females of *R. constrictus* reached greater carapace lengths when compared to males. Boschi (1989) affirmed that it represents a general rule established for penaeids and it characterizes the sexual dimorphism observed for this species (Garcia et al. 2016), as well as for other penaeids (Castilho et al. 2012; Sancinetti et al. 2015; Castilho et al. 2015ab). Males also reached the sexual maturity earlier when compared to females. Similarly, in the Ubatuba region, Costa and Fransozo (2004a) observed lower values of sexual maturity, estimated at $CL_{50\%}$= 7.8 mm (females) and $CL_{50\%}$= 7.0 mm (males); whereas in the Cananéia region, Garcia et al. (2016) estimated $CL_{50\%}$= 10.5 mm (females) and $CL_{50\%}$= 8.2 mm (males). The differences observed for the onset of sexual maturity varies considerably among species, between populations of the same species and between individuals of the same population, and is generally related to the maximum range of a particular individual size (Fonteles-Filho 1989). Considering that females reach greater body sizes when compared to males, it is reasonable for them to present higher sizes at onset of sexual maturity when compared to males.

According to Bauer (1992), the reproduction of benthic marine invertebrates commonly follows a latitudinal paradigm and tends to be continuous in the tropics, while seasonal at higher latitudes. It may happen due to the relatively homogeneous and elevated water temperatures observed year round in such tropical areas, allowing reproduction to take place continuously (Sastry 1983). Several penaeoid shrimp species followed this classical paradigm, such as *Artemesia longinaris* Spence Bate 1888 (Castilho et al. 2007; Semensato and Di Beneditto 2008), *Pleoticus muelleri* (Bate 1888) (Castilho et al. 2008a), *Sicyonia dorsalis* Kingsley 1878 (Castilho 2008b), and *Xiphopenaeus kroyeri* (Heller 1862) (Grabowski et al. 2016). It also seems to hold true for *R. constrictus*, as previously described in the literature by Garcia et al. (2016), who observed a seasonal reproduction in a subtropical region, while Costa and Fransozo (2004a) reported continuous reproduction on a tropical region. The present study strengthen this statement, since reproductive females were registered along the entire sampled period, suggesting a continuous reproduction for this species in southeastern Brazil.

Besides the continuous reproductive pattern, we identified two main peaks of reproductive females, in most of the years, suggesting that even though reproduction in this area is continuous, there may be two main peaks. According to Pauly et al. (1984), penaeid shrimps generally present two spawning peaks per year indeed, which is common even at low latitudes (Dall et al. 1990). Similar patterns to those observed in this study were verified for the *R. constrictus* by Costa and Fransozo (2004a), who have found peaks of higher reproductive activities during summer, and lower in winter; and for *X. kroyeri* (Semensato and Di Beneditto 2008; Grabowski et al. 2016). Dall et al. (1990) stated that a large number of penaeid shrimp species presents two main reproductive peaks yearly, generally in September-November and March-May; however, each species may respond in different ways to peculiar local environmental features. Briefly, penaeid species distributed close to the equator generally tend to exhibit a continuity in their spawning, even though not totally homogeneous throughout the months.

Even though Costa and Fransozo (2004a) did not observe a significant correlation between the relative frequency of reproductive females and bottom water temperature, it is considered as an important regulating factor in the reproductive period for penaeids, and might directly affect the ovary development cycle (Bauer and Lin 1994). For instance, the eggs of the species of the genus *Rimapenaeus* (= *Trachypenaeus*) are pelagic, and thus, temperature would favor their embryonic and larval development (Dall et al. 1990). Actually, spawning in penaeids is generally concentrated in the warmer months (Bauer and Rivera Vega 1992). In the current study, it was possible to observe a significant positive relation between increases in the abundance of reproductive females and in the bottom water temperature, in time lags of 1 and 3. It suggests that the abundance of reproductive females increases as the bottom water temperature does, up to the third following months. It may be considered as an evidence that the variation in temperature acted as a proximate factor over reproduction (spawning), since variations in this factor influenced ovarian development. The same was reported for *R. constrictus* by Bauer and Lin (1994) and Garcia et al. (2016), as well as for other penaeiod shrimps (Castilho et al. 2015a; Costa et al. 2016).

The southeastern Brazilian coast is strongly influenced by the South Atlantic Central Water (SACW) mass, during late spring and summer. The arrival of SACW promotes decreases in the coastal water temperature (<20ºC), and causes other important changes in bottom-water characteristics (Castro-Filho et al. 1987), which considerable affect resident communities, either in a negative or in a positive way. In a wide temporal scale study, we detected the SACW intrusion during late spring for most of the years (except for 1998). Although the arrival of SACW induced decreases in bottom water temperatures in the same periods where we observed peaks in the frequency of reproductive females, the amount of nutrients brought along with the SACW may also have influenced the reproductive activity (especially in summer and spring) in this region, explaining the reproductive peaks recorded even at low (not favorable) temperatures.

According to Vega-Pérez (1993), in the Ubatuba region, the chlorophyll-*a* levels (phytoplankton production) increase in specific months, a likely effect of the intrusion of the SACW. It results in a higher phytoplankton production, which stimulates a subsequent production of zooplankton. In several marine organisms, the mainly reproductive (spawning) periods follow the annual increases of phytoplankton and zooplankton (i.e. larval food) production. Cushing (1975) proposed that the maximum reproductive investment of marine planktotrophic species coincides with the maximum seasonal abundances of phytoplankton. Likewise, Castilho et al. (2007; 2008ab; 2015a) reported this spring-summer reproductive investment, in long-term studies (5.5 years) with *A. longinaris*, *P. muelleri*, *S. dorsalis* and *X. kroyeri*. Thus, we strongly agree with Thorson (1950)'s hypothesis, which states that temperature may act as a proximate factor, while food availability for protozoeal larvae may be an ultimate factor (selective pressure) responsible for the reproductive period in *R. constrictus* (for details, see introductive section above).

Bauer (1989) found an episodic recruitment when analyzing the oscillation in the abundance of juveniles (immature) in nine shrimp species, i.e., in which it was not possible to clearly identify seasonal peaks in this parameter. In this long-term study, even though no significant relation was found between reproduction and recruitment (episodic pattern), the main recruitment peaks may be considered a consequence of the major reproductive periodicity (spawning and subsequent recruitment 2 or 3 months later). In this sense, the recruitment peaks observed around autumn would be a result of the reproductive activities recorded in summer, as it follows. Therefore, the main recruitment periods observed in our study are in agreement with the recruitment curves obtained in the growth analysis performed by Lopes et al. (2017). Analyzing the growth curves obtained by these authors, together to the recruitment periods we observed in our study, one may infer that the individuals composing the smaller size classes around autumn for both studies would be descendants from the spawning processes taking place in late spring and during summer. Similarly, previous studies reported no seasonal trends in recruitment periodicity for the same species as here concerned (Bauer and Lin 1994; Costa and Fransozo 2004a; Garcia et al. 2016), as well as for other penaeoids, such as *A. longinaris* (Castilho et al. 2007), *P. muelleri* (Castilho et al. 2008a) and *X. kroyeri* (Castilho et al. 2015a).

Several conditions can lead to episodic recruitment in penaeid shrimps, such as large variations in the mortality of planktonic larvae and early developmental stages (Bauer 1989), associated to the variation in phytoplankton production (larval food). In penaeid shrimps, particular environmental conditions observed in each location can influence the complex stock-recruitment relationship. For instance, it is possible to cite the presence of predators, larval food availability and water changes induced by SACW intrusion (Castilho et al. 2007; 2015a). Thus, it may be possible that the specific environmental conditions observed in the region contributed to the absence of a clear recruitment pattern in our study. However, it is noteworthy that other studies addressing the species, under different environmental situations (Bauer and Lin 1994; Garcia et al. 2016), also reported the absence of a clear recruitment pattern, and thus, one should also consider that intrinsic factors or other parameters not considered in our study may act as a stimuli over this process.

The significant correlation found between reproductive and ISP females in a time lag of 0 and -2 suggests that the main copulation period may occur at the same time as reproduction (lag = 0) and 2 months prior to it (lag = -2), confirming that ISP females take a few months to mature their gonads (thus becoming reproductive). Besides, it also could be considered an evidence for the continuous reproduction previously reported for this species (Costa and Fransozo 2004a), as well as in our results. For *R. constrictus*, the presence of a plug in ISP females can be considered as an evidence of copulation. In our study, it was possible to be confirmed by the positive correlation found between ISP females and reproductive males with no time lag (0), supporting the assumption that that species with a closed thelycum copulate immediately after ecdysis (when females are in the spent gonadal stage) (Dall et al. 1990).

The copulation period in *R. constrictus* was continuous, since ISP females were observed continuously in the entire period. Peaks were evident mainly in summer and spring, similarly to the main reproductive peaks. According to Coelho and Santos (1993), in copulation and growth areas males and females are equally distributed, being susceptible to the same action of the fishing gears. On the other hand, in the reproductive (spawning) areas, there is female aggregation and, therefore, they end up being more vulnerable to the fishing gears.

In our study, we sampled a higher abundance of females, when compared to males. Similar results were previously reported for not only the studied species (Garcia et al. 2016) but also for other penaeoidean shrimp species, such as *A. longinaris* (Castilho et al. 2015b), *X. kroyeri* (Grabowski et al. 2016), *Sicyonia dorsalis* (Castilho et al. 2008b). Thus, general abundance here observed consists an evidence that *R. constrictus* follows the theory purposed by Wenner (1972), which attests that several crustaceans tend to exhibit a sexual proportion different from 1:1. On the other hand, in Fisher (1930)'s theory, it is observed that gonocorical species tend to exhibit a sex ratio close to 1:1 as a rule.

Based on the results obtained in the crosscorrelation analyses, we observed that during the copulation period, the individuals involved in this process (reproductive males and ISP females) tend to present a similar distribution throughout the year, i.e., both demographic classes seem to occupy the same areas, simultaneously. Deviations towards females in the 1:1 sex ratio may occur due to differential sex-related occupation of niches. According to Dall et al. (1990), in species with closed thelycum, males would court females when they were close to moulting, since it is when females signal their sexual receptivity using pheromones. In several crustacean species, the copulation seems to be tied to a sex pheromone secreted in the female urine and its receiving by the males (near the basis of their antennules), which may be considered a mating stimulating factor (Misamore and Browdy 1996), and consequently attracting males to copulate. Thus, it seems reasonable to attest that in this study, the sex ratio got closer to 1:1 only during the supposed copulation periods, mainly in its peaks (especially during Summer-Spring). It suggests that males may migrate to copulate since they are attracted to, and thus their population will be found to present a 1:1 proportion mainly (or only) during this period. It is also in agreement with the assumptions purposed by Castilho et al. (2008b), who explained that variations in the 1:1 sex ratio could occur due to differences in migration and habitat use, among other factors. Likewise, Belcari and Viva (2003) reported an increase in the males' percentage of *Aristaemorpha foliacea* (Risso, 1827) during the copulation period, whereas in the other months, females were more abundant.

Garcia et al. (2016) and Lopes et al. (2017) verified a sex ratio skewed toward females of *R. constrictus*, suggesting that it was an exception to the rule proposed by Fisher (1930). Although both studies analyzed the overall population, instead of a specific period, they suggest that it can be associated with several factors, such as migration. Thus, here we propose that for *R. constrictus*, the intrinsic processes involved in the species' reproduction may induce a sexual proportion of 1:1 during the copulation period.

In our study, we could describe the population dynamics of a bycatch species over a 5-year period. Such an accurate description of the population dynamics is essential to the creation of responsible and effective fishing management plan, since not only the economically interesting species undergo the consequences of overfishing, but also other organisms that inhabit the same area. Together with data regarding the Brazilian commercial species, the results here presented may be fundamental in the adjustment of the Brazilian fisheries closure period. We strongly encourage further studies on both commercial and ecological important species, regardless of their economic interest, addressing their long-term population dynamics. Only by knowing such traits will we be able to find a balance between the anthropic interests and the conservation of the local biodiversity.

References

Bauer RT, 1989. Continuous reproduction and episodic recruitment in nine shrimp species inhabiting a tropical seagrass meadow. Journal of Experimental Marine Biology and Ecology, 127(2): 175-187.

Bauer RT, 1992. Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. Invertebrate Reproduction and Development, 22: 193-202.

Bauer RT and Rivera Vega LW, 1992. Pattern of reproduction and recruitment in two sicyoniid shrimp species (Decapoda: Penaeoidea) from a tropical seagrass habitat. Journal of Experimental Marine Biology and Ecology, 161: 223-240.

Bauer RT and Lin J, 1994. Temporal patterns of reproduction and recruitment in populations of the penaeid shrimps *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson) (Crustacea: Decapoda) from the Northcentral Gulf of Mexico. Journal of Experimental Marine Biology and Ecology, 182(2): 205-222.

Belcari P and Viva C, 2003. Fishery and biology of *Aristaeomorpha foliacea* (Risso, 1827) (Crustacea, Decapoda) in the Northern Tyrrhenian Sea (Western Mediterranean). Journal of Northwest Atlantic Fishery Science, 31: 195-204.

Boschi EE, 1989. Biología pesquera del langostino del litoral patagonico de Argentina. Instituto Nacional de Desarollo Pesquero, Mar del Plata (Argentina).

Branco JO, 2005. Biologia e pesca do camarão sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862) (Crustacea, Penaeidae), na Armação do Itapocoroy, Penha, Santa Catarina, Brasil. Revista Brasileira de Zoologia, 22(4): 1050-1062.

Castilho AL, Costa RC, Fransozo A, Boschi EE, 2007. Reproductive pattern of the South American shrimp *Artemesia longinaris* (Decapoda: Penaeoidea), off São Paulo State, Brazil. Revista de Biologia Tropical, 55(1): 39-48.

Castilho AL, Costa RC, Fransozo A, Negreiros-Fransozo ML, 2008a. Reproduction and recruitment of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. Marine Biology Research, 4: 361-368.

Castilho AL, Furlan M, Costa RC, Fransozo V, 2008b. Reproductive biology of the rock shrimp *Sicyonia dorsalis* (Decapoda: Penaeoidea) from the southeastern coast of Brazil. Invertebrate Reproduction and Development, 52 (1-2): 59-68.

Castilho AL, Wolf MR, Simões SM, Bochini GL, Fransozo V, Costa RC, 2012. Growth and reproductive dynamics of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. Journal of Marine Systems, 105: 135-144.

Castilho AL, Bauer RT, Freire FAM, Fransozo V, Costa RC, Grabowski RC, Fransozo A, 2015a. Lifespan and reproductive dynamics of the commercially important sea bob shrimp *Xiphopenaeus kroyeri* (Penaeoidea): synthesis of a 5-year study. Journal of Crustacean Biology, 35: 30-40.

Castilho AL, Grabowski RC, Simões SM, Santos APF, Costa RC, Fransozo A, 2015b. Lifespan and population dynamics of the endemic South American shrimp *Artemesia longinaris* (Crustacea: Penaeidae) in southeastern Brazil. Anais da Academia Brasileira de Ciências, 87(4): 2123-2138.

Castro-Filho BM, Miranda LB, Miyao SY, 1987. Condicões hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. Boletim do Instituto Oceanográfico 35: 135-151.

Chu KH, 1995. Aspects of reproductive biology of the shrimp *Metapenaeus joyneri* from the Zhujiang Estuary, China. Journal of Crustacean Biology, 15: 214-219.

Coelho PA and Santos MCF, 1993. Época da reproducão do camarão rosa, *Penaeus subtilis* Pérez-Farfante, 1967 (Crustacea, Decapoda, Penaeidae) na região de Tamandaré, PE. Boletim Técnico-Científico do CEPENE, 1(1): 57-72.

Costa RC, Fransozo A, Melo GAS, Freire FAM, 2003. Chave ilustrada para identificação dos camarões Dendrobranchiata do litoral norte do estado de São Paulo, Brasil. Biota Neotropica 3: 1-12.

Costa RC and Fransozo A, 2004a. Reproductive biology of the shrimp *Rimapenaeus constrictus* (Decapoda, Penaeidae) in the Ubatuba region of Brazil. Journal of Crustacean Biology, 24(2): 274-281.

Costa RC and Fransozo A, 2004b. Abundance and ecologic distribution of the shrimp *Rimapenaeus constrictus* (Crustacea: Penaeidae) on the northern coast of São Paulo State, Brazil. Journal of Natural History, 38(7): 901-912.

Costa RC, Bochini GL, Simões SM, Lopes M, Sancinetti GS, Castilho AL, Fransozo A, 2016. Distribution pattern of juveniles of the pink shrimps *Farfantepenaeus brasiliensis* (Latreille, 1817) and *F. paulensis* (Pérez-Farfante, 1967) on the southeastern Brazilian coast. Nauplius, 24: e2016024.

Crocos PJ and Van Der Velde TD, 1995. Seasonal, spatial and interanual variability in the reproductive dynamics of the grooved tiger prawn *Penaeus semisulcatus* in Albatross Bay, Gulf of Carpentaria, Australia: the concept of effective spawning. Marine Biology, 122: 557-570.

Cushing DH, 1975. Marine Ecology and Fisheries. Cambridge University Press, Great Britain, 278p.

Dall W, Hill BJ, Rothlisberg PC, Sharples DJ, 1990. The biology of the Penaeidae. In: Blaxter JHS, Southward AJ eds. Advances in Marine Biology. Academic Press, Manhattan. 489p.

D'Incao F, Valentini H, Rodrigues LF, 2002. Avaliação da pesca de camarões nas regiões sudeste e sul do Brasil. Atlântica, 24(2): 103-116.

Fisher RA, 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

Fonteles-Filho AA, 1989. Recursos pesqueiros, biologia e dinâmica populacional. Imprensa Oficial do Ceará, 296p.

Food and agriculture organization of the United Nations (FAO), 2015. Transforming wasted resources for a sustainable future. The sustainable management of bycatch in Latin America and Caribbean trawl fisheries. Fisheries and Aquaculture Department, 8p.

Garcia JR, Wolf MR, Costa RC, Castilho AL, 2016. Growth and reproduction of the shrimp *Rimapenaeus constrictus* (Decapoda: Penaeidae) from the southeastern coast of Brazil. Regional Studies in Marine Science, 6: 1-9.

García S, 1988. Tropical penaeid prawns. In: Gulland JA. Fish Population Dynamics: the Implications for Management. Wiley and Sons Ltd, Chichester. 249p.

Grabowski RC, Negreiros-Fransozo ML, Castilho AL, 2016. Reproductive ecology of the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) in a coastal area of Southern Brazil. Chinese Journal of Oceanology and Limnology, 34(1): 125-135.

Hiroki KAN, Fransozo A, Costa RC, Castilho AL, Shimizu RM, Almeida AC, Furlan M, 2011. Bathymetric distribution of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) (Decapoda, Penaeidae) in two locations off the southeastern Brazilian coast. Marine biology research, 7(2): 176-185.

Keunecke KA, Vianna M, Fonseca DB, D'Incao F, 2007. The pink-shrimp trawling bycatch in the northern coast of São Paulo, Brazil, with emphasis on crustaceans. Nauplius, 15(2): 49-55.

Lopes AEB, Grabowski RC, Garcia JR, Fransozo A, Costa RC, Hiroki KA, Castilho AL, 2017. Population dynamics of *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea) on the southeastern Brazilian coast: implications for shrimp fishing management from a 5-year study on a bycatch species. Anais da academia Brasileira de Ciências, 89(2): 1013-1025.

Mantelatto FL, Bernardo CH, Silva TE, Bernardes VP, Cobo VJ, Fransozo A, 2016. Composição e distribuição de crustáceos decápodes associados à pesca do camarão-sete-barbas *Xiphopenaeus kroyeri* (Heller, 1862) no litoral norte do estado de São Paulo. Boletim do Instituto de Pesca, 42(2): 307-326.

Misamore MJ and Browdy CL, 1996. Mating behavior in the white shrimps *Penaeus setiferus* and *P. vannamei*: a generalized model for mating in *Penaeus*. Journal of Crustacean Biology, 16(1): 61-70.

Orton JH, 1920. Sea temperature, breeding and distribution of marine animals. Journal of the Marine Biological Association of the United Kingdom, 12(2): 339-366.

Pauly D, Ingles J, Neal R, 1984. Application to shrimp stocks to objective methods for the estimation of growth, mortality and recruitment-related parameters from length-frequency data (ELEFAN I and II). In: Gulland J and Rothschild B. Penaeid Shrimp, Their Biology and Management. Great Britain: New Books. 234p.

Robert R, Borzone CA, Natividade CD, 2007. Os camarões da fauna acompanhante na pesca dirigida ao camarão-sete-barbas (*Xiphopenaeus kroyeri*) no litoral do Paraná. Boletim do Instituto de Pesca, 33(2): 237-246.

Sancinetti GS, Azevedo A, Castilho AL, Fransozo A, Costa RC, 2015. Population biology of the commercially exploited shrimp *Artemesia longinaris* (Decapoda: Penaeidae) in an upwelling region in the Western Atlantic: comparisons at different latitudes. Brazilian Journal of Biology, 27(2): 305-313.

Sastry AN, 1983. Ecological aspects of reproduction. In: Vernberg, FJ and Vernberg WB. The Biology of Crustacea, 8: New York: Academic Press. 210p.

Semensato XEG and Di Beneditto APM, 2008. Population dynamic and reproduction of *Artemesia longinaris* (decapoda, penaeidae) in Rio de Janeiro state, South-eastern brazil. Boletim do Instituto de Pesca de São Paulo, 34(1): 89-98.

Somerton DA, 1980. A computer technique for estimating the size of sexual maturity in crabs. Canadian Journal of Fisheries and Aquatic Sciences, 37: 1488-1494.

Statsoft, 2011. Statistica: Data Analysis Software System, version 10.0. StatSoft, Tulsa.

Thorson G, 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Review, Cambridge 25: 1-45.

Vega-Pérez LA, 1993. Estudo do zooplâncton da região de Ubatuba, Estado de São Paulo. Publicação Especial do Instituto Oceanográfico 10: 65-84.

Wenner AM, 1972. Sex ratio as a function of size in marine crustacean. The American Naturalist, 106(949): 321-350.

Considerações finais

Até o momento, a escassez de estudos desenvolvidos com *R. constrictus*, em comparação às demais espécies de peneídeos, reforça a grande necessidade de estudos que descrevam com maior abrangência o conhecimento sobre o seu ciclo de vida. Estas pesquisas se tornam indispensáveis tendo em vista principalmente dois fatores: os impactos ecológicos da pesca de camarões, os quais, embora sejam consideráveis, ainda não são suficientemente compreendidos; e segundo, o fato de *R. constrictus* ser uma das espécies compondo o *bycatch* e, portanto, sendo tão influenciada quanto as próprias espécies de interesse pesqueiro (espécies-alvo).

Em sua proposta de gestão para o uso sustentável dos camarões marinhos no Brasil, Dias Neto (2011) considera de conhecimento mundial a necessidade de redução do impacto ambiental da pesca de arrasto no ecossistema; para atingir tal meta, o primeiro objetivo seria garantir a sustentabilidade da fauna acompanhante. Entretanto, o autor reconhece que pouco tem sido feito no sentido de minimizar os impactos pesqueiros no ecossistema, devido principalmente à escassez de estudos, ou à falta de aprofundamento e abrangência dos existentes, evidenciando a relevância do presente estudo. Além disso, há a necessidade de mais estudos que abordem não apenas *R. constrictus*, mas também outras espécies componentes do *bycatch*. A partir de estimativas que caracterizem os parâmetros do ciclo de vida das espécies, preferencialmente em uma ampla escala espaço-temporal, é possível analisar os prováveis impactos pesqueiros sobre os organismos. Assim, a partir da fácil acessibilidade às informações, torna-se viável o desenvolvimento de propostas de políticas de conservação e manejo dos estoques pesqueiros, a fim de evitar futuros impactos ecológicos sobre as espécies e a cadeia trófica marinha como um todo.

A partir das considerações realizadas, destacamos a seguir os principais resultados obtidos para a espécie neste estudo:

- A maior longevidade observada para as fêmeas quando comparada aos machos possivelmente é consequência do alto coeficiente de crescimento (k) observado nos machos, uma vez que uma atividade metabólica mais acelerada contribuiria para o envelhecimento celular mais rápido. Propomos também que o mesmo fator pode ter sido o principal motivo para o desvio da razão sexual a favor das fêmeas nas maiores classes de tamanho, considerando que os machos não foram encontrados nestas, provavelmente devido à sua menor taxa de longevidade (maior mortalidade);

- O paradigma do efeito latitudinal parece não se aplicar a *R. constrictus* na costa sudeste do Brasil, uma vez que em uma região tropical a espécie apresentou maior comprimento assintótico, longevidade e coeficiente de crescimento, quando comparados a outro estudo em uma região subtropical (Cananéia). Características ambientais peculiares da região de Ubatuba provavelmente influenciaram os processos biológicos de diferentes maneiras e intensidades, resultando em tais padrões;
- Dentre as 16 curvas de crescimento encontradas para fêmeas e 8 para machos, a maioria foi constituída por coortes de indivíduos jovens, e não inclusas nos meses abrangidos no período de defeso. Tal resultado justifica a proposta de adequação do período de defeso ao recrutamento da espécie na região sudeste do Brasil, reforçando assim a necessidade de preservação dos estoques;
- A reprodução contínua e bimodal observada para a espécie reafirmou os padrões reprodutivos latitudinais observados, tendendo a ser contínua em ambientes tropicais e com maior sazonalidade em maiores latitudes;
- A temperatura da água de fundo teve relação significativa com a abundância de fêmeas reprodutivas, provavelmente devido ao fato de que esta influencia o desenvolvimento ovariano dos organismos;
- Acredita-se que a quantidade de nutrientes para as larvas oriundos da ACAS podem ter influenciado de forma mais seletiva do que a temperatura da água, no que diz respeito à atividade reprodutiva. Tal fator explicaria os picos reprodutivos que foram observados mesmo em períodos nos quais foram observadas temperaturas mais baixas (não favoráveis ao desenvolvimento ovariano);
- O recrutamento foi episódico, não tendo assim relação com as abundâncias de fêmeas reprodutivas. Entretanto, os principais picos de recrutamento observados, próximos aos meses de outono, provavelmente seriam consequência das atividades reprodutivas observadas no verão;
- Analisando o período de cópula, os machos reprodutivos e as fêmeas RU inseminadas foram encontrados em períodos concomitantes (sem intervalo de tempo entre a abundância das duas classes demográficas). Isto sugere que os machos provavelmente migrem para copular (uma vez que são atraídos pelas fêmeas), e, neste caso, a proporção sexual observada durante este período seria de 1:1.

Referências

Dias Neto J, 2011. Proposta de plano nacional de gestão para o uso sustentável de camarões marinhos do Brasil. Brasília: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis e Ministério do Meio Ambiente. IBAMA, 59 (1): 242p.

Anexo

Anais da Academia Brasileira de Ciências (2017) 89(2): 1013-1025
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
http://dx.doi.org/10.1590/0001-3765201720160567
www.scielo.br/aabc

Population dynamics of *Rimapenaeus constrictus* (Stimpson, 1874) (Penaeoidea) on the southeastern Brazilian coast: implications for shrimp fishing management from a 5-year study on a bycatch species

ANA ELISA B. LOPES[1], RAPHAEL C. GRABOWSKI[1], JOYCE R. GARCIA[1], ADILSON FRANSOZO[1], ROGÉRIO C. DA COSTA[2], KÁTIA A.N. HIROKI[3] and ANTONIO L. CASTILHO[1]

[1]Universidade Estadual de São Paulo/UNESP, Instituto de Biociências de Botucatu, Departamento de Zoologia, Rua Professor Doutor Antonio Celso Wagner Zanin, s/nº, Distrito de Rubião Júnior, 18618-689 Botucatu, SP, Brazil
[2]Universidade Estadual de São Paulo/UNESP, Faculdade de Ciências, Departamento de Ciências Biológicas, Avenida Luiz Edmundo Carrijo Coube, nº 14-01, Vargem Limpa, 17033-360 Bauru, SP, Brazil
[3]Universidade Federal do Triângulo Mineiro/UFTM, Instituto de Ciências Exatas, Naturais e Educação, Departamento de Ciências Biológicas, Avenida Doutor Randolfo Borges, 1400, Univerdecidade, 38064-200 Uberaba, MG, Brazil

Manuscript received on August 26, 2016; accepted for publication on November 28, 2016.

ABSTRACT

This is the first study to evaluate in broad spatiotemporal scales the growth parameters and population structure of *Rimapenaeus constrictus*, a barely damaged species composing the bycatch from shrimp fishing in the Western Atlantic. The abundance and size-class frequency distribution, growth, longevity and sex ratio were evaluated from monthly samples obtained in the northern littoral of São Paulo state from Jan/1998 to Jun/2003. We measured 5,812 individuals in which the sex ratio was skewed toward females; this was more evident in size classes greater than 10 mm in CL (carapace length) (binomial test, $p<0.05$). We selected 16 growth cohorts of females, and 8 of males, the majority consisting of younger individual cohorts excluded from the fisheries closure period. Growth estimates resulted in a CL_∞ of 17.42 mm, a growth coefficient of 0.008 and a longevity of 579 days (1.60 year) for females, as well as a CL_∞ of 16.3 mm, a growth coefficient of 0.01 and a longevity of 425 days (1.17 year) for males. Our results provide information of incontestable relevance to our knowledge of fishing management. We therefore strongly recommend that the fisheries closure period be changed to protect this species' recruitment period and consequently its adult individuals.

Key words: Fisheries biology, latitudinal variation, recruitment cohorts, roughneck shrimp, stock conservation.

INTRODUCTION

Crustacean fisheries production has been declining throughout the southeastern Brazilian Coast, mainly in the Ubatuba region, which within a 10-year period (2005-2015) has shown a 64% of reduction in biomass landings (Instituto de Pesca, São Paulo: www.pesca.sp.gov.br). Commercial fishery trawling in the Brazilian Southeastern region targets species such as *Farfantepenaeus brasiliensis* (Latreille, 1817), *F. paulensis* (Pérez-

Correspondence to: Ana Elisa Bielert Lopes
E-mail: anaelisa_lopes@hotmail.com

Farfante 1967), *Litopenaeus schmitti* (Burkenroad, 1938), *Xiphopenaeus kroyeri* (Heller, 1862), *Artemesia longinaris* Spence Bate, 1888 and *Pleoticus muelleri* (Spence Bate, 1888) (D'Incao et al. 2002). In Brazilian Southeastern coast, the use of motor boats for shrimp trawling from March 1st to May 31st is forbidden by the Brazilian Institute of Environment and Natural Renewable Resources (IBAMA 2016). During this season (the fisheries closure period), fishermen are prohibited from using such gear to capture economically marketable shrimp species or to transport, stock or commercialize these animals. This measure aims to protect their regular population structure, reproduction and recruitment period (normative instruction available at: www.ibama.gov.br).

Trawling activity uses non-selective fishing gear, i.e., along with the target species, many non-target organisms (bycatch fauna) are incidentally caught. According to Dias Neto (2011), a minority of the bycatch fauna is landed and is locally commercialized (often at very low prices), on the other hand, most is discarded back to the sea already dead due to their negligible commercial value. On average, in a trawl to obtain tropical shrimp, the captured bycatch is 3 to 15 times larger than the captured target species (FAO 2015). The ecological impacts resulting from shrimp fishing are still poorly understood, but are known to be considerable. One of the main effects of the bycatch capture on the ecosystem is the alteration in the species composition and/or in the stock size of the bycatch species (Dias Neto 2011). Theoretically, species with no economic value (bycatch), such as *Rimapenaeus constrictus* (Stimpson, 1874), are protected by the fisheries closure period as well, since the bycatch and economically important species are not being captured during this period.

Rimapenaeus constrictus exhibits a broad geographical distribution ranging from Nova Scotia (Canada) to Santa Catarina (Brazil). This species is among those most often accidentally caught during fishery activities, and due to its small size, it is not commercially exploited. However, it plays an important ecological role as part of the trophic web chain within its habitat range (Pérez-Farfante and Kensley 1997, Costa and Fransozo 2004b).

The biological knowledge about species and estimates of their population parameters (size class distributions, growth rates, sex ratios, etc.) are highly relevant to provide essential information about the management of fishing resources (Gab-Alla et al. 1990, Bauer and Rivera Vega 1992, Castilho et al. 2015a). With regard to shrimp growth studies, the most accepted (and consequently most utilized) methodology is the von Bertalanffy (1938) growth model, which estimates the age of an individual of a given body size according to a mathematical equation. This methodology is necessary due to the impossibility of periodic tissue tagging, since crustaceans do not have permanent skeletal structures (Hartnoll 2001, Fonseca and D'Incao 2003, Campos et al. 2011, Castilho et al. 2015b).

However, only a few studies have been undertaken to guide and clarify the basic biology of the population dynamics and life history of this species. In the northern littoral of São Paulo state, Costa and Fransozo (2004a, b) studied its reproductive biology and its abundance and ecological distribution, respectively, and Hiroki et al. (2011) investigated its bathymetric distribution. In the southern littoral of São Paulo, only the study addressing its growth and lifespan carried out by Garcia et al. (2016) is available in a different region. In addition to the studies conducted on the Brazilian coast, Bauer and Lin (1994) evaluated the reproductive and recruitment periods of the congeneric species, *Rimapenaeus similis* (Smith, 1885) and *R. constrictus*, in the Gulf of Mexico.

It is important to point out that to date, no studies have been done concerning growth and longevity of *R. constrictus* in the Ubatuba region or on the northern coast of São Paulo state; thus, this is a pioneer study for this approach. It is therefore necessary to strengthen our biological knowledge about the bycatch by obtaining appropriate data. These findings are essential to substantiate the implementation of management and sustainable use measures for marine shrimp fishing along the Brazilian coast, especially since current knowledge is insufficient to make scientifically based decisions (Dias Neto 2011).

On the basis of this scenario, we here describe the population structure and sex ratio and estimate the growth parameters for *R. constrictus* across a wide temporal scale, for 5 years, in Ubatuba in the northern littoral of São Paulo state. Additionally, we tested the hypothesis that such parameters undergo alterations induced by environmental features related to the latitude and compared our results to the studies on *R. constrictus* available to date. For the first time, a growth analysis covers the whole bathymetric distribution of this species on the Brazilian coast, and distinct results can therefore be observed. Thus, we could determine whether the commonly referred to "latitudinal effect paradigm" proposed by Bauer (1992) and Castilho et al. (2007b) is applicable to the growth parameters of the species concerned here, as it was already reported to apply to its reproductive aspects (Costa and Fransozo 2004a). We also verified the applicability of the current fisheries closure period to this species with regard to its functionality for the recruitment observed during the study period.

MATERIALS AND METHODS

STUDY AREA

The Ubatuba region presents an extremely indented coastline, resulting in the creation of many bays with particular environmental conditions exhibiting very irregular internal limits that are favorable to the establishment of the local fauna. It is a result of the peculiar characteristics and ecological needs of each species and the consequent development of particular marine faunas (Negreiros-Fransozo et al. 1991).

The main oceanographic feature structuring ecosystems on the southeastern and southern Brazilian continental shelf is the presence of the South Atlantic Central Waters, a water mass characterized by low temperature and salinity (SACW: T<18º C; S<36) (Pires-Vanin 2001, Soares-Gomes and Pires-Vanin 2003). In addition, the northern coast of São Paulo state is strongly influenced by two other water masses, each showing specific characteristics and distinct models of distribution between summer and winter: Coastal Water (AC: high temperature (>20º C) and low salinity [<36]) and Tropical Water (TW: high temperature (>20º C) and high salinity [>36]) (Castro-Filho et al. 1987).

The SACW approaches from the continental shelf in the bottom water layers, reaching the coastal zone and causing the low water temperatures recorded during spring and early summer (minimum values of 15º C). This process creates a thermocline at depths of 10 to 15 m due to the presence of cold water in the bottom layers of the water column and warm water in the remaining layers (Castro-Filho et al. 1987).

BIOLOGICAL SAMPLING

Samplings were carried out monthly from Jan/1998 to Jun/2003, with a gap between January 2001 to June 2001, along the northern coast of São Paulo state in the Ubatuba region. Samples were obtained during the day using a shrimp-fishing boat outfitted with double-rig nets (mesh size: 20 mm knot-to-knot in the body and 15 mm in the cod end). Trawls were extended for two kilometers for 30 minutes each, sampling a total area of 18,000 m².

Carapace length (CL) was adopted as a standard measurement in this study, corresponding to the linear distance from the post-orbital angle and the posterior margin of the carapace, which has been widely used in investigations concerning penaeid shrimps (Castilho et al. 2015a, b). CL size frequencies were distributed in 1-mm classes to each sex, separately. Both were compared by a Kolmogorov-Smirnov two-sample test in which the null hypothesis adopted was that size distribution among sexes did not differ (Castilho et al. 2008a). Recruitment was estimated as the percentage of the population sampled in the lower 25% of all possible size classes (males+females). Thus, for the purposes of measuring recruitment, all individuals with a CL less than 9.4 mm were considered recruits (Bauer and Rivera Vega 1992, Castilho et al. 2008a).

SEX RATIO

Individuals were classified to sex according to the presence of a petasma (males) or a thelycum (females) (Pérez-Farfante 1988). The sex ratio was estimated as the quotient between the number of males and the total number of individuals in the monthly samples. Differences in the expected ratio of 1:1 (males:females) were tested with the binomial test ($\alpha=0.05$) (Wilson and Hardy 2002, Grabowski et al. 2014).

GROWTH AND LONGEVITY

Growth and longevity were analyzed separately for each sex according to the von Bertalanffy (1938) growth model and using the methodology purposed by Simões et al. (2013). Modal values were determined for each CL frequency using the software Peakfit 4.0 (Automatic Peak Fitting Detection and Fitting, Method I-Residual, no Data Smoothing) in size classes of 1.0 mm. The models were plotted on a scatter graph vs. age to verify the growth rhythm of the cohorts. Growth parameters (CL_∞: asymptotic carapace length; k: growth coefficient (day-1); t_0: theoretical age at size 0) were estimated using the SOLVER supplement in Microsoft Excel, which applies the von Bertalanffy growth model: $CL_t=CL_\infty[1-exp-k^{(t-t0)}]$ (CL_t: carapace length at age t). The cohort data were pooled, and the growth parameters estimated. The estimated growth curves for each sex were compared by an F test (p=0.05) (Cerrato 1990). Longevity was calculated using the inverse von Bertalanffy growth model with a modification suggested by D'Incao and Fonseca (1999) given by $longevity = 0-(1/k)ln[1-(CL_t/CL_\infty)]$ (considering $t_0= 0$, and $CL_t/CL_\infty= 0.99$). Cohorts including the modal peaks of recruitment size (<9.4 mm CL) were identified as recruitment cohorts, and the age at which individuals become adult was estimated by the equation purposed by King (1995): $t = t_0-(1/k).ln(1-(CL_t/CL_\infty)$.

RESULTS

POPULATION STRUCTURE

During this study 5,812 individuals were sampled, including 1,458 males and 4,354 females. Carapace length varied from 4.2 to 17.9 mm in males (mean: 9.21 mm ± 1.31 SD [standard deviation]) and from 3.4 to 19.2 mm in females (mean: 12.1 mm ± 2.31 SD). Males were more abundant in the 5 to 9 mm size classes and females, from 10 to 19 mm, with a peak abundance observed at 12 mm (Figure 1). The size class distributions for males and females showed a statistically significant difference (Kolmogorov-Smirnov, $d_{max}= 0.61$; p= 0.04).

SEX RATIO

Throughout the sampling period, we observed a female-biased sex ratio (binomial test, p<0.05), as they were more abundant compared to the number of males (Figure 2).

From the size class distribution for adult individuals, it was possible to observe a male-biased sex ratio in the smaller size classes (5-9 mm). From 10 mm on, the sex ratio was exclusively female biased (Figure 3).

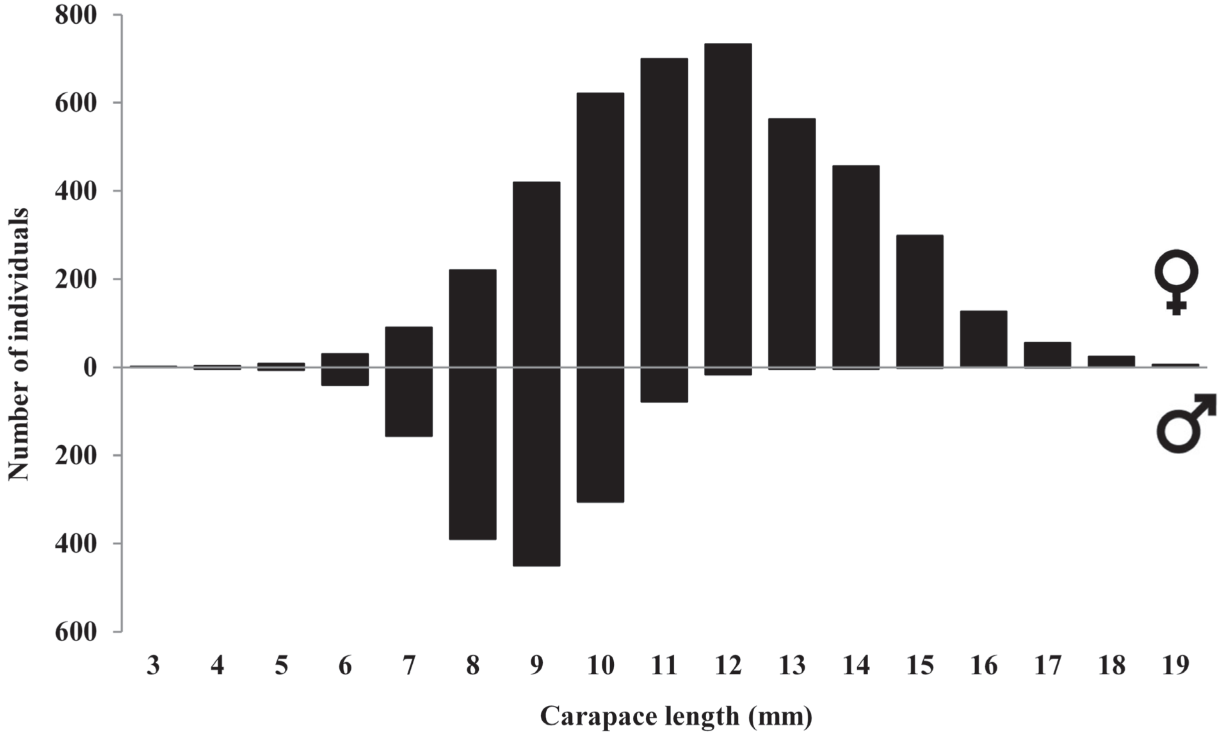

Figure 1 - *Rimapenaeus constrictus*. Size class distributions of males and females for samples obtained from January 1998 to June 2003 at the northern littoral of São Paulo state.

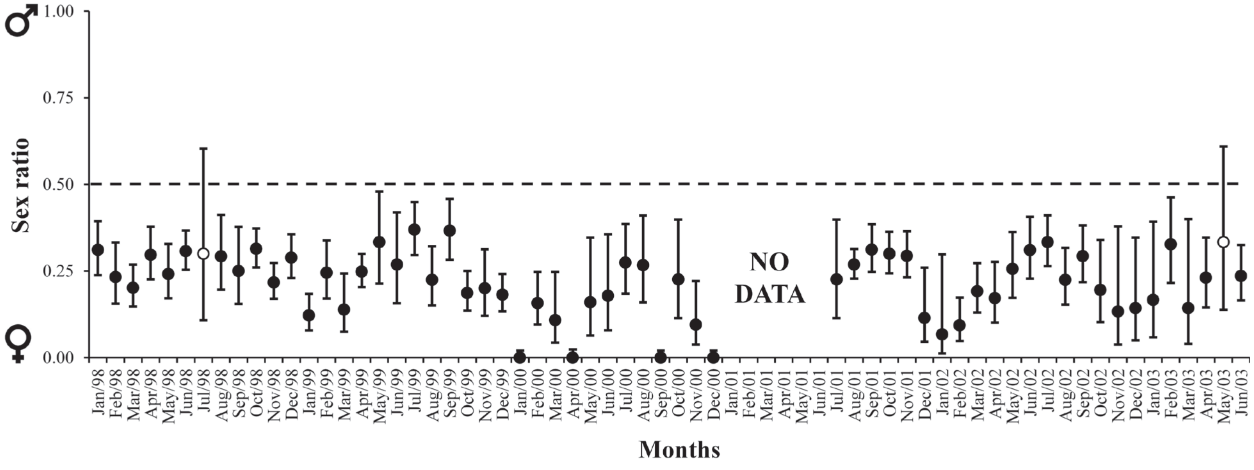

Figure 2 - *Rimapenaeus constrictus*. Monthly sex ratio (estimate ± standard error) for samples from January 1998 to June 2003 from the northern littoral of São Paulo state. Black circles indicate a significant deviation from a 1:1 (M:F) sex ratio (binomial test, $p<0.05$).

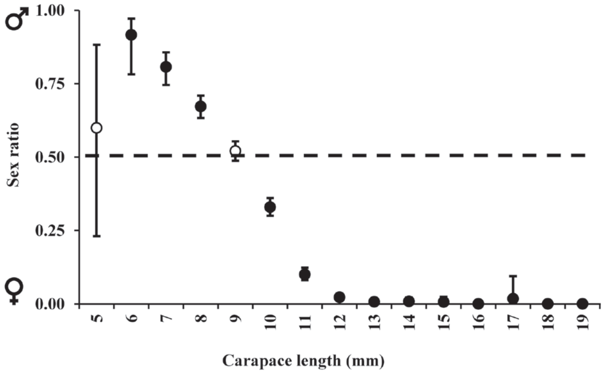

Figure 3 - *Rimapenaeus constrictus*. Sex ratio observed among the size classes (estimate ± standard error) for individuals sampled from January 1998 to June 2003 from the northern littoral of São Paulo state. Black circles indicate a significant deviation from a 1:1 (M:F) sex ratio (binomial test, p<0.05).

GROWTH AND LONGEVITY

We identified 16 female and 8 male cohorts (Figures 4 and 5). For males, only 2 recruitment cohorts (< 9.4mm CL) (cohorts 3 and 7) were set in the fisheries closure periods from the time of their emergence until reaching adult size. This condition is even more critical for females because only 3 recruitment cohorts (cohorts 5, 15 and 16) were set in the fisheries closure periods from their emergence until reaching adult size. Moreover, the majority of the remaining cohorts including recruitment sizes were identified in December and February (females: cohorts 2, 6 and 10; males: cohorts 1, 4 and 8). Estimates of the growth parameters resulted in CL_{∞}: 17.42 mm, k: 0.008 and t_0: -1.50 days for females, and CL_{∞}: 16.3 mm, k: 0.01 and t_0: -0.60 days for males (Figures 6 and 7). From the growth curves, longevity was estimated as 579 days (1.60 year) for females and 425 days (1.17 year) for males. Growth curves for males and females showed a significant difference through an F test ($F_{critical} = 2.688 < F_{calculated} = 4.124$; p= 0.008). The time necessary for recruits to reach the adult size here proposed (9.4 mm CL) was estimated as 85 and 95 days for males and females, respectively.

DISCUSSION

In our study, we observed that females reached larger sizes than males, which was previously observed for the same species by Costa and Fransozo (2004a) in the Ubatuba region and by Garcia et al. (2016) in the Cananéia region, as well as in studies of other penaeoid shrimps (Semensato and Di Beneditto 2008, Castilho et al. 2008a, b, 2015b, Grabowski et al. 2014, 2016). Such sexual dimorphism is considered a general rule among penaeids (Boschi 1989), indicating a likely adaptation to increase egg production (Gab-Alla et al. 1990, Yamada et al. 2007). In addition, Simões et al. (2013), studying *Acetes americanus* Ortmann, 1893, also found such differential growth between the sexes. Such growth differences thus occur in both superfamilies included in the Dendrobranchiata (Penaeoidea and Sergestoidea).

The theory purposed by Fisher (1930) states that gonochoristic species present equal abundances between the sexes, which runs counter to the results of Wenner (1972) in which several crustacean species show exceptions to this pattern. Recent studies carried out along the Brazilian coast also run counter to Fisher's (1930) theory, including *Sicyonia dorsalis* Kingsley 1878 (Castilho et al. 2008a), *A. longinaris* (Castilho et al. 2007a, 2015b), *P. muelleri* (Castilho et al. 2008b) and *X. kroyeri* (Castilho et al. 2015a, Grabowski et al. 2014, 2016). In this study, *R. constrictus* constitutes an exception to Fisher's (1930) theory and also agrees with previous studies carried out on the species (Costa and Fransozo 2004a, Garcia et al. 2016).

Deviations from a 1:1 sex ratio can be a result of the interaction of countless factors, such as differential growth rates, migration patterns and mortality rates between the sexes (Wenner 1972). In addition, certain growth parameters (higher growth coefficient and lower asymptotic length in males) can induce female-biased sex ratios (Simões et al. 2013). Garcia et al. (2016) also observed

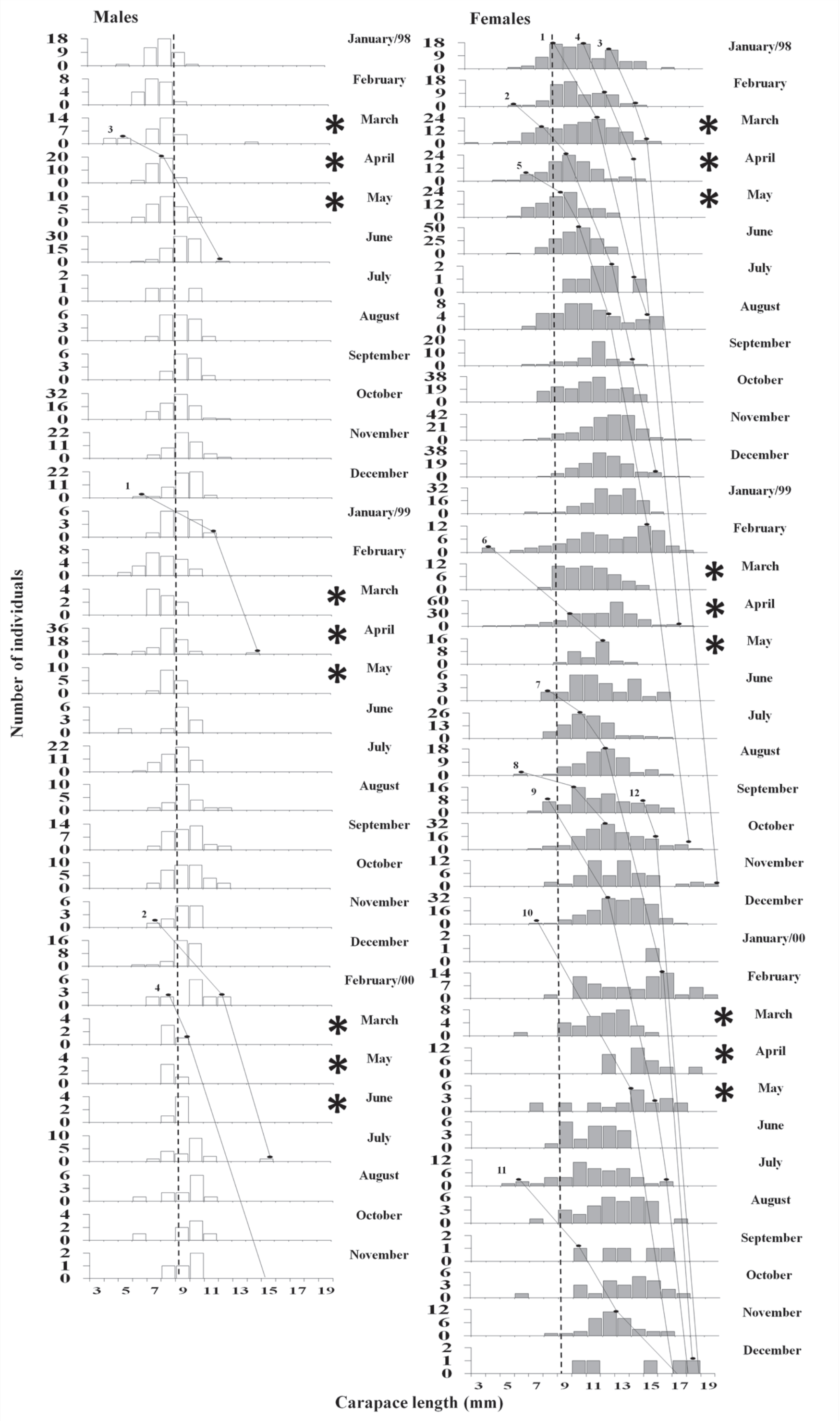

Figure 4 - *Rimapenaeus constrictus*. Selected cohorts (lines) for growth analyses performed on data sampled from January 1998 to December 2000 at the Northern littoral of São Paulo state. Dotted lines: recruitment size (9.4 mm CL); *: periods in which shrimp-fishing activities are prohibited by the responsible federal environmental agency.

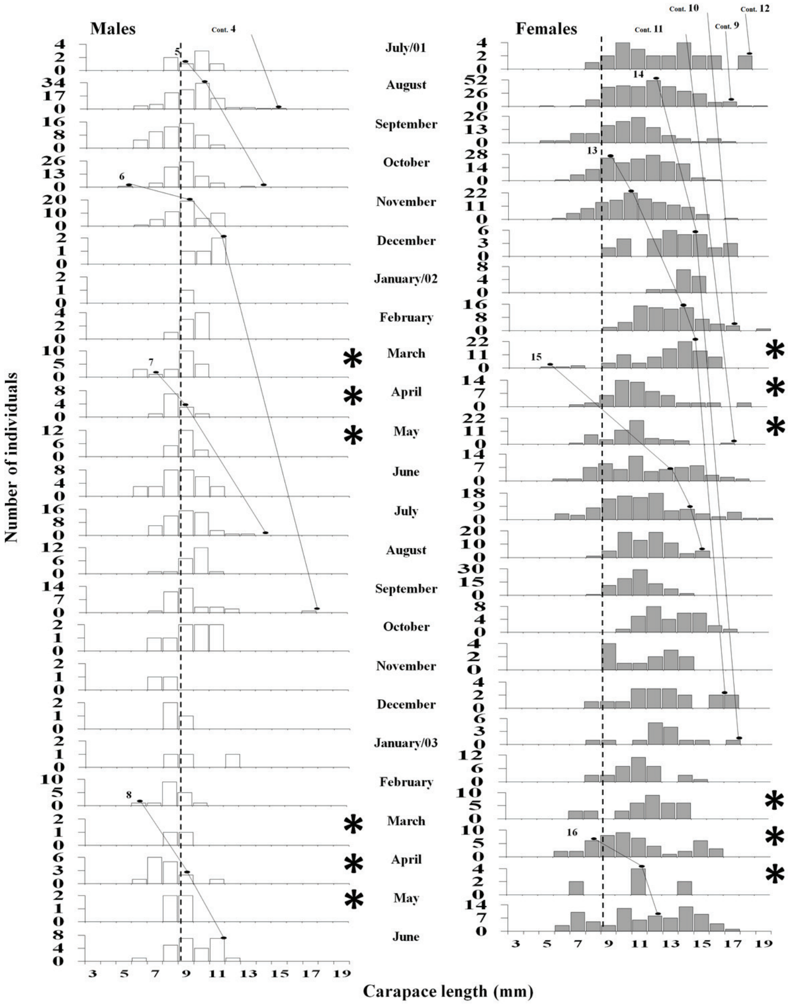

Figure 5 - *Rimapenaeus constrictus*. Selected cohorts (lines) for growth analyses performed on data sampled from July 2001 to June 2003 at the Northern littoral of São Paulo state. Dotted lines: recruitment size (9.4 mm CL); *: periods in which shrimp-fishing activities are prohibited by the responsible federal environmental agency.

female-biased sex ratios for *R. constrictus*, as in our study. According to the authors, the female-biased sex ratios in higher size classes can also be a consequence of the lower longevity observed for males.

The longevity observed in wild animals is highly variable and may be equal for both sexes of certain species or even differ between them (Vogt 2012). However, it is quite common to observe penaeoid males showing a lower longevity than females, as previously described in the literature (Simões et al. 2013, Grabowski et al. 2014, Castilho et al. 2015a, b) and as observed in our results. Vogt (2012) pointed out some factors that can influence the discrepancy observed in this parameter, such as geographical latitude, habitat, differences in mortality rates, energy costs of reproduction, and hormonal issues. Additionally, penaeoid males generally present a higher growth coefficient (k) and consequently a lower asymptotic length (CL_∞) (Garcia and Le Reste 1986, Boschi 1969, Petriella and Boschi 1997), as well as lower longevity (Castilho et al. 2012).

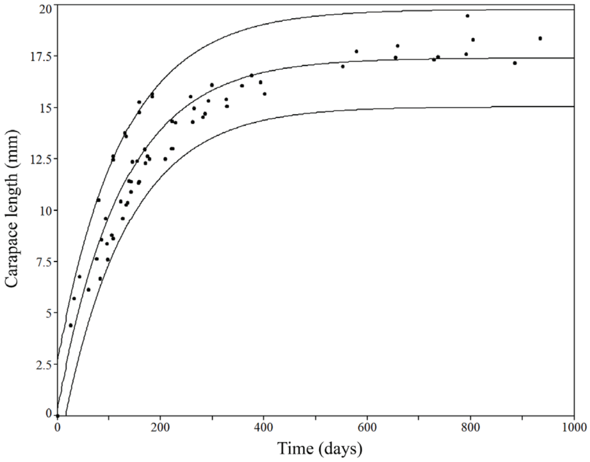

Figure 6 - *Rimapenaeus constrictus*. Mean estimated growth curve based on the von Bertalanffy growth model for females sampled from July 1998 to June 2003 in the Ubatuba region, northern São Paulo state. Outer lines: 95% prediction intervals.

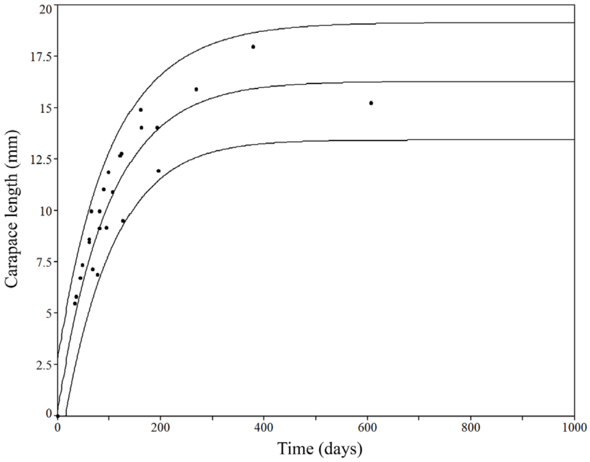

Figure 7 - *Rimapenaeus constrictus*. Mean estimated growth curve based on the von Bertalanffy growth model for males sampled from July 1998 to June 2003 in the Ubatuba region, northern São Paulo state. Outer lines: 95% prediction intervals.

Garcia et al. (2016) propose that the lower longevity (and consequent lower asymptotic length) of males is due to their higher metabolic rate, which leads to a cellular senescence induced by the higher investment in the growth rate (a higher *k* than for the females). This could also explain the tendency for males to show higher mortality rates compared to females (Gab-Alla et al. 1990). We therefore propose that the lower longevity of males is the main reason for the female-biased sex ratio, even though we do not discard the possible influence of other factors. Among them, are the higher susceptibility of females to sampling gear as a function of their search for food during the period of ovary maturation (Kevrekidis and Thessalou-Legaki 2006), migratory activities, and differential habitat occupation (Wenner 1972), among others.

Many studies have observed that some marine crustaceans can experience differential environmental influences at latitudinal scales that can impact their life history parameters (Castilho et al. 2015a, Garcia et al. 2016). Bauer (1992) and Castilho et al. (2007b) state that penaeoid life history aspects such as longevity and size at the onset of sexual maturity can vary according to the environmental conditions related to latitude, such as water temperature and nutrient availability. According to this "latitudinal effect paradigm", in subtropical and temperate regions, individuals tend to exhibit a slower growth rhythm and a higher longevity, likely influenced by the lower water temperatures found in these areas (Bauer 1992).

To date, Garcia et al. (2016) have provided the only available data on *R. constrictus* growth estimates carried out on the Brazilian Coast. This study, carried out in the Cananéia region at higher latitudes values (25°S) than Ubatuba, reports lower asymptotic lengths (females: 16.40 mm; males: 11.74 mm), longevities (females: 415 days [1.14 year]; male: 267 days [0.73 year]) and growth coefficients (females: 0.011; males: 0.017) compared to our results, suggesting that the latitudinal effect paradigm is not applicable to this species' population dynamics between these two regions.

To comprehend this scenario, it is necessary to keep in mind that physical processes influence the biological ones (Castro-Filho et al. 1987). Cananéia (southern littoral) and Ubatuba (northern littoral) show distinct physical features and thus have distinct biological processes. We propose, therefore, that uncountable factors related to the peculiar features of the Ubatuba region (different from Cananéia) influenced the biological processes in different ways and intensities, resulting in such exceptions to the latitudinal pattern. We propose three possible factors that can be held responsible for such a situation, which are listed below.

The first of these, typical of Ubatuba, is the water temperature, which is strongly molded by water masses such as the SACW which approaches the coastal zone during late spring and early summer, causing a decrease in bottom water temperature (<18º C) and salinity (<36) (Castro-Filho et al. 1987). According to Mantelatto and Fransozo (1999), the approaching SACW exerts a strong influence on the water temperature close to the bottom and causes considerable changes in the local communities. The SACW-induced low water temperatures possibly influence the environmental patterns so that Ubatuba presents subtropical rather than tropical environmental features (since shrimp seem to grow more slowly, reach larger sizes, and live longer).

Bauer (1992) points out that some taxa may have planktotrophic larvae, which are affected by very different pressures in the plankton (oscillations in the food supply and predators, for instance) that may influence larval success and recruitment in a variety of ways. Thus, the second factor is based on the statement by Vega-Pérez (1993) asserting that during the approaching SACW the chlorophyll values are higher due to an increase in phytoplankton production, confirming the tendency for water enrichment along the continental shelf during summer (Castro-Filho et al. 1987). Therefore, we propose here that the amount of nutrients in the water column might also have influenced the life history parameters observed in this study. Because the SACW may provide an important source of nutrients and allow a greater larval success, it also makes sense that individuals would be able to reach greater sizes and longevities.

The third and last proposed influencing factor is the type of sediment found in this region, which was characterized by Mantelatto and Fransozo (1999) and shown to be composed mainly of very coarse, coarse, and medium sand. This type of sediment favors not only a higher retention of organic matter content (a possible food resource) but also favors this species' common burrowing behavior. Such behavior may play a fundamental role in the defense of these organisms against predators (Dall et al. 1990), which could also correspond to a higher longevity. According to Negreiros-Fransozo et al. (1991), the distribution of different types of sediment is controlled by water currents. The sinuous littoral observed in Ubatuba (Ab'Sáber 1955) provides great barriers to the entry of seawater, possibly decreasing the intensity with which currents approach this region, which would stir the sediment, forcing animals to emerge and making them more susceptible to capture and predation.

Castilho et al. (2015b) observed that the geographical proximity between regions could establish migratory connections between groups that are part of the same population. However, despite the latitudinal proximity between Cananéia (23ºS) and Ubatuba (25ºS), we strongly suggest that the peculiar oceanographic conditions from Ubatuba (particularly, the above-mentioned effects of the SACW) produced the factors that most likely led to the exceptions.

Several studies carried out with different penaeoidean species suggest the necessity for adaptations to the fisheries closure period. Studies on *P. muelleri*, *X. kroyeri* and *A. longinaris* (Castilho et al. 2012, 2015a, b, respectively) show only 1, 11 and 2 growth curves protected in the fisheries closure seasons, from 15, 37 and 14 curves, respectively. We also observed that most of the recruitment cohorts do not arise during the months included in the closed fishery period (see figs. 5 and 6), thus strengthening this idea. Thus, it is reasonable to infer that the highest efficiency for protecting the species would be realized with an adaptation to the fisheries closure period in the months in which we can observe recruitment cohorts. Therefore, we propose here that the shrimp fishing closed season include late spring and early summer (from December to February) in addition to the already established closed months (March to May).

On the other hand, it is comprehensible that increasing the number of months covered by the fisheries closure period could induce social and economic issues (Castilho et al. 2015a). It is important to remember that the fishery activity is an essential source of income, employment and livelihood for millions of families, which are partially or totally dependent on it. Therefore, Castilho et al. (2015a) suggest further migration studies concerning the locations of the main stocks of reproductive and recruitment individuals in different areas. These data could be crucial for determining the zones and periods of total fishery prohibition, protecting not only the economically important species, but also the bycatch taxa. Additionally, Silva et al. (2013) attest that the management effectiveness of the shrimp fishery is not only achieved by closed fishing seasons, but also by the number of fishing licenses issued, the engine size and dimensions of fishing vessels, minimum mesh sizes and other characteristics as well.

We can infer that *R. constrictus* completes its ontogeny in the studied region since we sampled individuals in a wide range of size classes from juveniles to adults. We strongly believe that the growth coefficient was directly related to the longevity of the individuals and that the growth parameters ran counter to the expected latitudinal effect paradigm, likely in response to the environmental conditions observed in Ubatuba. The present study provides information of undoubted relevance to the field of fishing management, since we present a basis for the establishment of sustainable capture policies. On the basis of such results, therefore, we strongly recommend that the fisheries closure period be changed to protect this species' recruitment period and, consequently, also its adult individuals. It is important to keep in mind that scientifically based knowledge is indispensable for protecting with greater efficiency the ecologically important stocks and avoiding their collapse in the near future. To achieve excellence in such activities, it is crucial to support additional studies at a wide geographical scale in order to understand the influence of latitudinal variations in the growth dynamics of this species.

ACKNOWLEDGMENTS

We thank many colleagues from the NEBECC group who helped with sampling and laboratory analyses; and the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) for granting permission to collect the shrimps. This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (Biota # 98/07090-3, # 2010/50188-8; Scholarships # 97/12106-8, # 07/56733-5, # 2015/13639-5); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Ciências do Mar (CAPES – CIMAR) (# 23038.004310/2014-85) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (Research Scholarships PQ # 305919/2014-8; PQ 308653/2014-9).

REFERENCES

AB'SÁBER AN. 1955. Contribuição à geomorfologia do litoral paulista. Rev Bras Geogr 17: 3-48.

BAUER RT. 1992. Testing generalizations about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. Invertebr Reprod Dev 22: 193-202.

BAUER RT AND LIN J. 1994. Temporal patterns of reproduction and recruitment in populations of the penaeid shrimps *Trachypenaeus similis* (Smith) and *T. constrictus*

(Stimpson) (Crustacea: Decapoda) from the Northcentral Gulf of Mexico. J Exp Mar Biol Ecol 182: 205-222.

BAUER RT AND RIVERA VEGA LW. 1992. Pattern of reproduction and recruitment in two sicyoniid shrimp species (Decapoda: Penaeoidea) from a tropical seagrass habitat. J Exp Mar Biol Ecol 161: 223-240.

BOSCHI EE. 1969. Crecimiento, migración y ecología del camarón comercial *Artemesia longinaris* Bate de Mar del Plata. FAO Fish Rep 57: 833-846.

BOSCHI EE. 1989. Biología pesquera del langostino del litoral patagonico de Argentina (*Pleoticus muelleri*). Inst Nac Invest Desarr Pesq 646: 5-71.

CAMPOS BR, BRANCO JO AND D'INCAO F. 2011. Crescimento do camarão-sete-barbas (*Xiphopenaeus kroyeri* (Heller 1862)), na Baía de Tijucas, Tijucas, SC (Brasil). Atlântica 33: 201-208.

CASTILHO AL, BAUER RT, FREIRE FAM, FRANSOZO V, COSTA RC, GRABOWSKI RC AND FRANSOZO A. 2015a. Lifespan and reproductive dynamics of the commercially important sea bob shrimp *Xiphopenaeus kroyeri* (Penaeoidea): synthesis of a 5-year study. J Crust Biol 35: 30-40.

CASTILHO AL, COSTA RC, FRANSOZO A AND BOSCHI EE. 2007a. Reproductive pattern of the South American endemic shrimp *Artemesia longinaris* (Decapoda: Penaeoidea), off São Paulo state, Brazil. Rev Biol Trop 55: 39-48.

CASTILHO AL, COSTA RC, FRANSOZO A AND NEGREIROS-FRANSOZO ML. 2008b. Reproduction and recruitment of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the Southeastern coast of Brazil. Mar Biol Res 4: 361-368.

CASTILHO AL, FURLAN M, COSTA RC AND FRANSOZO V. 2008a. Reproductive biology of the rock shrimp *Sicyonia dorsalis* (Decapoda: Penaeoidea) from the southeastern coast of Brazil. Invertebr Reprod Dev 52: 59-68.

CASTILHO AL, GAVIO MA, COSTA RC, BOSCHI EE, BAUER RT AND FRANSOZO A. 2007b. Latitudinal variation in population structure and reproductive pattern of the endemic South American shrimp *Artemesia longinaris* (Decapoda: Penaeoidea). J Crust Biol 27: 548-552.

CASTILHO AL, GRABOWSKI RC, SIMÕES SM, SANTOS APF, COSTA RC AND FRANSOZO A. 2015b. Lifespan and population dynamics of the endemic South American shrimp *Artemesia longinaris* (Crustacea: Penaeidae) in southeastern Brazil. An Acad Bras Cienc 87: 2123-2138.

CASTILHO AL, WOLF MR, SIMÕES SM, BOCHINI GL, FRANSOZO V AND COSTA RC. 2012. Growth and reproductive dynamics of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. J Mar Syst 105-108: 135-144.

CASTRO-FILHO BM, MIRANDA LB AND MIYAO SY. 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. Bol Inst Oceanogr 35: 135-151.

CERRATO RM. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can J Fish Aquat Sci 47: 1416-1426.

COSTA RC AND FRANSOZO A. 2004a. Reproductive biology of the shrimp *Rimapenaeus constrictus* (Decapoda, Penaeidae) in the Ubatuba Region of Brazil. J Crust Biol 24: 274-281.

COSTA RC AND FRANSOZO A. 2004b. Abundance and ecologic distribution of the shrimp *Rimapenaeus constrictus* (Crustacea: Penaeidae) on the northern coast of São Paulo State, Brazil. J Nat Hist 38(7): 901-912.

DALL W, HILL BJ, ROTHLISBERG PC AND SHARPLES DJ. 1990. The Biology of the Penaeidae. In: Blaxter JHS and Southward AJ (Eds), Advances in Marine Biology. San Diego: Academic Press, 489 p.

DIAS NETO J. 2011. Proposta de plano nacional de gestão para o uso sustentável de camarões marinhos do Brasil. Brasília: Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis e Ministério do Meio Ambiente. IBAMA 59(1): 242.

D'INCAO F AND FONSECA DB. 1999. Performance of the von Bertalanffy growth curve in penaeid shrimps: a critical approach. In: von Vaupel Klein JC and Schram FR (Eds), The Biodiversity Crisis and Crustacea: Proceedings of the Fourth International Crustacean Congress. Amsterdam (The Netherlands), Brill Academic Publishers, Leiden, The Netherlands, p. 733-737.

D'INCAO F, VALENTINI H AND RODRIGUES LF. 2002. Avaliação da pesca de camarões nas regiões Sudeste e Sul do Brasil. Atlântica 24: 103-116.

FAO - FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS. 2015. Transforming wasted resources for a sustainable future. The sustainable management of bycatch in Latin America and Caribbean trawl fisheries. Fisheries and Aquaculture Department, 8 p.

FISHER RA. 1930. The genetical theory of natural selection. New York Dover Publications, 318 p.

FONSECA DB AND D'INCAO F. 2003. Growth and reproductive parameters of *Kalliapseudes schubartii* in the estuarine region of the Lagoa dos Patos (southern Brazil). J Mar Biol Ass UK 5: 931-935.

GAB-ALLA AAFA, HARTNOLL RG, GHOBASHY AF AND MOHAMMED SZ. 1990. Biology of penaeid prawns in the Suez Canal lakes. Mar Biol 107: 417-426.

GARCIA JR, WOLF MR, COSTA RC AND CASTILHO AL. 2016. Growth and reproduction of the shrimp *Rimapenaeus constrictus* (Decapoda: Penaeidae) from the southeastern coast of Brazil. Reg Stud Mar Sci 6: 1-9.

GARCÍA S AND LE RESTE L. 1986. Ciclos vitales, dinámica, explotación y ordenación de las poblaciones de camarones peneidos costeros. FAO Doc Téc Pesca 203: 180.

GRABOWSKI RC, NEGREIROS-FRANSOZO ML AND CASTILHO AL. 2016. Reproductive ecology of the seabob shrimp *Xiphopenaeus kroyeri* (Heller, 1862) in a coastal area of Southern Brazil. Chin J Oceanol Limnol 34: 125-135.

GRABOWSKI RC, SIMÕES SM AND CASTILHO AL. 2014. Population structure, sex ratio and growth of the seabob shrimp *Xiphopenaeus kroyeri* (Decapoda, Penaeidae) from coastal waters of southern Brazil. In: Wehrtmann IS and Bauer RT (Eds), Proceedings of the Summer Meeting of the Crustacean Society and the Latin American Association of Carcinology, Costa Rica. ZooKeys 457: 253-269.

HARTNOLL RG. 2001. Growth in Crustacea - twenty years on. Hydrobiologia 449: 111-122.

HIROKI KAN, FRANSOZO A, COSTA RC, CASTILHO AL, SHIMIZU RM, ALMEIDA AC AND FURLAN M. 2011. Bathymetric distribution of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) (Decapoda, Penaeidae) in two locations off the southeastern Brazilian coast. Mar Biol Res 7: 176-185.

IBAMA - INSTITUTO BRASILEIRO DO MEIO AMBIENTE E DOS RECURSOS NATURAIS RENOVÁVEIS. 2016. < www.ibama.gov.br >. Acesso em Maio de 2016.

KEVREKIDIS K AND THESSALOU-LEGAKI M. 2006. Catch rates, size structure and sex ratio of *Melicertus kerathurus* (Decapoda: Penaeidae) from an Aegean Sea trawl fishery. Fish Res 80: 270-279.

KING M. 1995. Fisheries biology, Assessment and Management. Fishing News Books, Oxford, UK, 341p.

MANTELATTO FLM AND FRANSOZO A. 1999. Characterization of the physical and chemical parameters of Ubatuba Bay, northern coast of São Paulo state, Brazil. Rev Bras Biol 59: 23-31.

NEGREIROS-FRANSOZO ML, FRANSOZO A, PINHEIRO MAA, MANTELATTO FLM AND SANTOS S. 1991. Caracterização Física e Química da Enseada de Fortaleza, Ubatuba, SP. Rev Bras Geociênc 21: 114-120.

PÉREZ-FARFANTE I. 1988. Illustrated key to Penaeoid shrimps of commerce in the Americas. NOAA Tech Rep NMFS 64: 1-32.

PÉREZ-FARFANTE I AND KENSLEY B. 1997. Penaeoid and Sergestoid shrimps and prawns of the World. Keys and diagnoses for the families and genera. Paris, Éditions du Muséum National d Histoire Naturalle, 233 p.

PETRIELLA AM AND BOSCHI EE. 1997. Crecimiento en crustáceos decápodos: resultados de investigaciones realizadas en Argentina. Investig Mar 25: 135-157.

PIRES-VANIN AMS. 2001. Identifying the components of ecological variation in a marine benthic megafauna. Rev Bras Oceanogr 49: 29-38.

SEMENSATO XEG AND DI BENEDITTO APM. 2008. Population dynamic and reproduction of *Artemesia longinaris* (Decapoda, Penaeidae) in Rio de Janeiro State, South-Eastern Brazil. Bol Inst Pesca 34: 89-98.

SILVA CNS, BROADHURST MK, MEDEIROS RP AND DIAS JH. 2013. Resolving environmental issues in the southern Brazilian artisanal penaeid-trawl fishery through adaptive co-management. Mar Pol 42: 133-141.

SIMÕES SM, D'INCAO F, FRANSOZO A, CASTILHO AL AND COSTA RC. 2013. Sex ratio, growth and recruitment of the pelagic shrimp *Acetes americanus* on the southeastern coast of Brazil. J Crust Biol 33: 1-9.

SOARES-GOMES A AND PIRES-VANIN AMS. 2003. Padrões de abundância, riqueza e diversidade de moluscos bivalves na plataforma continental ao largo de Ubatuba, São Paulo, Brasil: uma comparação metodológica. Rev Bras Zool 20: 717-725.

VEGA-PÉREZ LA. 1993. Estudo do zooplâncton da região de Ubatuba, Estado de São Paulo. Publ Esp Inst Oceanogr 10: 65-84.

VOGT G. 2012. Ageing and longevity in the Decapoda (Crustacea): A review. Zool Anz 251: 1-25.

VON BERTALANFFY L. 1938. A quantitative theory of organic growth. Human Biology 10: 181-213.

WENNER AM. 1972. Sex ratio as a function of size in marine crustacean. Am Nat 106: 321-350.

WILSON K AND HARDY ICW. 2002. Statistical analysis of sex ratio: an introduction. In: Hardy ICW (Ed), Sex ratios: concepts and research methods. Cambridge University Press, Cambridge, p 48-92.

YAMADA R, KODAMA K, YAMAKAWA T, HORIGUCHI T AND AOKI I. 2007. Growth and reproductive biology of the small penaeid shrimp *Trachysalambria curvirostris* in Tokyo Bay. Mar Biol 151: 961-971.