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TESE DE DOUTORADO

DISTRIBUIÇÃO ESPAÇO-TEMPORAL DA COMUNIDADE ZOOPLANCTÔNICA NO ESTUÁRIO DO TAPERAÇU (BRAGANÇA-PARÁ-BRASIL): BIOMASSA E PRODUÇÃO SECUNDÁRIA DAS PRINCIPAIS ESPÉCIES DE COPÉPODOS

NATÁLIA DA ROCHA LEITE

BRAGANÇA – PA
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Tese de Doutorado apresentada ao Programa de Pós-Graduação em Biologia Ambiental da Universidade Federal do Pará, Campus Universitário de Bragança, como parte dos requisitos necessários à obtenção do título de Doutor em Biologia Ambiental.

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NATÁLIA DA ROCHA LEITE

Tese apresentada para obtenção do título de Doutor em Biologia Ambiental: ênfase em Recursos Biológicos da Zona Costeira Amazônica do Programa de Pós-Graduação em Biologia Ambiental, Universidade Federal do Pará.

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RESUMO

O presente estudo objetivou estudar a composição e a distribuição da comunidade zooplanctônica no estuário do Taperaçu avaliando, em escala temporal e espacial, a contribuição das principais espécies de copépodos para a biomassa e produção em termos de carbono orgânico no ambiente em estudo. Para tanto, foram realizadas coletas bimestrais (zooplâncton e variáveis hidrológicas) de junho de 2012 a junho de 2013, em três estações fixas situadas ao longo do estuário, totalizando 45 amostras. A comunidade zooplanctônica do Taperaçu foi aparentemente homogênea, não sendo detectadas variações significativas relacionadas aos ciclos circadianos (dia/noite) e de maré (enchente/vazante), no que se refere aos atributos biológicos. Elevados valores de densidade de *Paracalanus quasimodo*, *Labidocera fluviatilis*, e *Pseudodiaptomus marshi* foram observados. A ausência de um padrão nictimeral e de maré, esteve possivelmente relacionada às características morfodinâmicas do estuário do Taperaçu, tais como a presença de bancos de areia em sua porção central, a ausência de uma descarga fluvial, a pequena área de captação, as baixas profundidades e as fortes correntes de maré, as quais facilitam os processos de mistura horizontal e vertical da coluna de água. Quando analisados em uma escala mensal e espacial, foi observada a influência dos períodos sazonais sobre a dinâmica desses organismos, estando estas diretamente relacionadas às variações da salinidade, turbidez e concentrações de clorofila-a. A comunidade zooplanctônica esteve dominada pelos copépodos, em especial *Acartia tonsa* (22.230,9±46.145,7 ind.m^{-3}), *Acartia lilljerborgi* (4.011,6±10.326,5 ind.m^{-3}), *P. marshi* (3.267,3±4.565,1 ind.m^{-3}), *P. quasimodo* (9.270,7±17.593,3 ind.m^{-3}) e *Oithona oswaldocruzi* (30.221,9±28.328,4 ind.m^{-3}), juntamente com *Oikopleura dioica* (15.284,6±26.060,6 ind.m^{-3}). A diversidade média das espécies variou de 2,0±0,6 bits.ind^{-1} a 3,8±0,4 bits.ind^{-1}, enquanto que a equitabilidade variou de 0,5±0,1 a 0,7±0,03. De modo geral, a variabilidade temporal (mensal e sazonal) e espacial observada na estrutura e dinâmica populacional do zooplâncton esteve principalmente relacionada às flutuações nas taxas de precipitação, as quais afetaram diretamente a salinidade da água e, consequentemente, a densidade desses organismos. Adicionalmente, conclui-se que a presença de espécies tipicamente marinhas, tais como *P. quasimodo* e *Oikopleura dioica* pode estar relacionada ao aumento significativo da salinidade, resultado da redução das chuvas em 2012. A biomassa e produção de *A. tonsa* e *A. lilljeborgi* estiveram diretamente relacionadas à precipitação local, visto que *A. tonsa* apresentou elevados valores durante todo o período, e não apenas no período chuvoso, como anteriormente observado neste mesmo estuário. Os estágios imaturos (C1-C5) de *A. tonsa* foram as formas dominantes, com destaque para o estágio C4 (839,88±1.518,80 mgC.m^{-3}), enquanto que para *A. lilljeborgi* os mais elevados valores foram obtidos para os adultos (499,95±1.347,84 mgC.m^{-3}). As taxas de produção secundária obtidas foram mais elevadas do que àquelas descritas para outros estuários localizados ao redor do mundo, podendo estes resultados estarem associados as elevadas temperaturas registradas durante todo o ano, bem como a observação de águas ricas em nutrientes e matéria orgânica particulada derivados dos manguezais adjacentes ao Taperaçu. De forma geral os resultados obtidos indicam que a influência das variações climáticas sobre as variáveis hidrológicas, em especial a temperatura, salinidade, bem como sobre as concentrações de clorofila-a foram os principais responsáveis pela dinâmica das espécies mesozooplanctônicas identificadas no estuário do Taperaçu.

Palavras-chave: Zooplâncton, pluviosidade, variáveis ambientais, estuário tropical.

ABSTRACT

This study aimed to determine the composition and distribution of zooplankton in the estuary Taperaçu evaluating, in temporal and spatial scales, the contribution of the main species of copepods for biomass and production in terms of organic carbon in the environment under study. Therefore, samples were taken bimonthly (zooplankton and hydrologic variables) from June 2012 to June 2013, in three fixed stations located along the estuary, totaling 45 samples. The zooplankton community was apparently homogeneous. With regard to biological attributes, significant variations related to circadian cycles (day/night) and tidal periods (flood/ebb) were not detected. High values of abundance of *Paracalanus quasimodo*, *Labidocera fluviatilis* and *Pseudodiaptomus marshi* were observed. The absence of a nichtemeral and tidal patterns, was possibly related to the morphodynamic characteristics of the estuary Taperaçu, such as the presence of sandbanks in its central portion, the absence of a river discharge, the small catchment area, low depths and strong tidal currents, which facilitate the processes of horizontal and vertical mixing of the water column. When analyzed on a monthly and spatial scale, it was observed the influence of seasonal periods on the dynamics of these organisms, these being directly related to variations in salinity, turbidity and chlorophyll-a concentrations. The zooplankton community was dominated by copepods, especially *Acartia tonsa* (22,230.9±46,145.7 ind.m^{-3}), *Acartia lilljerborgi* (4,011.6±10,326.5 ind.m^{-3}), *P. marshi* (3,267.3±4,565.1 ind.m^{-3}), *P. quasimodo* (9,270.7±17,593.3 ind.m^{-3}) and *Oithona oswaldocruzi* (30,221.9±28,328.4 ind.m^{-3}), together with *Oikopleura dioica* (15,284.6±26,060.6 ind.m^{-3}). The average diversity of species ranged from 2.0±0.6 bits.ind^{-1} to 3.8±0.4 bits.ind^{-1}, while the evenness ranged from 0.5±0.1 to 0.7±0:03. Overall, the temporal variability (monthly and temporal) and spatial observed in the structure and dynamics of zooplankton population was mainly related to fluctuations in precipitation rates, which directly affect the salinity of the water and consequently the abundance of these organisms. In addition, it was also concluded that the presence of typically marine species such as *P. quasimodo* and *O. dioica* may be related to the significant increase in salinity as a result of reduced rainfall in 2012. Biomass and production *A. tonsa* and *A.*

lilljeborgi were directly related to the local rainfall since, *A. tonsa* showed high values throughout the period, not only in the rainy season as previously observed in this same estuary. The immature stages (C1-C5) of *A. tonsa* were the dominant forms, especially the C4 stage (839.88±1518.80 mgC.m^{-3}), while for *A. lilljeborgi* the highest values were obtained for adults (1,347.84±499.95 mgC.m^{-3}). The obtained rates of secondary production were higher than those described for other estuaries located around the world, and these results are associated with the high temperatures recorded during the year as well as the observation of water rich in nutrients and particulate organic matter derived from adjacent to mangroves Taperaçu. In general, the results indicate that the influence of climate changes on the hydrological variables especially temperature, salinity, as well as the concentration of chlorophyll-a were the main responsible for the dynamics of mesozooplanctônicas species identified in the estuary of Taperaçu.

Keywords: Zooplankton, rainfall, environmental variables, tropical estuary.

INTRODUÇÃO GERAL

1. INTRODUÇÃO

Os estuários são classicamente definidos como corpos de água costeiros semi-fechados que têm uma ligação livre com o mar e nos quais a água do mar se dilui, de forma mensurável, com água doce proveniente da drenagem terrestre. (Cameron & Pritchard, 1963). Pode ser definido também como uma interação entre duas massas de água com diferentes características físicas e químicas, que desenvolvem padrões sedimentológicos e biológicos característicos (Carter, 1988). Estes ecossistemas, desempenham função importante como áreas de reprodução e desenvolvimento para muitas espécies de vertebrados e invertebrados aquáticos, tornando-se áreas de refúgio e proteção contra a ação de predadores e outros competidores (Blaber, 1997; Whitfield, 1999), aumentando a sobrevivência e o crescimento destas espécies nos estágios mais críticos de seu ciclo de vida (Araújo et al., 2003).

Geralmente as águas estuarinas são biologicamente mais produtivas do que os sistemas de água doce e o oceano adjacente, devido à circulação hidrodinâmica característica destes ambientes e a retenção de nutrientes, estimulando assim a sua produção (Miranda et al., 2002).

Estes ecossistemas caracterizam-se por serem altamente dinâmicos, apresentando variações sazonais de salinidade, temperatura, e das concentrações de oxigênio e nutrientes dissolvidos (Summerhayes & Thorpe, 1998; Park & Marshall, 2000). Esta variabilidade nos componentes abióticos se reflete na dinâmica das populações biológicas, determinando assim os padrões de flutuação da composição e da distribuição espaço-temporal da biota residente e transitória destes ecossistemas (Little, 2000).

A compreensão das relações tróficas e a influência dos fatores abióticos sobre a distribuição e abundância dos organismos aquáticos constituem um dos principais objetivos da ecologia. Os organismos aquáticos apresentam relações intra e inter-específicas, através das quais competem pela utilização de espaço, nutrientes e alimento disponíveis na coluna d’água (Valiela, 1995). Dentre os organismos aquáticos que habitam o ambiente estuarino, destacam-se àqueles pertencentes à comunidade planctônica, cujo conhecimento é de importância prioritária, pois, enquanto o fitoplâncton produz a matéria orgânica através da fotossíntese, o zooplâncton constitui um importante elo na transferência de energia oriunda do fitoplâncton – bacterioplâncton ou de detritos orgânicos particulados para os demais níveis tróficos (Leandro et al., 2007; Islam et al., 2006; Magalhães et al., 2015). Este grupo de organismos é bastante heterogêneo e está constituído por quase todos os grupos de invertebrados aquáticos, além de ovos e larvas de peixes, apresentando formas permanentemente planctônicas (holoplâncton), bem como espécimes que vivem temporariamente no plâncton (meroplâncton).

Os organismos zooplanctônicos apresentam espécies bioindicadoras, as quais fornecem importantes informações sobre os processos atuantes nos ecossistemas aquáticos, uma vez que suas comunidades são diretamente influenciadas pelas variáveis abióticas e bióticas do meio (Linton & Warner, 2003), e que respondem rapidamente às flutuações ambientais (Gomez-Gutiérrez & Peterson, 1999).

Entre os organismos que compõem o mesozooplâncton estuarino e marinho, os copépodos são o grupo dominante compreendendo entre 80 e 90% da densidade total dos organismos desta comunidade (Leandro et al., 2006, Magalhães et al., 2015).

Estudos referentes às variações espaciais e temporais da densidade, biomassa e produção dos copépodos são de grande importância para determinação de seu papel na produção e fluxo de matéria orgânica particulada e dissolvida, bem como para o entendimento da trofodinâmica estuarina (Perissinotto et al., 2003, Miyashita et al., 2009; Leandro et al., 2014). São importantes também na avaliação de estoques pesqueiros, visto que estes organismos, tanto na fase larval (Payne & Rippingale, 2001) como na fase adulta (Camargo & Isaac, 2004) constituem um dos elementos básicos da dieta alimentar de muitas espécies de peixes zooplanctófagos (Xie & Yang, 2000; Evjemo et al., 2003; Magalhães et al., 2015). Além disto, estudos recentes vêm evidenciando também o papel dos copépodos na utilização do carbono produzido pela alça microbiana (Putzeys & Hernández-Léon, 2005; Camacho, 2012; Zingel et al., 2016).

As estimativas de produção secundária em ecossistemas pelágicos marinhos e estuarinos de uma dada região, permitem não apenas agregar conhecimentos sobre o estado nutricional e fisiológico das comunidades, mas também elaborar modelos sobre o funcionamento destes ecossistemas

(Huntley & Lopez, 1992; Runge & Roff, 2000; Melo, 2009). Dentro da comunidade zooplanctônica, os copépodos constituem o principal grupo abordado nos estudos de produção secundária nos ambientes estuarinos e marinhos, uma vez que são numericamente abundantes na maioria dos ambientes pelágicos (Turner, 2004; Schminke, 2007).

As variáveis físicas, químicas, e biológicas influenciam diretamente a estrutura e distribuição do zooplâncton estuarino (Magalhães et al., 2015), afetando consequentemente as taxas de produção secundária destes organismos. Embora as estimativas de produtividade secundária sejam de grande importância para a caracterização do fluxo energético nas teias alimentares estuarino-marinhas, estas tornam-se cada vez mais desafiadoras devido à escassez de métodos disponíveis para estimar a produção desta comunidade, não havendo, desta forma, uma metodologia padrão devido à grande diversidade de espécies zooplanctônicas e o amplo espectro dimensional observado nesta comunidade.

As estimativas de biomassa das espécies zooplanctônicas são frequentemente realizadas por meio de equações morfométricas empíricas que relacionam o peso dos espécimes com o tamanho do prossoma (Chisholm & Roff, 1990; Webber & Roff, 1995; Hopcroft et al., 1998; Ara, 2004; Miyashita et al., 2009). A produção de um organismo, por sua vez, é definida como a biomassa acumulada em um dado intervalo de tempo, independentemente do destino final desta nova matéria (Clarke et al., 1946), sendo expressa em “$mgC.m^{-3}.dia^{-1}$”. (Rigler & Downing, 1984). As estimativas da produção secundária são geralmente obtidas usando-se a equação $P=B\times g$, onde “P” é a produção, “B” é a biomassa em carbono do indivíduo, e “g” é a taxa de crescimento (Kimmerer, 1987; Huntley & Lopez, 1992; Hirst & Bunker, 2003).

Na literatura científica existe uma gama de métodos para avaliação das taxas de crescimento dos organismos zooplanctônicos, tais como as análises de coorte (Mullin, 1969; Greze, 1978; Uye, 1982) e técnicas de “coortes artificiais” (Kimmerer & Mckinnon, 1987); métodos baseados na estimativa de produção de ovos (Marshall & Orr, 1955; Sekiguchi et al., 1980; Poulet et al., 1995; López et al., 2007; Melo Junior, 2009); frequência de mudas (Burkill & Kendal 1982; Peterson et al., 1991; Hutchings et al., 1995); e a medição de taxas metabólicas (Omori & Ikeda, 1984; Le Borgne, 1986), além do conteúdo de DNA e RNA (Ikeda et al., 2007; Speekmann et al., 2007), ou baseados em relações bioquímicas e atividades de enzimas relacionadas ao crescimento (Berges et al., 1990; Biegala e Bergon, 1998; Avila et al., 2011). No entanto, tais técnicas têm apresentado algumas limitações em seu uso e aplicação, tais como a incapacidade de se aplicar a mesma técnica em diferentes grupos taxonômicos, bem como a impossibilidade de agregar mais de uma espécie, ou mesmo mais de uma fase de desenvolvimento nas análises (Kimmerer & McKinnon, 1987; Melo Junior, 2009).

Dentre as metodologias disponíveis, a aplicação de modelos empíricos globais para o cálculo das taxas de crescimento e consequentemente da produção, tem sido amplamente empregada como alternativa para a determinação da produtividade secundária do zooplâncton. Tais modelos matemáticos utilizam principalmente a temperatura e a disponibilidade de alimento associadas a outras variáveis (Huntley & Lopez, 1992; Hirst & Shaedar, 1997; Hirst & Limpitt, 1998; Hirst & Bunker, 2003). Não obstante, vale ressaltar que diversos fatores biológicos influenciam a abundância e a distribuição do zooplâncton, repercutindo diretamente na produção secundária dos mesmos (Magalhães et al., 2015).

No modelo de Huntley & Lopez (1992), a taxa de crescimento dos copépodos é dependente apenas da temperatura, e independente do tamanho do prossoma e da espécie considerada, pois, baseia-se no fato de que as reações enzimáticas envolvidas na síntese proteica de organismos pecilotérmicos marinhos são dependentes da temperatura.

Este modelo, por sua vez, é bastante simples, visto que não são considerados os efeitos da qualidade e quantidade do alimento disponível no ambiente para o crescimento dos organismos. Além disto, podem superestimar as taxas de crescimento em regiões oligotróficas (Calbet & Agustí, 1999).

Os modelos empíricos de Hirst & Shaedar (1997) e Hirst & Limpitt (1998) consideram que a taxa de crescimento dos copépodos é dependente tanto da temperatura quanto do peso corporal dos indivíduos analisados. Ambos os modelos fornecem valores menores de produção secundária que os obtidos pelo modelo de Huntley & Lopez (1992), uma vez que a temperatura não é o único fator levado em consideração. Entretanto, uma das grandes limitações do modelo de Hirst & Lampitt (1998) é o fato de que o mesmo leva em consideração que as populações dos organismos analisados (neste caso, copépodos) crescem continuamente. Desta forma, populações que não apresentam crescimento contínuo, ou que estão em estado de latência, não podem ter sua produção calculada através desta técnica (Gomes, 2007).

Mais recentemente, Hirst & Bunker (2003) propuseram um modelo no qual foram englobados o crescimento dos copépodos e informações referentes à temperatura e às concentrações de clorofila-a. Como este modelo considera a disponibilidade de alimento, que é limitante para a maioria das espécies de copépodos pelágicos de áreas costeiras tropicais e subtropicais, as estimativas obtidas podem ser mais realísticas do que as obtidas através dos modelos de Hirst & Shaedar (1997) e Hirst & Lampitt (1998).

Embora as estimativas de produção sejam amplamente difundidas, nos ecossistemas costeiros do Brasil, os estudos sobre as estimativas de biomassa e produtividade secundária, estiveram restritos as regiões nordeste (Eskinazi-Sant'anna, 2000; Melo Junior et al., 2007), e sudeste do Brasil (Rocha & Tundisi, 1984; Ara, 2001; 2002; 2004; Eskinazi-Sant'anna & Bjornberg, 2006; Muxagata et. al., 2011; Miyashita et al., 2009, entre outros). Na costa norte do Brasil, apesar dos esforços aplicados para o conhecimento das estimativas da biomassa e produção dos copépodos, pouco se conhece a respeito deste tema. Os primeiros estudos realizados em ecossistemas amazônicos dentro desta temática foram os realizados por Krumme & Liang (2004), com copépodos em um canal de maré do estuário do rio Caeté, através do qual estes autores observaram que *Pseudodiaptomus marshi* dominou sobre a comunidade de copépodos em termos de biomassa, sendo responsável por 66% da biomassa do mesozooplâncton total, seguida por *P. richardi*, *Acartia tonsa* e *A. lilljeborgi*. Ainda nesse mesmo estuário, Magalhães et al. (2006) e Magalhães et al. (2010), verificaram que a variabilidade espacial e temporal de três espécies da família Pseudodiaptomidae (*P. richardi*, *P. acutus* e *P. marshi*), de forma geral, estiveram diretamente associadas às flutuações nos gradientes de salinidade.

Em estudos recentes, estimativas de produção secundária para a costa norte do Brasil foram realizadas por Magalhães et al. (2011) em um estuário do litoral paraense para os adultos da espécies *P. marshi*, *A. lilljeborgii*, *A. tonsa* e *Subeucalanus pileatus*, e por Magalhães et al., (2013) com os copépodos *A.*

tonsa e *A. lilljeborgi*. Em ambos os estudos, as estimativas da produção foram realizadas utilizando-se o modelo empírico global de Hirst & Sheader (1997) nas estimativas da taxa de crescimento destes organismos. As taxas de produtividade foram determinadas em escala diária, com os resultados sendo posteriormente relacionados às variáveis hidrológicas. Estes resultados revelaram que a produção dos copépodos esteve sujeita a uma forte sazonalidade, a qual foi principalmente associada às flutuações nas taxas de precipitação, que afetaram diretamente a salinidade e consequentemente os processos de sucessão ecológica e dinâmica populacional das espécies identificadas.

Desta forma este estudo apresenta pela primeira vez, através de amostragens simultâneas ao longo do estuário do Taperaçu, como as oscilações das variáveis hidrológicas e hidrodinâmicas, influenciam as variações espaciais e temporais da abundância das principais espécies de copépodes, bem como a biomassa e produção dos copepoditos e adultos de *Acartia tonsa* e *A. lilljeborgi*.

2. POSTULADO TEÓRICO E OBJETIVOS

2.1. HIPÓTESE GERAL

Esta tese está baseada em três questões norteadoras:

i) Como o ciclo circadiano e os períodos de maré afetam a dinâmica da comunidade zooplanctônica no estuário do Taperaçu?

ii) Como os efeitos da precipitação atuam sobre a abundância, diversidade específica e a equitabilidade das espécies zooplanctônicas no estuário do Taperaçu, e quais as correlações destas com as variáveis ambientais?

iii) Quais os efeitos, em escala temporal e espacial, das variáveis ambientais sobre a abundância, biomassa e produção secundária de copepoditos e adultos (machos e fêmeas) de *Acartia tonsa* e *A. lilljeborgi*?

2.2. OBJETIVOS

2.2.1. Objetivo Geral

O presente estudo teve por objetivo geral, estudar a composição e distribuição zooplanctônica no estuário do Taperaçu – nordeste do Pará, assim como avaliar em escala temporal e espacial, a contribuição das principais espécies de copépodos para a biomassa e produção em termos de carbono orgânico no ambiente em estudo e suas inter-relações com as variáveis ambientais, podendo, desta forma, servir como embasamento para estudos futuros de modelagem trófica no ambiente em estudo, bem como em ecossistemas estuarinos amazônicos com características semelhantes.

2.2.2 Objetivos Específicos

i) Determinar o efeito do ciclo circadiano (dia e noite) e dos períodos de maré (enchente e vazante) sobre as variáveis ambientais e sobre a estrutura da comunidade zooplanctônica do estuário do Taperaçu;

ii) Avaliar em escala espacial e temporal de curto e médio prazo (diária, mensal e sazonal) os efeitos da precipitação sobre a abundância, diversidade específica e a equitabilidade das espécies zooplanctônicas no estuário do Taperaçu, bem como as correlações destas com as variáveis ambientais (temperatura, salinidade, pH, oxigênio dissolvido, turbidez, concentrações de clorofila-a e nutrientes inorgânicos dissolvidos;

iii) Estudar os efeitos temporais das variáveis ambientais sobre a abundância, biomassa e produção secundária de copepoditos e adultos (machos e fêmeas) de *Acartia tonsa* e *A. lilljeborgi* no estuário do Taperaçu;

2.2.3. ESTRUTURA DA TESE

Esta tese está estruturada em três capítulos:

- *Capítulo I*: artigo publicado no periódico Journal of Coastal Research. Este artigo apresenta questões relacionadas a influência do ciclo circadiano e dos períodos de maré sobre a dinâmica da comunidade zooplanctônica no estuário do Taperaçu.

- *Capítulo II:* artigo publicado no periódico Journal of Coastal Research. Este artigo aborda os efeitos da sazonalidade sobre a abundância, diversidade específica e equitabilidade das espécies zooplanctônicas no estuário do Taperaçu e suas correlações com as variáveis ambientais

- *Capítulo III:* artigo que será submetido ao periódico Journal of Marine Systems. Este artigo estima através de modelos empíricos de crescimento a abundância, biomassa e produção secundária de copepoditos e adultos (machos e fêmeas) de *Acartia tonsa* e *A. lilljeborgi*, em escala temporal e espacial, e sua relação com as variáveis ambientais.

3. METODOLOGIA GERAL

3.1. Área de estudo

A zona costeira norte do Brasil, cuja extensão é de aproximadamente 2.250 km (Souza Filho, 2005), possui características hidrodinâmicas de alta energia e uma linha de costa extremamente entrecortada por baías e estuários com reentrâncias que alcançam até 45 km de extensão em direção ao continente (Souza-Filho et al., 2009).

No litoral nordeste do estado do Pará, encontra-se o estuário do Taperaçu, localizado a cerca de 200 km a sudeste da desembocadura do rio Amazonas, no município de Bragança. O Taperaçu (Figura 1), é classificado como um estuário permanentemente aberto, caracterizado por elevados valores de turbidez, (média de 378,1 NTU), profundidade média em torno de 4,2 m e correntes de maré de até 2,04 $m.s^{-1}$ (Asp et al., 2012; Andrade et al., 2016). Morfologicamente o estuário possui forma de funil, com extensos bancos de areia em sua porção mediana, 21 km^2 de superfície de lâmina de água e uma pequena área de drenagem de aproximadamente 40 km^2 (Araújo Jr & Asp, 2013), formada principalmente por áreas alagadas e florestas de mangue, que margeiam o corpo estuarino quase que exclusivamente (Pereira et al., 2010; Asp et al., 2012). As áreas de mangue incluem vários canais de maré que ligam o Taperaçu à Baía do Maiaú e ao estuário do rio Caeté.

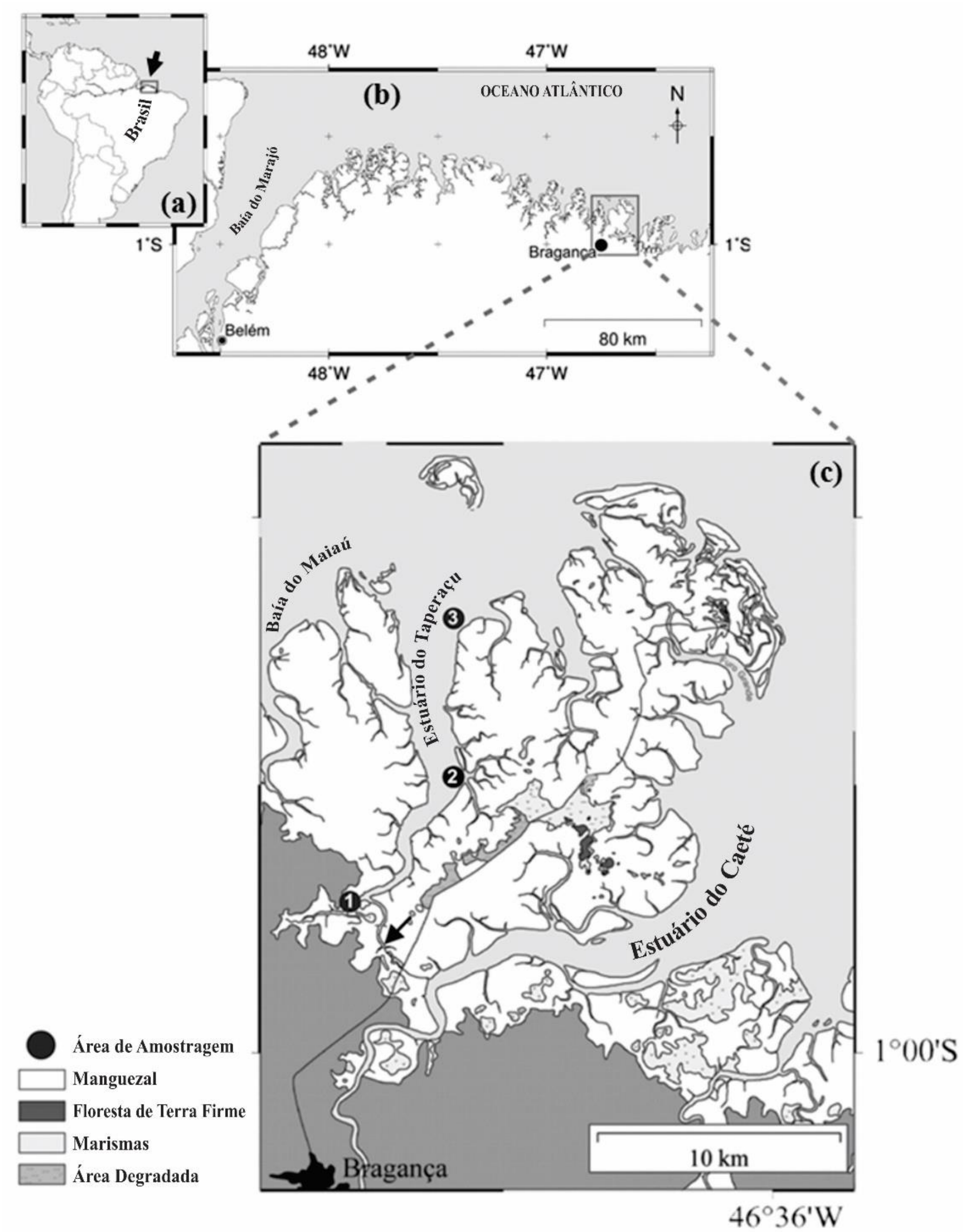

Figura 1. (a) América do Sul; (b) localização do estuário do Taperaçu (00º50’–00º57’ S and 46º42’–46º45’ W) sobre a costa nordeste do Brasil; (c) localização geográfica das três estações amostrais localizadas na porção superior (1), média (2), e inferior (3) do estuário. A seta negra indica a localização do canal do Taici, o qual conecta o estuário do Taperaçu ao estuário do Caeté (Modificado de Mehlig, 2001).

Assim como outros estuários localizados ao norte do Brasil (Matos et al., 2011; Magalhães et al., 2015) o estuário do Taperaçu apresenta um regime de meso/macro-marés semidiurnas com alturas de maré em torno de 5 m, podendo alcançar valores de até 6 m durante as marés equinociais de sizígia (DHN, 2015). Neste sentido, a morfodinâmica do Taperaçu é conduzida primariamente pelos regimes de macro-marés, sendo os ventos locais e as ondas geradas pelos ventos no estuário de relevância secundária ao longo da costa e sua propagação para o estuário substancialmente reduzida por bancos de areia e deltas de maré vazante (Asp et al., 2012, 2013).

O estuário do Taperaçu, não possui uma descarga fluvial efetiva (Asp, eta al., 2012), sendo as únicas fontes de água doce para o estuário, provenientes dos campos alagados e do canal de maré do Taici, o qual apresenta uma extensão média de 3 km, com cerca de 15 m de largura, que conecta a parte superior do Taperaçu com o setor médio do estuário do rio Caeté (Perillo, 2009; Araújo Jr. & Asp, 2013).

Devido à ausência de uma descarga fluvial efetiva, as variações sazonais são mais evidentes e ocorrem em resposta às oscilações da precipitação, cujos valores médios de salinidade oscilam entre 42 e 07, em períodos de menor e maior pluviosidade, respectivamente. Em termos de produtividade primária, as concentrações de clorofila-a são relativamente elevadas, alcançando em alguns meses valores superiores a 30 $mg.m^{-3}$ (Magalhães et al., 2013; Leite et al., 2013; Costa et al., 2013).

O clima da região é equatorial quente e úmido apresentando duas estações, uma estação chuvosa nos primeiros meses do ano (janeiro a junho) e uma estação seca (menos chuvosa), compreendendo os meses de julho a dezembro (Figura 2), com a umidade relativa do ar oscilando entre 80 e 91% (Moraes et al., 2005). A temperatura média e a pluviosidade anual são de 25,5 ºC e 2.500 mm, respectivamente, com 75 a 85% da precipitação ocorrendo na estação chuvosa (INMET, 2015). Este padrão climático reflete o efeito do deslocamento da Zona de Convergência Intertropical (ZCIT) sobre a região, a qual permanece em latitudes em torno de 14°N durante agosto e setembro, migrando para o sul até cerca de 2°S durante março e abril, exatamente sobre a Amazônia (Marengo, 1995; Souza Filho et al., 2009).

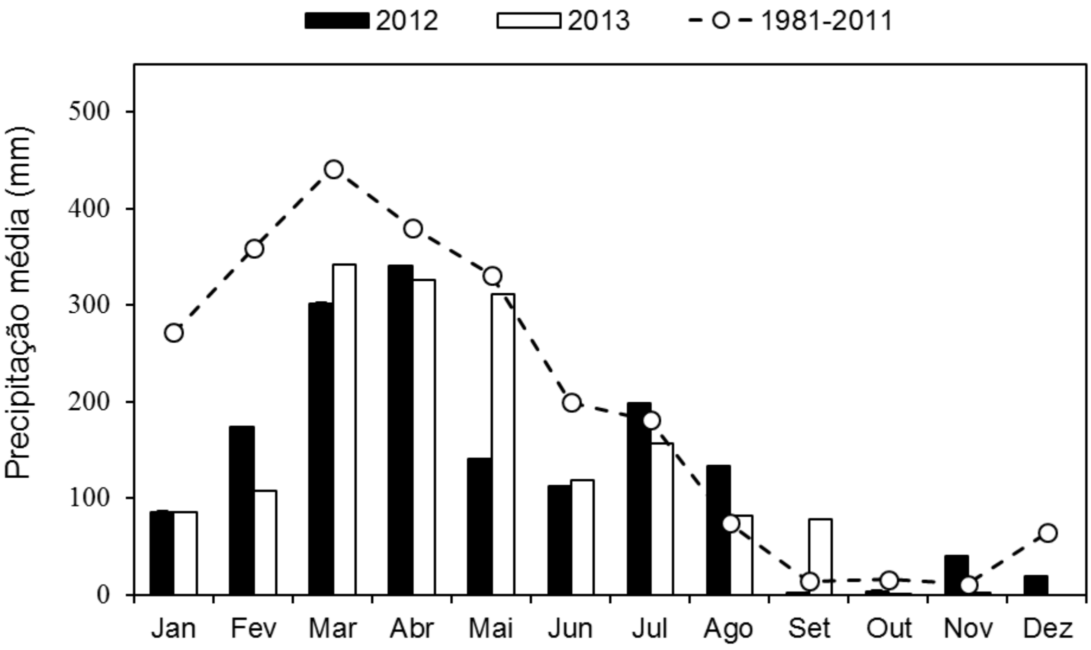

Figura 2. Precipitação média mensal (mm) dos últimos trinta anos (1981-2011) e dos anos de 2012 e 2013 da estação meteorológica de Tracuateua, Pará (01º05'S e 47º10'W) (Fonte: INMET).

A área de estudo faz parte da Unidade de Conservação Federal de Uso Sustentável – RESEX Marinha Caeté-Taperaçu, criada oficialmente pela Portaria ICMBio nº 17 de 24 de setembro de 2007, com uma área de aproximadamente 42.068,086 hectares. Nesta RESEX, localizada no Nordeste Paraense, na Microrregião Bragantina, os recursos naturais renováveis são tradicionalmente utilizados pelas populações extrativistas residentes em sua área de abrangência.

A vegetação nas margens do Taperaçu, a partir da sua desembocadura, caracteriza-se pela presença de florestas de mangue relativamente densas e bem desenvolvidas, com aproximadamente 20 m de altura, com três espécies dominantes na região: *Rhizophora mangle* Linnaeus, 1753, *Avicennia germinans* Linnaeus, 1764 e *Laguncularia racemosa* Linnaeus, 1807, todas pertencentes à província de manguezal do Atlântico (Menezes, 2008).

3.2 Amostragens de campo

As coletas foram realizadas bimestralmente, no estuário do Taperaçu, de abril de 2012 a setembro 2013, em marés de quadratura, durante 25 horas, simultaneamente em um perfil longitudinal composto por três estações fixas situadas ao longo do estuário, E1 (046º46'26.9"S e 00º56'58.4"W) situada na região mais interna e distante 7,5 km da E2 (046º44'00"S e 00º55'06.8"W), a qual está localizada na porção intermediária do estuário e distante 10 km da E3 (046º43'02.4"S e 00º50'30.9"W), esta última situada na desembocadura do estuário (Figura 1).

As amostras de zooplâncton (total de 171 amostras), foram obtidas através de arrastos horizontais subsuperficiais, realizados a cada três horas, utilizando-se redes de plâncton cônicas de 200 µm de abertura de malha e 50 cm de diâmetro de boca, providas de fluxômetros mecânicos para determinação do volume de água filtrada pelas redes. Ao fim das coletas, os organismos foram armazenados em recipientes plásticos, contendo formol a 20% (concentração final de 4%), neutralizado com tetraborato de sódio, segundo Newell & Newell (1975).

O volume de água filtrado pelas redes foi determinado pela seguinte fórmula:

$$V = a * n * c$$

onde: V é o volume de água filtrada pela rede após cada arrasto (m^3); a corresponde à área da boca da rede (m^2); n é o número de rotações do fluxômetro após os arrastos (FF – FI); c é o fator de aferição do fluxômetro após a calibração desse aparelho em metros por rotações.

As medidas de elevação da maré, temperatura, salinidade e turbidez, bem como as concentrações de oxigênio dissolvido na água foram realizadas *in situ* através de marégrafos e CTDO’s (RBR, modelo XR-420) com sensores de turbidez, os quais permaneceram fundeados durante todo período de amostragem (cerca de 25h) a aproximadamente 1,7 m de profundidade. Adicionalmente, foram coletadas 500 ml de amostras de água para determinação das concentrações de clorofila-a, pH e nutrientes inorgânicos dissolvidos (nitrito, nitrato, fosfato e silicato). Após as coletas, as amostras de água foram acondicionadas em recipientes plásticos de 500 ml, previamente descontaminados, e congeladas a -20 ºC até o momento da realização das análises em laboratório.

Os dados referentes à precipitação de 2012 a 2013, foram cedidos pelo Instituto Nacional de Meteorologia (INMET) e são provenientes da estação meteorológica de Tracuateua, Pará, distante 17 km da sede municipal de Bragança.

3.3 Análises de laboratório

3.3.1 Variáveis Ambientais

As concentrações de clorofila-a foram determinadas de acordo com a metodologia descrita por Parsons & Strickland (1963) e UNESCO (1996), enquanto os valores de pH foram determinados com o auxílio de um pHmetro eletrônico de bancada Labmeter PH2 (PHS–3B).

As análises dos nutrientes dissolvidos (nitrito, nitrato, fosfato e silicato) foram realizadas através de métodos espectrofotométricos, de acordo com a metodologia descrita por Strickland & Parsons (1972) e Grasshoff et al. (1983).

3.3.2 Zooplâncton

Para as análises quali-quantitativas dos organismos zooplanctônicos, as amostras foram fracionadas em um subamostrador tipo *Folsom*, (McEwen et al., 1954), sendo esta metodologia descrita por Boltovskoy (1981). Os organismos presentes nas subamostras foram identificados ao menor nível taxonômico possível e quantificados, utilizando-se microscópios estereoscópicos (Zeiss-Stemi, 2000), placas de Petri quadriculadas e chaves taxonômicas (Trégouboff & Rose, 1957; Boltovskoy, 1981, 1999; Bradford-Grieve et al., 1999; Sabatini, 1990 e Björnberg, 1972).

As contagens levaram em consideração o valor encontrado na alíquota multiplicado pelo fator de subamostragem para obtenção do valor total de organismos.

Os dados quantitativos foram utilizados para calcular a abundância absoluta e relativa, biomassa, produção, além dos índices ecológicos (diversidade e equitabilidade) das espécies zooplanctônicas.

A densidade dos organismos foi calculada através da seguinte equação:

$$D = N / V$$

onde, D= densidade zooplanctônica (ind.m^{-3}); N= número total de indivíduos da amostra; V= volume de água filtrada pela rede durante o arrasto.

A abundância relativa de cada táxon identificado foi expressa em termos de porcentagem, utilizando-se a seguinte fórmula:

$$A = (ni.100) / N$$

onde, ni= número de indivíduos da espécie 'i' observados na amostra; N= número total de indivíduos da amostra.

Os índices de diversidade (Shannon, 1948) e equitabilidade (Pielou, 1977) foram aplicados com o intuito de avaliar a complexidade da estrutura da comunidade zooplanctônica, sendo descritos, respectivamente, pelas equações:

$$H' = - \Sigma(pi.\log_2 pi)$$

onde, H' = índice de diversidade de Shannon-Wienner; pi = proporção do número de indivíduos da espécie presente na amostra, e:

$$J' = H' / \log_2 S$$

onde, J'= equitabilidade; S= número total de espécies presentes na amostra.

A riqueza de espécies foi determinada como sendo o número total de espécies presentes na amostra.

A biomassa em termos de peso seco dos copépodos foi calculada através da fórmula:

$$B = P\text{s} \times 10^{-3}.D$$

onde, B é a biomassa (mgPs.m^{-3}); Ps (mg) é o peso seco de cada indivíduo determinado a partir do comprimento do cefalotórax, através das equações de regressão espécie-específicas, da relação entre o comprimento do corpo e o peso seco, sendo estas obtidas da literatura (Ara, 2001). Tais regressões foram selecionadas segundo a fonte geográfica das mesmas, ou seja, somente regressões provenientes de estudos realizados em regiões tropicais e subtropicais foram utilizadas. As medidas do comprimento do cefalotórax dos copépodos (C1 a C6) (Figura 3) foram tomadas com auxílio de uma régua ocular micrométrica, e realizadas dorsalmente. Para os estágios C6 de *A. lilljeborgii*, o comprimento dos espinhos situados na porção posterior do cefalotórax não foram considerados, uma vez que o ângulo e o comprimento dos mesmos variam dependendo do adulto (ARA, 1998).

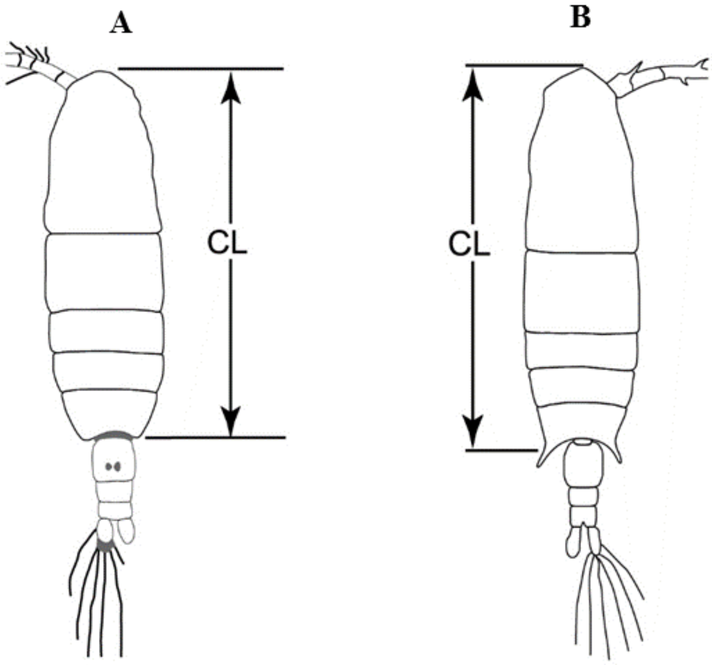

Figura 3. Medidas do comprimento do cefalotórax das espécies *A. tonsa* (A) e *A. lilljeborgi* (B).

Por último, *D* corresponde à densidade (ind.m^{-3}). Assim, a biomassa de uma espécie por unidade de volume de água foi expressa através da fórmula:

$$B = \Sigma\, P\mathrm{s}\; x10^{-3}.D$$

A biomassa em termos de carbono por unidade de volume de água foi expressa como:

$$Bc = B.Cp / 100$$

onde, *Bc* é a biomassa (mg C m^{-3}); *Cp* é o conteúdo de carbono de cada espécie, expresso em peso seco, assumindo que *Cp*= 0,506 para *A. tonsa* e 0,47 para *A. lilljeborgi* (Leite et al., dados não publicados).

A taxa de produção diária das principais espécies do zooplâncton foi estimada pela seguinte equação:

$$\boldsymbol{Pc = \Sigma\, D.Wc.g}$$

onde, *P* é a produção (mgC.m^{-3}.d^{-1}); *D* é a densidade (ind.m^{-3}); *Wc* representa o peso individual em carbono (µg C); *g* é a taxa instantânea de crescimento (d^{-1}).

No presente estudo, os valores de *g* foram estimados utilizando os modelos de crescimento de Hirst & Sheader (1997) e Hirst & Bunker (2003). No primeiro modelo, a taxa de crescimento é dependente do peso do corpo em termos de carbono (*Pc*, µgC) e da temperatura (*T*, ºC), sendo descrito pela seguinte equação:

$$\boldsymbol{Log10(g)=-1.1355+[0.0246*(T)]-[0.2962*log10\ (Dw)]}$$

O modelo de Hirst & Bunker (2003) utilizado para copepoditos adultos e juvenis, retentores e dispersores de ovos, é expresso pela seguinte equação:

$$\boldsymbol{Log_{10}g = 0.0186T - 0.288\ log_{10}DW + 0.417\ log_{10}Cl - 1.209}$$

Onde, *g* é a taxa de crescimento (d^{-1}), *T* é a temperatura (°C), *DW* é o peso seco em carbono (mg.C) e *Cl* representa as concentrações de clorofila (mg.m^{-3}).

Para as análises do conteúdo de carbono orgânico os indivíduos foram separados sob o microscópio óptico. Em seguida, os indivíduos foram lavados com uma pequena quantidade de água destilada (0,5-1 ml) e colocados em cápsulas de estanho de 2 ml, as quais foram deixadas em estufa a 50ºC durante 24 horas. Após este período, as amostras foram levadas ao dessecador durante meia hora e posteriormente, após estabilização da temperatura, foram pesadas em balanças apropriadas. Após a pesagem, foram adicionados 0,2 ml de ácido clorídrico (0,1 N) a fim de remover os carbonatos inorgânicos do exoesqueleto dos copépodos, visto que os carbonatos tendem a aumentar o $\delta^{13}C$. Outros componentes bioquímicos tais como proteínas, carboidratos e quitina também contribuem para o aumento de $\delta^{13}C$, e podem ser encontrados em outras categorias taxonômicas dentro do zooplâncton, sendo estes em seguida levados a estufa a 50 ºC por 24 h e colocados posteriormente em dessecador com sílica gel para a redução da temperatura.

Após estes procedimentos as amostras foram levadas ao autoanalisador de carbono, hidrogênio, nitrogênio (CHN-O) para as medições do conteúdo de carbono.

3.3.2 Análises Estatísticas

Para a análise estatística dos dados, estes foram primeiramente transformados log (x+1) e em seguida, testou-se normalidade e a homocedasticidade das variâncias através dos testes de Levene e Cochran, respectivamente (Underwood, 1997; Zar, 2010).

A análise de variância (ANOVA one way e two-way, $\alpha<0,05$) foi utilizada para comparar os dados hidrológicos e biológicos em escala espacial (estações de amostragem), temporal (mensal, sazonais, períodos de maré e ciclo circadiano), bem como as análises com os fatores combinados. O teste de Fisher-LSD (*Least Significant Difference Method*), indicado por ser considerado um teste robusto (não precisa que as médias sejam muito diferentes para que acuse a existência de diferenças significativas) e de rigidez intermediária (diferenças intermediárias já são indicadas como significativas), foi utilizado como método de comparação das médias *a posteriori* sempre que foram registradas diferenças significativas pelo teste de ANOVA. Para todas estas análises, adotou-se o nível de significância de 5% (Underwood, 1997; Zar, 2010).

Para investigar as relações existentes entre as espécies do zooplâncton e os meses de coleta, os períodos sazonais (seco/chuvoso), os períodos de maré (enchente/vazante) e as estações de amostragem foram utilizadas análises de agrupamento, as quais foram realizadas com base em matrizes de similaridade, calculadas utilizando-se o índice de Bray-Curtis, a partir dos dados de densidade das espécies por amostra. Estes dados foram transformados pelo log (x+1) (Clarke & Warwick, 1994), sendo a construção do dendrograma realizada utilizando-se o método de ligação *Weighted Pair Group Method-Arithmetical Averages* (WPGMA). Adicionalmente, quando detectada a formação de grupos foi realizada a análise do percentual de similaridade (SIMPER) para identificar os táxons mais importantes para a formação destes grupos nos dendrogramas, através da contribuição das espécies para a similaridade interna dos grupos e para a dissimilaridade entre eles (Clarke & Warwick, 1994).

A análise de similaridade ANOSIM foi utilizada para testar a significância das diferenças entre os grupos formados nos dendrogramas, onde o coeficiente *R* indica o grau de similaridade das amostras, acompanhado do nível de significância "*p*". Nesta análise os valores de *R* variam entre - 1 e + 1, sendo que *R* +1 indica que todas as amostras dentro do grupo são mais similares que qualquer outra amostra de grupos diferentes e *R* -1 aponta que a similaridade dentro e entre grupos é, em média, a mesma.

Com o intuito de investigar as relações existentes entre as variáveis ambientais e a densidade das espécies zooplanctônicas foram utilizados os coeficiente de Correlação de Spearman (*rs*) e a Análise de Componentes Principais (ACP), sendo nesta última análise a abundância das principais espécies introduzidas como variáveis suplementares.

Todos os testes estatísticos foram realizados com o auxílio dos softwares STATISTICA® v8 (StatSoft, 2009) e Plymouth Routines Multivariate Ecological Research (PRIMER), version 6, segundo Clarke e Warwick (1994).

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CAPÍTULO I

Diel variation in the zooplankton of a highly dynamic Amazonian estuary

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Diel variation in the zooplankton of a highly dynamic Amazonian estuary

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ABSTRACT

The short-term dynamics (circadian and tidal cycles) of the zooplankton community were investigated in the Taperaçu estuary in northern Brazil. The plankton samples were collected in April (rainy season) at a fixed station, located in the middle sector of this estuary, through horizontal tows (plankton net with 200 μm mesh), every 3 hours over a 24-hour period, during the spring tide. Altogether, 51 zooplankton taxa were identified, of which the copepods *Paracalanus quasimodo* (34.6 to 13,852.8 ind.m^{-3}; mean: 2,320.8±3,842.2 ind.m^{-3}), *Labidocera fluviatilis* (2.0 to 3,209.2 ind.m^{-3}; mean:484.5±804.4 ind.m^{-3}), *Pseudodiaptomus marshi* (9.7 to 1,599.6 ind.m^{-3}; mean:453.9±580.5 ind.m^{-3}), and *Acartia tonsa* (27.6 to 3,953.6 ind.m^{-3}; mean:694.4±1,269.4 ind.m^{-3}) were the dominant species. While no significant short-term variation was observed in hydrological or biological parameters, fluctuations related to tidal height were recorded in abiotic parameters and the density of the principal zooplankton taxa. The temporal variation in copepod populations tended to reflect that of total zooplankton abundance. Mean zooplankton density varied from 509.1 ind.m^{-3} (ebb tide, at 16:30 h) to 25,514.3 ind.m^{-3} (flood tide, at 10:30 h), with an overall mean of 5,872.1±8,286.4 ind.m^{-3}. Oscillations in the density of *P. quasimodo*, *L. fluviatilis*, and *P. marshi* were influenced by the morphological and morphodynamic characteristics of the Taperaçu estuary, associated with the recruitment of individuals from the adjacent Caeté estuary, which constitutes an important factor determining the structure of the zooplankton community recorded in this study.

Additional index words: *Copepoda, density, short-term trend, tropical estuary, Brazil.*

INTRODUCTION

Estuaries are transitional environments that link continental, limnic environments to marine systems, and are characterized primarily by the constant dynamic of the tidal cycle (Schaeffer-Novelli, 1995), which provokes daily variation in abiotic variables such as salinity, temperature, dissolved oxygen and nutrient concentrations, and tidal currents (Park and Marshall, 2000). This variability is reflected in the structure of the resident and/or transitional populations of different organisms, and determines fluctuations in the composition of ecological communities, and the spatial-temporal variation in the distribution of species (Little, 2000).

These environments are also considered to be natural nurseries, providing important spawning grounds for an ample variety of aquatic vertebrates and invertebrates, and constitute one of the most productive biological systems in the world. The productivity of phyto- and zooplankton, and zoobenthic organisms is especially marked.

The zooplankton has a special role in the estuarine biota, occupying a key role in the trophic web of these systems, including nutrient recycling and the regulation of phytoplankton populations through the consumption of these organisms. The zooplankton is an important link in the transfer of energy and organic material between the primary producers and the system’s principal consumers (Parsons *et al.*, 1984). The analysis of the spatial and temporal variation in the density, biomass, and productivity of the zooplankton is fundamentally important to the understanding of the role of these organisms in the processing of particulate and dissolved organic matter, and estuarine trophodynamics in general (Perissinotto *et al.*, 2003). In this context, it is essential to understand the interaction between local climatic and hydrographic parameters and the biological characteristics of these organisms.

Copepods tend to be the principal component of the estuarine and marine mesozooplankton, corresponding to 60-80% of the total biomass of this group. These organisms contribute directly to the recycling of the material produced by the microbial loop (Champalbert and Pagano, 2002; Osidele and Beck, 2004), as well as regulating fishery stocks, both in the larval (Payne and

Rippingale, 2001) and adult phases (Camargo and Isaac, 2004), and providing one of the main components of the diets of many zooplanktophagous fishes (Evjemo *et al.*, 2003).

The present study investigated the daytime variation (circadian and tidal cycles) in the density and diversity of the zooplankton of the Taperaçu estuary in northern Brazil, in relation to the variation in hydrological parameters.

METHODS

Study area

The Taperaçu estuary (Figure 1) is located about 200 km east of the mouth of the Amazon River, in the municipality of Bragança, northern Brazil. It is considered as a permanently open estuary, characterized by high turbidity (mean: 378.1 UNT), shallow depths (mean = 4.2 m) and strong tidal currents of up to 2.04 $m.s^{-1}$ (Asp et al., 2012). This estuary, like others in northern Brazil (Krumme *et al.*, 2004; Giarrizzo & Saint-Paul, 2008), has a semidiurnal tidal range of approximately 5 m, which may reach 6 m during the equinoctial spring tides (DHN, 2008). The local climate is equatorial humid, with a rainy season that usually extends from January to July, while the dry (or less rainy) season is from August to December (Moraes *et al.*, 2005). Considerable variation in the distribution of precipitation may be observed in some years, however. This seasonal pattern is controlled primarily by shifts in the position of the Intertropical Convergence Zone (ITCZ), which provoke intense convective activity during the first half of the year. Mean annual rainfall is 2,401 mm (INMET, 2012), of which 75% is recorded during the rainy season. Mean monthly air temperatures are between 25.2°C and 26.7°C, ranging between 20.4°C and 32.8°C during the day (Schories and Mehlig, 2000).

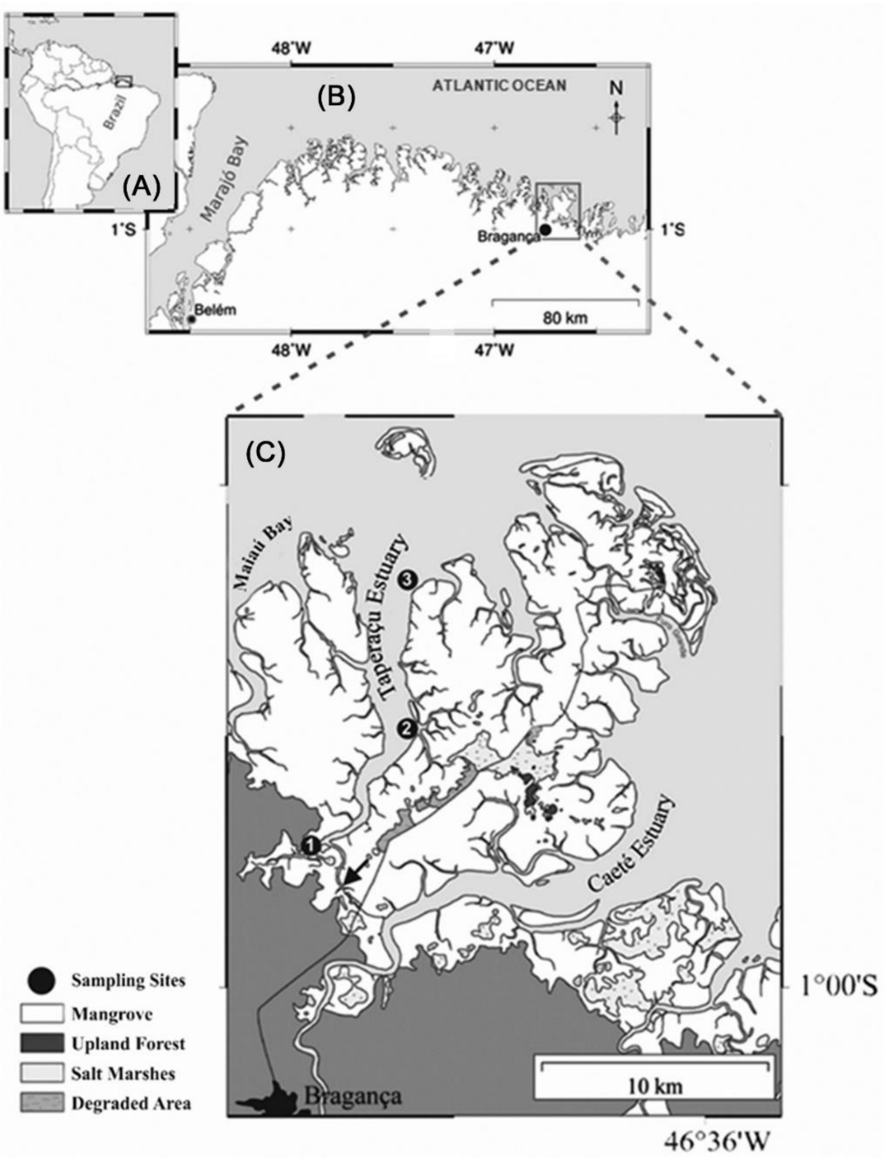

Figure 1. Location of the study area showing the sampling site (●) in the Taperaçu estuary, northern Brazil (Modified from Mehlig, 2001). The Taici creek, which connects the Taperaçu and Caeté estuaries, is also shown in detail.

Sampling and laboratory procedures

Zooplankton was sampled in April, 2012 (rainy season), at a fixed station (00º55'06.8"S and 46º44'0"W), located in the middle sector of the Taperaçu estuary (Figure 1). Samples were collected at 3-hour intervals over a 24 hour period during the spring tide. Each sample consisted of a 3 min sub-surface horizontal tow of a conical plankton net (200 µm mesh) fitted with a mechanical flowmeter to estimate the volume of water filtered through the net. After collection, the samples were transferred to 600 ml plastic bottles and preserved in 4% buffered formalin-seawater solution (sodium tetraborate). Salinity and dissolved oxygen concentrations were measured *in situ* using a CTD and CTDO. Additionally, water samples (600 ml) were collected from the sub-surface with a Niskin oceanographic bottle for the laboratory determination of the hydrogenionic potential (pH meter), turbidity (turbidimeter), and the concentrations of suspended particulate material (adapted from Strickland and Parsons, 1972) and chlorophyll *a* (Parsons and Strickland, 1963). Water level data were acquired every 2 s and mean values were obtained every 10 min.

In the laboratory, the zooplankton samples were divided into aliquots using a Folsom splitter (McEwen *et al.*, 1954), to provide standardized subsamples containing approximately 1,000 individuals, which were then identified (Trégouboff and Rose, 1957; Björnberg, 1981; Bradford-Grievem *et al.*, 1999), classified taxonomically (WoRMS, 2012), and counted in a gridded Petri dish under a Zeiss Stemi-2000 stereomicroscope. The counts for each species were multiplied by the subsampling factor to obtain the estimate of the total number of individuals in the full sample. The quantitative data obtained for each sample were used to calculate density, relative abundance, and ecological indices (diversity, evenness) and species richness. Density was expressed as the number of individuals per m^3 ($ind.m^{-3}$). Ecological diversity was estimated by the Shannon-Wiener index (Shannon, 1948) and evenness by Pielou’s index (Pielou, 1977). Species richness was assumed to be equal to the number of species reported in each sample. Species contributing more than 5% of the total number of zooplankton in a given sample were classified as dominant. The organisms represented by lower percentages were classified as “other taxa”.

Numerical analysis

The parametric Student’s *t* test for independent samples and the nonparametric Mann-Whitney *U* were used to compare the two main zooplankton groups (total fauna and dominant species) and their ecological indices between circadian periods (day/night) and tides (flood/ebb). The relationship between physical, chemical, and biological parameters was assessed using Spearman’s correlation coefficient (Zar, 1999). These analyses were run in the STATISTICA 5.0 package, considering an α = 0.05 significance level. The similarity of samples obtained in different circadian and tidal periods was assessed using a hierarchical agglomerative cluster analysis, computed using the Bray-Curtis similarity index for log-transformed (x+1) density data. A one-way analysis of similarity (ANOSIM) was subsequently used to test whether the community structure differed significantly between groups. In addition, similarity percentage analysis (SIMPER) was used to identify the species that most contributed to the similarities within and dissimilarities between the groups formed by the cluster analysis. These analyses were run in the Plymouth Routines Multivariate Ecological Research (PRIMER), version 6, software package, following Clarke and Warwick (1994).

RESULTS AND DISCUSSION

Environmental parameters

The tides on the Amazon coastal systems are semi-diurnal, and are thus quite distinct from those of other Brazilian coastal regions (Joyeux *et al*, 2004; Ferreira *et al*, 2010). At Taperaçu, tides ranged between 1.2 m (ebb tide, 16:30 h) and 4.5 m (flood tide, 10:30 h)

Salinity was meso-polyhaline, ranging from 15.0 (ebb tide, 16:30 h) to 20.6 (flood tide, 10:30 h), with an overall mean (±SD) of 18.3±1.8 over the course of the day. Although no short-term pattern was observed in the other abiotic parameters, salinity always increases during the flood tide and decreases during the ebb tide, whatever the time of day. As the Taperaçu estuary lacks any effective fluvial discharge, it seems likely that the decrease in salinity observed during the ebb tide was related to the input of oligohaline waters from the Caeté estuary (Magalhães, 2012), which is connected to the Taperaçu estuary by the Taici creek (see Figure 1). The opposite trend was recorded in turbidity, which oscillated from 35.8 NTU during the flood tide (22:30 h) to 532.0 NTU on the ebb tide (16:30 h), with an overall mean of 285.7±178.5 NTU (Figure 2). The Taperaçu estuary has relatively turbid waters, which are likely related to its shallow depths and strong tidal currents, which cause recurring re-suspension of autochthonous and allochthonous particulate matter.

Dissolved oxygen concentrations (3.4 to 4.7 mg.L^{-1}; mean = 4.0±0.4 mg.L^{-1}) varied little, with relatively values low being recorded in comparison with those from the same site in previous studies (Costa *et al.*, 2008; Magalhães *et al.*, 2011), as well as other coastal tropical environments around the world (Brugnoli-Olivera and Morales-Ramírez, 2008; Sousa *et al*., 2009). The pH was alkaline overall, and varied from 7.7 to 8.2 (mean = 7.9±0.1). This lack of variation is typical of marine and estuarine ecosystems, in which the pH is controlled primarily by the buffering effect of the seawater (Sousa *et al*., 2009), as well as the high primary productivity which increases the consumption of CO_2, resulting in an increase in the pH of the water (Branco *et al*., 2002; Bastos *et al*., 2005). Concentrations of chlorophyll *a* (14.1 to 42.8 mg.m^{-3}; mean = 27.4±11.2. mg.m^{-3}) and suspended particulate material, or SPM (13.7 to 122.5 mg.L^{-1}; mean = 50.1±34.7 mg.L^{-1}) were not only relatively high, but also presented considerable daily variation (Figure 2). Sassi and Kutner (1982) concluded that the higher phytoplankton biomass found in coastal ecosystems during the rainy season is due to the expansion in the availability of dissolved nutrients resulting from the increased runoff from the continental zone. The high concentrations of SPM during the ebb tide resulted from the leaching of the floodplain, which is an important mechanism for the transportation of organic material and nutrients to the adjacent estuaries and coastal zones.

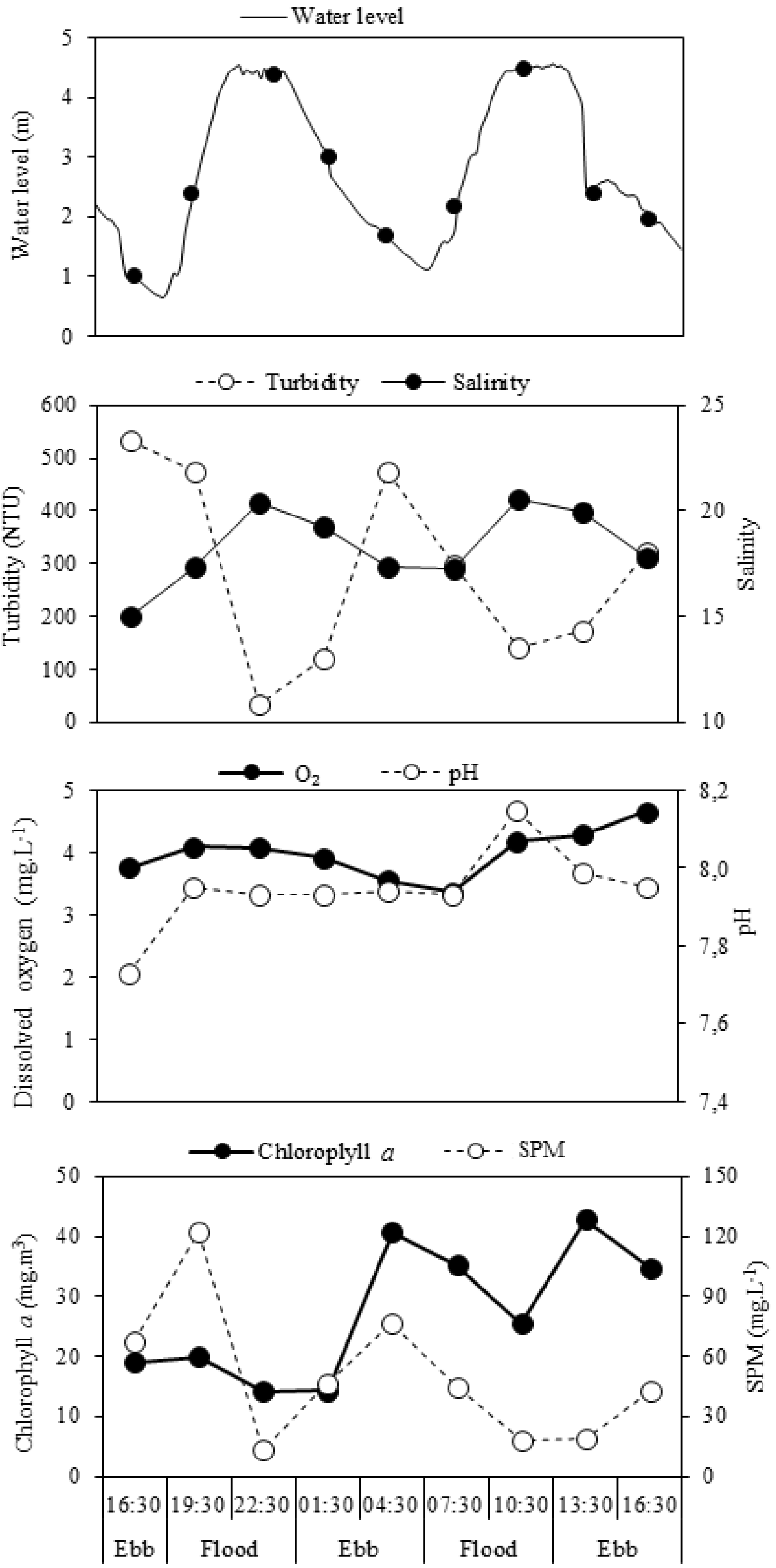

Figure 2. Short-term variation (circadian and tidal cycles) in environmental parameters in the Taperaçu estuary, northern Brazil

Zooplankton community structure

A total of 51 zooplankton taxa were identified. Copepods were the most diverse, being represented by four orders (Calanoida, Poecilostomatoida, Cyclopoida, and Harpacticoida) and twenty species, of which *Pseudodiaptomus marshi* Wright S., 1936, *Paracalanus quasimod*o Bowman, 1971, *Acartia tonsa* Dana, 1849 and *Labidocera fluviatilis* F. Dahl, 1894, were numerically dominant.

Total zooplankton density varied from 509.1 ind.m^{-3} (ebb tide, 16:30 h) to 25,514.3 ind.m^{-3} (flood tide, 10:30 h), with a mean of 5,872.1±8,286.4 ind.m^{-3}. Copepod density oscillated between 387.8 ind.m^{-3} on the ebb tide (16:30 h) and 23,671.5 ind.m^{-3} on the flood tide (10:30 h), with an overall mean of 4,5125±7,408.6 ind.m^{-3} (Figure 3). There was no evidence of any significant variation in zooplankton or copepods in relation to either tidal level or the circadian cycle. This may be the result of the peculiar morphological and morphodynamic characteristics (presence of sand banks and the absence of a connection with a river) of the Taperaçu estuary (Magalhães *et al.*, 2011), which is strongly influenced by coastal waters, given the lack of fluvial discharge and the small catchment area, which leads to sporadic freshwater inflow. The lack of circadian variations recorded by these last authors appears to be the result of the interactive effect of shallow water and strong tidal currents, which facilitate both the horizontal and the vertical mixing of the water column, mediating the effects on the composition and density of zooplankton during the course of the day. Similar patterns were recorded in *P. quasimodo* (34.6 to 13,852.8 ind.m^{-3}; mean: 2,320.8±3,842.2 ind.m^{-3}), *L. fluviatilis* (2.0 to 3,209.2 ind.m^{-3}; mean: 484.5±804.4 ind.m^{-3}), *P. marshi* (9.7 to 1,599.6 ind.m^{-3}; mean: 453.9±580.5 ind.m^{-3}), and *A. tonsa* (27.6 to 3,953.6 ind.m^{-3}; mean: 694.4±1,269.4 ind.m^{-3}).

The cluster analysis nevertheless revealed a short-term change in the zooplankton community of the Taperaçu estuary. Two distinct groups of samples were delineated with 65% similarity (Figure 4a). The first group was characterized by the predominance of *P. quasimodo*, and included primarily late flood and early ebb tide samples. By contrast, the second group, which contained mainly late ebb and early flood tide samples, was characterized by a greatly reduced contribution of *P. quasimodo* and an increase in that of *P. marshi* (Figure 4b).

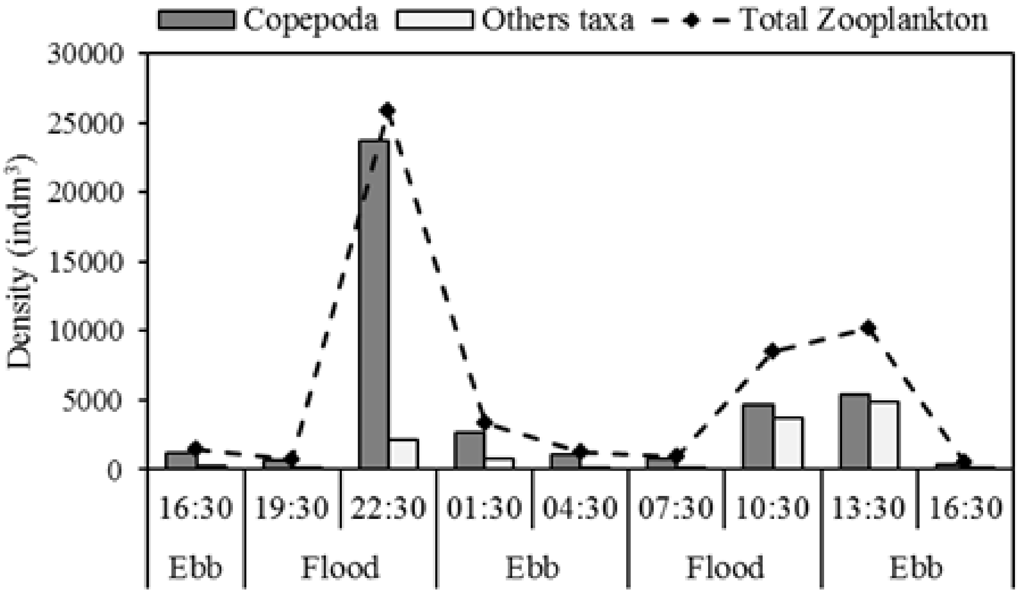

Figure 3. Short-term variation (circadian and tidal cycles) in the densities of total zooplankton, copepods, and non-copepod zooplankton in the Taperaçu estuary, northern Brazil.

The results of the cluster analysis were supported by the ANOSIM (Global $R = 0.8$, $p < 0.01$). Overall, *P. quasimodo*, *P. marshi*, *L. fluviatilis* and *A. tonsa* accounted for over 67% of the similarity within these groups, and for 43% of dissimilarity between them. The SIMPER indicated that *P. quasimodo* (28.9%) and *P. marshi* (29.8%) were the species that most contributed to the similarity within groups I and II, respectively, highlighting the importance of these species in the structural dynamics of the zooplankton community.

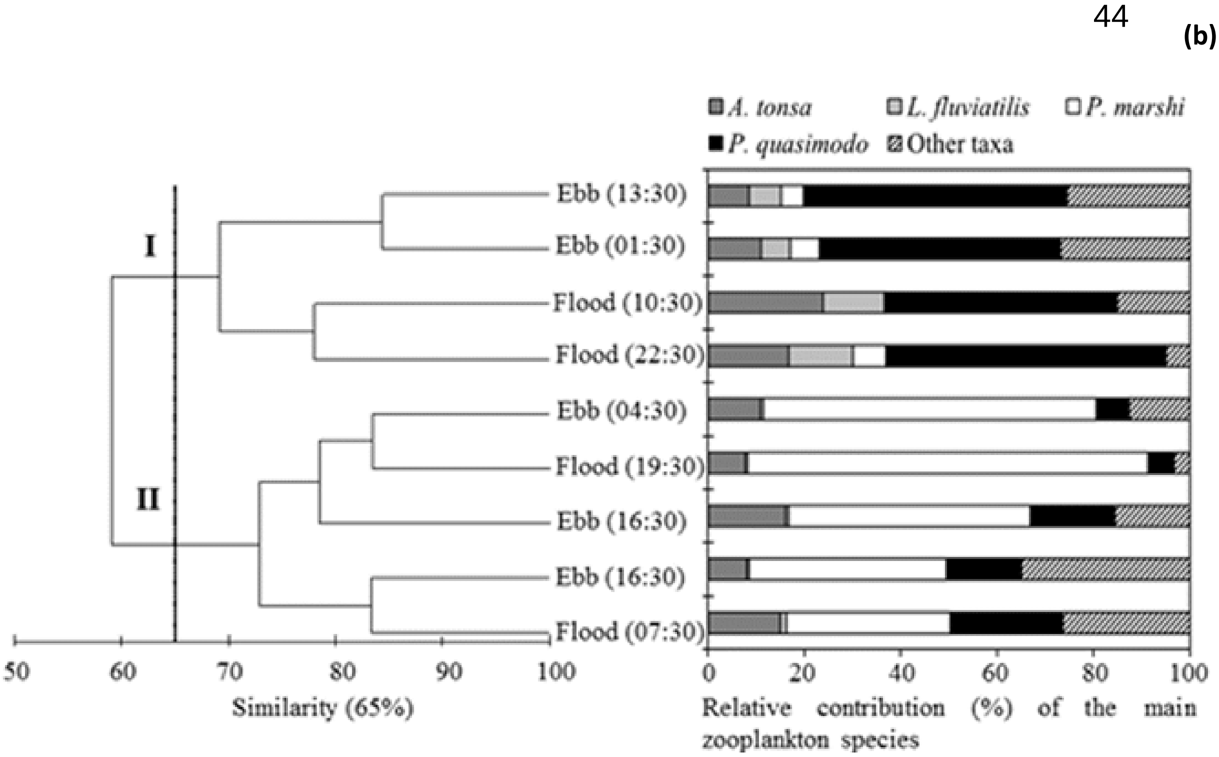

Figure 4. (a) Results of the cluster analysis and (b) relative contribution of the dominant species to total zooplankton abundance recorded during the study period in the Taperaçu estuary, northern Brazil.

A dominant species in most subtropical and tropical coastal zones of South America (Vega-Pérez and Hernandes, 1997; Araújo, 2006; Magalhães *et al.*, 2009), *P. quasimodo* presents marine-euryhaline behavior, occurring preferably in areas with high salinity (Lopes *et al*., 1998) and dominated by tides (Lopes, 1994; Eskinazi-Sant'Anna & Tundisi, 1996). An ability to tolerate moderate levels of salinity may nevertheless explain the dominance of *P. quasimodo* in the late flood tide and early ebb tide, when polyhaline conditions - as defined by the Venice system of classification (Anonymous, 1959) - prevailed (Figure 2). A similar tidal pattern was observed in *L. fluviatilis*, which suggests that the prevalence of both species in the study area depends on their recruitment from the adjacent coastal zone.

Pseudodiaptomus marshi is found on the Atlantic seaboard of the Neotropical region (Almeida Prado Por and Lansac-Toha 1984; Reid, 1990; Suárez-Morales, 2003), and is an important component of the mesozooplankton communities in many estuaries and tidal creeks of north (Krumme and Liang 2004; Costa *et al*, 2008) and northeastern Brazil (Silva et al. 1996). Given the lack of any effective fluvial discharge in the Taperaçu estuary, it seems likely that the increased contribution of *P. marshi* in the late ebb and early flood tide may be related to the recruitment of this species from the neighboring oligo-mesohaline Caeté estuary through the Taici creek (Figure 1) during the flood tide (Magalhães, unpublished results).

No clear tidal trend was identified in *A. tonsa*, which is a cosmopolitan species, distributed preferentially in estuarine and coastal areas (Paffenhöfer and Stearns, 1988; Tester and Turner, 1991), and tolerant of salinity of between 0 and 31.5 (Montú and Gloeden, 1986), albeit with an optimal range of 15-22 (Cervetto *et al.*, 1999). The lack of any tidal effects on *A. tonsa* was thus determined by its ecological affinity to the meso-polyhaline conditions, which predominated throughout study period.

In the present study, the circadian variation in the density of the dominant zooplankton taxa may be explained by the species-specific effects of salinity on the ability of each species to osmoregulate. This was confirmed by the significant correlation found between salinity and the density of *P. quasimodo* ($r_s = 0.6$, $p < 0.05$), *L. fluviatilis* ($r_s = 0.73$, $p < 0.05$), and *A. tonsa* ($r_s = 0.70$, $p < 0.05$). The density of these species also varied negatively with turbidity (*P. quasimodo*: $r_s = -0.75$, $p < 0.05$; *L. fluviatilis*: $r_s = -0.83$, $p < 0.05$; *A. tonsa*: $r_s = -0.73$, $p < 0.05$) and SPM concentrations (*P. quasimodo*: $r_s = -0.79$, $p < 0.05$; *L. fluviatilis*: $r_s = -0.72$, $p < 0.05$; *A. tonsa*: $r_s = -0.67$, $p < 0.05$). In estuarine environments, the zooplankton is potentially limited by turbidity and tidal currents (McLusky and Elliot, 2004; Marques *et al*., 2009). The presence of SPM reduces the penetration of sunlight into the water column, affecting phytoplankton growth (Menéndez *et al*, 2012), and consequently, the temporal variation in abundance and distribution of copepods (Marques *et al*., 2009).

Although no significant correlation ($r_s = -0.23$, $p > 0.05$) was recorded between salinity and the density of *P. marshi*, this species was more abundant when salinity was lower. Magalhães *et al.* (2010), who studied the population dynamics of *P. marshi* in the neighboring Caeté estuary, concluded that the reduced tolerance of this species to high salinity determined its temporal and spatial segregation, as observed in other tropical estuaries (Araujo, 1996).

The ecological indices recorded in the present study reinforced the homogeneity of the local zooplankton community. Diversity was relatively high in comparison with other equatorial coastal systems (Costa *et al.*, 2009; Costa *et al.*, 2012), with values ranging from 0.9 to 2.7 bits.ind^{-1} (mean: 2.1±0.6 bits.ind^{-1}). Evenness ranged between 0.3 and 0.7 (mean: 0.6±0.1), while richness varied from 10 to 16 (mean: 13.4.±2.4.). The effective lack of any systematic short term pattern – related to circadian or tidal cycles – may be related to the intensely coastal characteristics of the Taperaçu estuary, which is determined by the absence of any regular or effective source of freshwater.

CONCLUDING REMARKS

Overall, the structure of the zooplankton and copepod communities of the study area was characterized by its relative homogeneity. However, the abundance of some of the principal zooplankton species (*P. quasimodo*, *L. fluviatilis*, and *P. marshi*) varied systematically in relation to tidal height. This appeared to be related to a number of morphological and morphodynamic features of the Taperaçu estuary, associated with the recruitment of organisms from the adjacent Caeté estuary, through the Taici creek. This process constitutes an important factor for the understanding of changes in the structure of the zooplankton community on a fine temporal scale.

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CAPÍTULO II

Short and Medium Term Variation in the Dynamics of the Mesozooplankton Community of an Amazonian Estuary

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Short and Medium Term Variation in the Dynamics of the Mesozooplankton Community of an Amazonian Estuary

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ABSTRACT

The aim of this study was to investigate the short- and medium-term variation in the dynamics of the zooplankton community, in a macrotidal estuary (the Taperaçu) of the Amazon Coast of northern Brazil. This estuary has a characteristic funnel shape, with extensive sandbars running down the middle and current patterns typical of a shallow estuary, in addition to substantial seasonal variation. Fluctuations in zooplankton densities were analyzed in the context of the influence of the tidal cycle, temperature, salinity, turbidity, pH, dissolved oxygen concentration and chlorophyll-a concentrations. Data were collected in months of June, September and December 2012 and March, June, and September/2013. Samples were taken at three fixed stations, S1, S2, and S3 at 3-hour intervals over a nychthemeral cycle during the neap tide. The data were analyzed using a two-way ANOVA (to test the significance of the variation among stations, months, tides, and the circadian cycle) and PCA. Five principal species were identified–*A. tonsa*, *A. lilljerborgii*, *P. marshi*, *P. quasimodo*, *O. oswaldocruzi* and *O.dioica*. The results indicate that the patterns of variation (temporal, tidal, and spatial) in the zooplankton of the Taperaçu estuary were determined primarily by precipitation, salinity, turbidity, and chlorophyll-a concentrations, due to the strong local hydrodynamics and the unique morphodynamic characteristics of the estuary that provoke the constant mixing of its waters.

ADDITIONAL INDEX WORDS: *Estuaries, Amazonian, Zooplankton.*

INTRODUCTION

Zooplankton, especially copepods, are of major importance in pelagic systems in which, in addition to transferring organic material produced by the phytoplankton to higher trophic levels (Gismervik, 2006), the metabolic activity of these organisms is fundamentally important to the biogeochemical cycles and flow of energy into marine systems (Longhurst and Pauly, 2007). Most zooplanktonic organisms are omnivores, although many are primarily herbivores, carnivores or detritivores (Calbet, 2008; Kiørboe, 2008), and play an important role in the trophic web of aquatic ecosystems.

Previous studies of the composition, abundance, and biomass of the principal mesozooplankton species of the Taperaçu Estuary on different scales (spatial, seasonal and tidal cycle) have provided an important database on this community (Costa *et al*., 2008; Magalhães *et al*., 2015 and references therein).

However, the use of different methodological procedures has hampered the evaluation of the spatial variability of its biological and environmental features.

The present study is the first based on the simultaneous, nycthemeral collection of data throughout the length of the estuary, which permitted the systematic testing of the hypothesis that the Taperaçu Estuary supports significant spatial and temporal gradients in environmental variables, which are regulated by seasonal oscillations in precipitation rates and determine the spatiotemporal distribution of the organisms that constitute the local zooplankton community.

METHODS

The Taperaçu Estuary (46º42’–46º45’W and 00º50’–00º57”S) is located approximately 200 km to the southwest of the mouth of the Amazon River, and has a surface area of 21 km², and a drainage basin of 40 km² (Asp *et al*., 2012). It is classified as a permanently open basin, with shallow waters, of an average depth of 4 m (Asp *et al*., 2012). The tides are semidiurnal macrotides, with ranges of approximately 5 m, reaching 6 m during the equinoctial spring tides

(DHN, 2008). The Taperaçu is connected to the estuary of the Caeté River through the Taici creek (Figure 1), which is approximately 3 km long and 15 m wide (Araújo Jr. and Asp, 2013).

The creek, together with the runoff of precipitation from adjacent wetlands during the rainy season, provides the estuary's only input fresh/oligohaline water (Araújo Jr. and Asp, 2013). Annual precipitation is approximately 2,500 mm, of which, 75% falls during the rainy season (INMET, 2012).

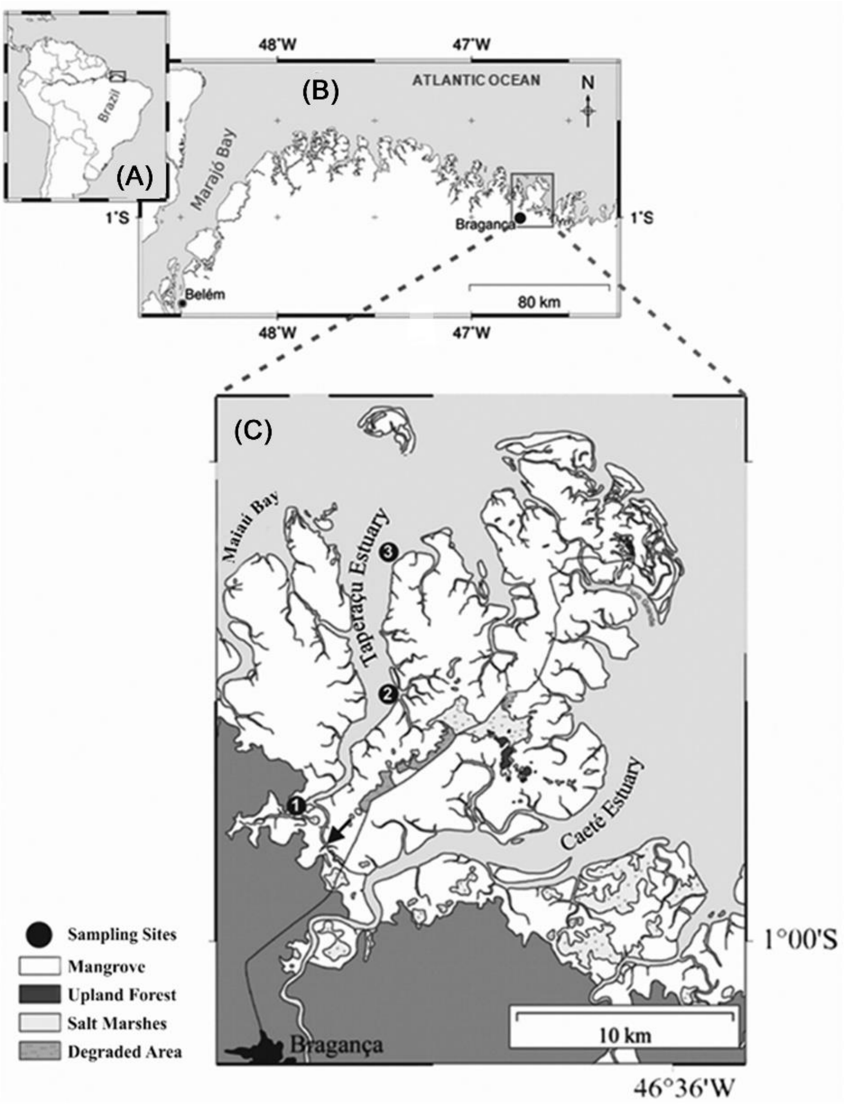

Figure 1. Study area: (a) South America; (b) location of the Taperaçu Estuary (00º50'–00º57' S and 46º42'–46º45' W) on the northern coast of Brazil; (c) location of the three data collection stations in the upper (1), middle (2) and

lower (3) sectors of the estuary (Source: Magalhães, 2015, modified from Mehlig, 2001).

Pluviometry, collection of samples and laboratory procedures

Precipitation data were obtained from the National Meteorological Institute's (INMET) Tracuateua station, 17 km from the municipality of Bragança.

Data were collected in June, September and December, 2012, and March, June and September, 2013, using subsurface trawls of the water column at three fixed stations (Figure 1), in the lower (station S3: 00°50'30.9" S, 46º43'02.4" W), middle (station S2: 00°55'06.8" S, 46º44'0" W), and upper (station S1:00°56'58.4" S, 46º46'26.9" W). The plankton samples were collected during neap tides at 3- hour intervals over a 25-hour period, using plankton nets with a mesh of 200 µm (50 m diameter mouth, 2 m in length), fitted with mechanical flowmeters. The physical and chemical parameters of the water (temperature, salinity, turbity and dissolved oxygen) were measured *in situ*, using CTDs. Subsurface samples of the water were also collected for the laboratory analysis of pH and chlorophyll-a concentrations, which were determined according to standard international methods

In the laboratory, the zooplankton samples were subsampled using a Folson splitter, counted, and identified in gridded Petri dishes under a stereo-microscope. The organisms were identified to the lowest possible taxonomic level and classified taxonomically. The quantitative data were used to calculate the density (ind. m^{-3}), the relative abundance (%), the indices of diversity and evenness.

Data analysis

A two-way analysis of variance (ANOVA) was applied to evaluate the effect of the sampling stations, tidal phases, and circadian cycle (day and night) on the environmental variables measured, the total zooplankton density, and that of the principal species, as well as the relevant ecological indices. All the statistical analyses were run in Statistica v 8.0, with a 5% significance level (α = 0.05). For the purposes of the present study, species were considered abundant when they had a relative mean monthly abundance of more than

20%. A Principal Components Analysis (PCA) was also run to evaluate the potential relationships among the environmental variables monitored during the study.

RESULTS

The initial statistical analyses found no significant differences among tidal phases or during the circadian cycle. Given this, all the parameters (biological and environmental data) were pooled (mean±standard deviation) and analyzed only in relation to the months of the study period and the sampling stations.

Environmental variables

Over the study period, precipitation in the region of the Taperaçu Estuary varied between 2 mm, in September 2012 and 342 mm in March 2013. In all months of the study period, except September 2013, the values recorded were lower than the historic means (1975-2011), with a reduction of 25.6% in June 2012 and 31.4% in March 2013 in comparison with the historic mean. The results of environmental variables are showm in figure 2.

Zooplankton

The analysis of the variation between the periods (day and night) of the nycthemeral cycle found no significant variation in any of the species analyzed, nor among tidal phases, allowed the data to be pooled (mean±standard deviation) for the analysis of monthly and spatial patterns, at the three sampling stations.

The Copepoda were the dominant taxon, representing 74.3% of the zooplankton community recorded during the study period as a whole. In the months of June (2012 and 2013), copepods reached their highest levels of relative abundance, contributing 76.8 and 80.7%, respectively. In these months, copepods of the genera *Acartia* and *Tisbe* were especially abundant. In March 2013, by contrast, the copepods contributed 59.9% of the organisms collected, while cirriped nauplii were found at high densities.

Total zooplankton density varied significantly ($p<0.05$) among months and sampling stations (Figure 3). High densities were recorded at station S1 in June, September and December 2012, but not during these same months in 2013. Clear differences were observed between the months of June in 2012 and 2013, with higher densities being recorded in 2012. The mean zooplankton densities ranged from 242.4±381.0 ind.m^{-3} at station S3 to 198,919.1±358,245.6 ind.m^{-3} at station S1, with both values being recorded in June 2012 (Figure 3).

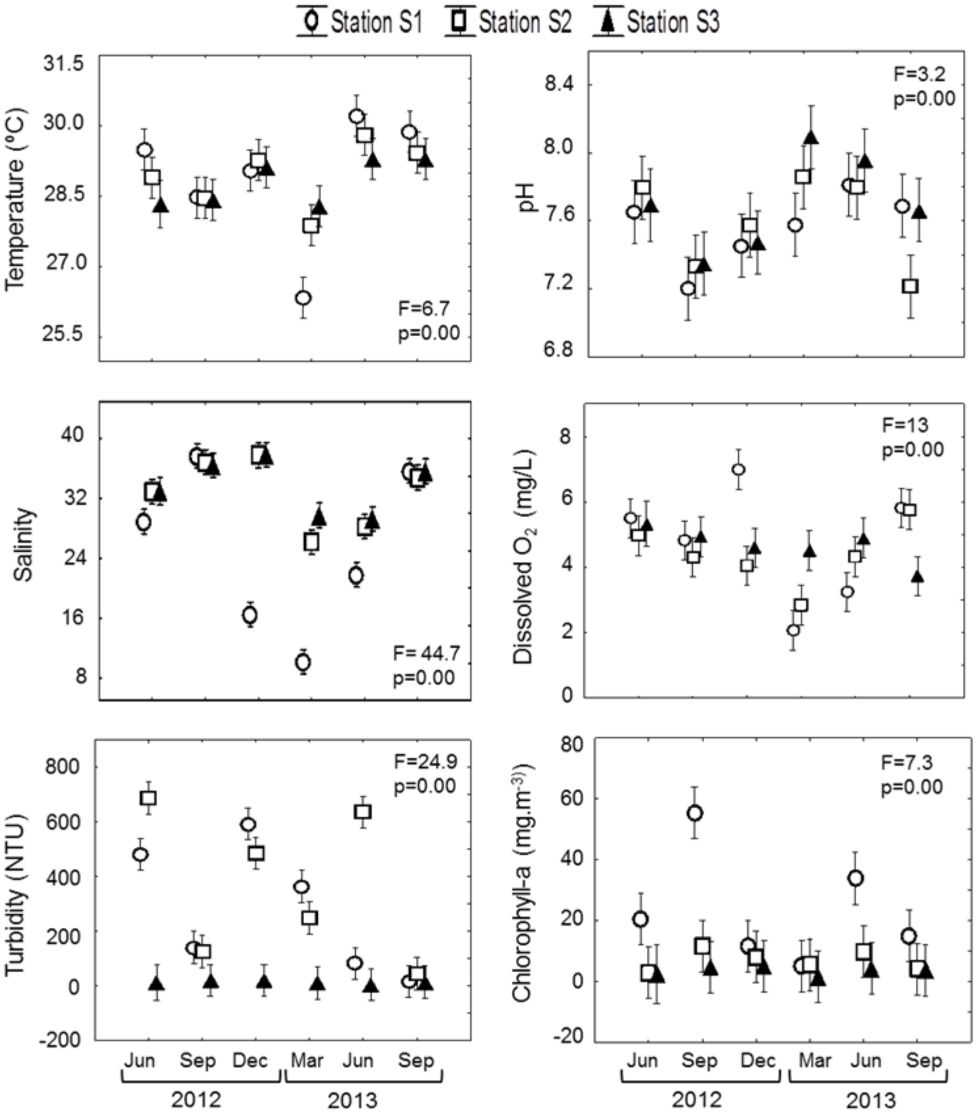

Figure 2. Results of the two-way ANOVA for the mean variation (± SD) in environmental variables recorded in the Taperaçu Estuary during the study period.

Acartia tonsa, *A. lilljerborgi*, *Pseudodiaptomus marshi*, *Paracalanus quasimodo* and *Oithona oswaldocruzi* were the most abundant copepod species overall, in both absolute and relative terms. The densities of *A.tonsa* varied significantly (p<0.05) among months and stations, with a peak being observed in June 2012 at station S1 (22,230.9±46,145.7 ind.m^{-3}). This species was observed at this station in June, September and December 2012, although it was not found in most samples collected in March 2013 (0.0 ind.m^{-3}). In September and December 2013, high densities of this species were recorded at station S2. The abundance of *A. lilljeborgi* followed a similar pattern, with significant (p<0.05) monthly and spatial variation. High mean densities were recorded at station S1 in June 2012 (4,011.6±10,326.5 ind.m^{-3}) and station S2 in June 2013 (1,579.9±2,742.3 ind.m^{-3}).

The density of *P. marshi* was significantly (p<0.05) higher than in other months at station S1 in June 2012 (3,267.3±4,565.1 ind.m^{-3}) and March 2013, with a mean of 2,678.8±6,353.08 ind.m^{-3} (Figure 3). Higher densities at station S1 were observed frequently during the study period, except for June 2013, when no significant spatial variation was found. *Paracalanus quasimodo* occurred at low densities in all months and sampling stations, except June 2012 (S1), when it contributed 75% of the total abundance of zooplankton recorded at this station. Significant (p<0.05) spatial variation was found in this species, with mean densities ranging from 5.4±7.6 ind.m^{-3} at station S3 in June 2012 and 9,270.7±17,593.3 ind.m^{-3} at station S1 in the same month (Figure 3).

Oithona oswaldocruzi was recorded in June and September 2012, with mean densities ranging from 3.9±5.7 ind.m^{-3} at station S3 in June 2013 and 30,221.9±28,328.4 ind.m^{-3} at station S1 (Figure 3). Significant (p<0.05) monthly and spatial differences were also found among months, with relatively high densities being recorded in June, September and December 2012 at station S1 (Figure 3).

Meroplanktonic organisms primarily *Oikopleura dioica*, contributed 25.2% of the total zooplankton density. As for the copepods the mean density of this species was highest (p<0.05) at station S1 in June 2012, with a density of 15,284.6±26,060.6 ind.m^{-3} (Figure 3).

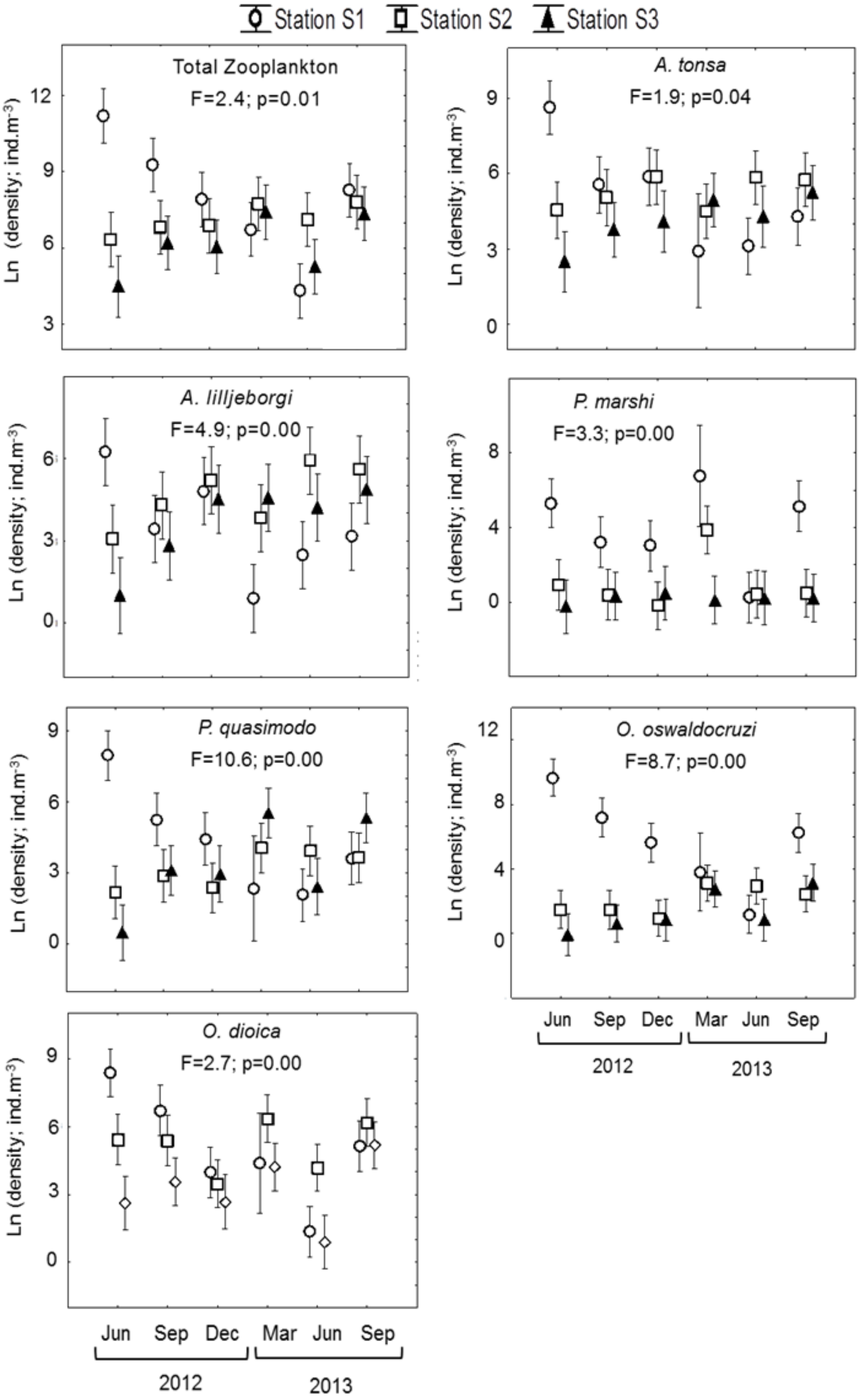

Figure 3. Two-way ANOVA showing the mean (± SD) variation in total zooplankton abundance, and that of the five principal copepod species and *O. dioica* in the Taperaçu Estuary. The scale of the y axis (density, ind.m^{-3}) was log-transformed using natural logarithms.

Mean species diversity ranged from 2.0±0.6 bits.ind^{-1} in March 2013 at station S1 and 3.8±0.4 bits.ind^{-1} in the same month at station S3, while evenness varied from 0.5±0.1 in March 2013 at station S1, and 0.7±0.03 at station S3 in September 2013. Considerable variability was observed among stations and study months ($p<0.05$), although the values recorded at station S3 were generally higher for both variables, indicating a high degree of spatial heterogeneity in the study region.

The PCA reflected the clear influence of environmental variables at the different sampling stations (S1, S2 and S3), with component 1 and component 2 explaining 59% of the variability at S1, 57% at S2, and 60% at S3 (Figure 4). All the environmental variables returned high correlation coefficients with PCA 1. Salinity was the most important variable at S1 and S3, with correlation coefficients of 0.84 and 0.82, respectively, while at S2, temperature was the most important variable (0.88 correlation with PCA 2).

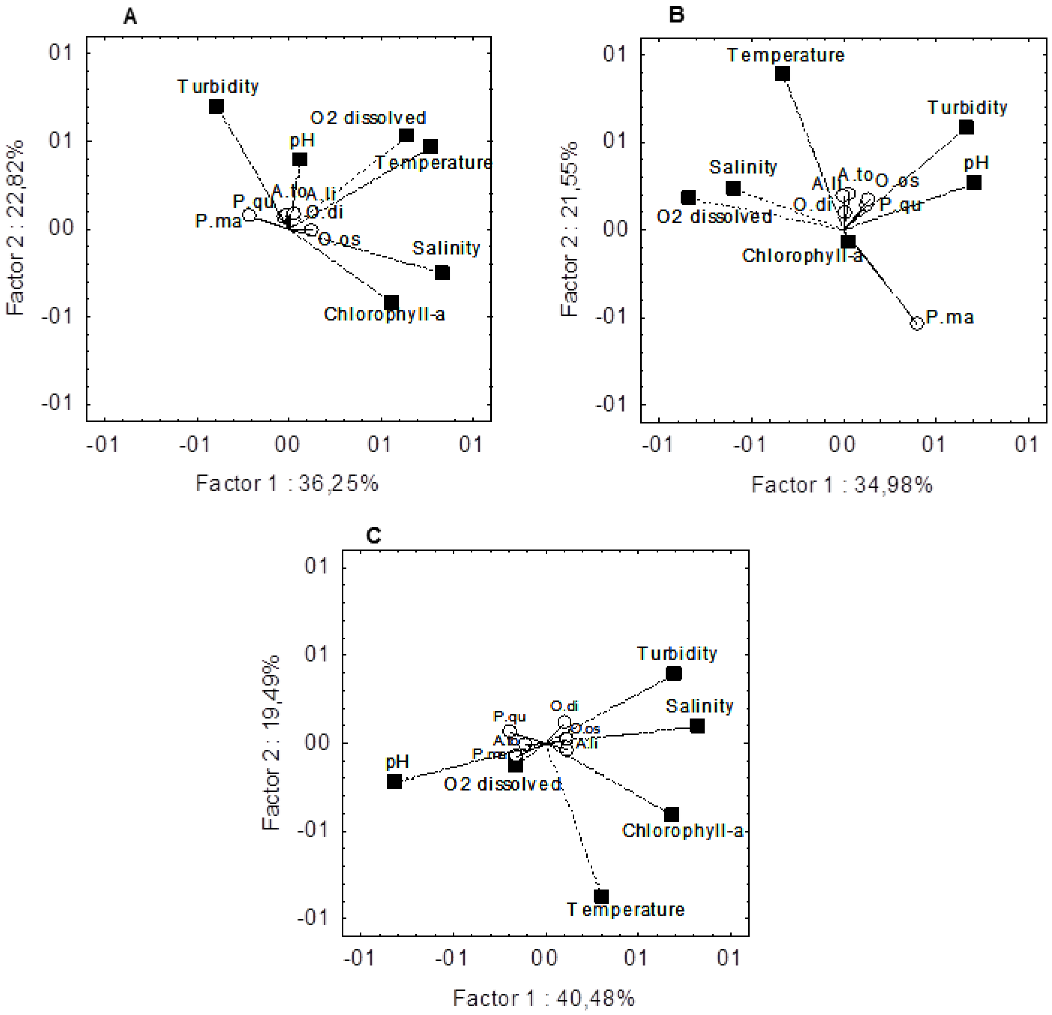

Figure 4. Results do PCA for the environmental variables analyzed at the three sampling stations (A: S1; B: S2; C: S3) located within the Taperaçu Estuary. The species (white circles) are: A.to = *Acartia tonsa*; A.li = *Acartia lilljerborgi*; P.ma = *Pseudodiaptomus marshi*; P.qu = *Paracalanus quasimodo*; O.os = *Oithona oswaldocruzi*; O.di = *Oikopleura dioica*.

DISCUSSION

In the Taperaçu Estuary, as in other tropical and subtropical regions around the world (Capo *et al*., 2006; Magalhães *et al*., 2009), seasonal variation in precipitation levels is the principal factor influencing monthly and seasonal fluctuations in environmental variables, with knock-on effects on the occurrence and distribution of zooplankton species. During the present study period (2012 and 2013), a significant reduction in precipitation rates was recorded in comparison with the historical average. This reduced rainfall may have provoked alterations in the environmental and biological parameters of the water, principally salinity. In the innermost portion of the estuary (S1), for example, a mean salinity of 28.9 was observed in June 2012, a period when values of less than 20 are normally recorded (Magalhães *et al*., 2015).

In addition to the influence of precipitation rates, the unique morphological and morphodynamic characteristics of the estuary contribute to the variation in the occurrence and distribution of the zooplankton, including the sandbars in the inner portion of the estuary, the absence of fluvial discharge, and the extremely small drainage basin, which reduces the input of freshwater to a sporadic minimum. This obviously favors the influence of coastal waters, and in particular the absence of freshwater species, especially in the outermost sector of the estuary. The estuary is also shallow, with strong currents (Asp *et al*., 2012), which facilitate the vertical and horizontal mixing of the water column, and hamper vertical migration in the zooplankton.

While the estuary lacks any significant fluvial discharge, considerable spatial differences were observed in the density of species, as well as the environmental variables measured, between station S1 and the other stations (S2 and S3) in 2012 and 2013. The Taperaçu is connected to the Caete Estuary through the tidal Taici Creek, through which fresh/oligohaline water flows during the highest flood tides, reinforcing the differences between station S1 and stations S2 and S3, located in the middle and outer estuary.

The density of mesozooplankton in the Taperaçu Estuary reflected the monthly and spatial variation in the copepod populations. These organisms were dominant in all months and at all sampling stations, and contributed 74.3% of the zooplankton collected during the study period. This group is common in estuaries around the world, where it typically contributes at least 80% of the total abundance (David *et al*., 2005; Menéndez *et al*., 2012). The zooplankton community was characterized by the predominance of the copepods *A.tonsa*, *A. lilljerborgi*, *P. marshi*, *P. quasimodo* and *O. oswaldocruzi* as well as *O. dioica* (Appendicularia), all of which occurred at high densities. A similar composition of the zooplankton community was recorded in previous studies of the same estuary (Magalhães *et al*., 2015) and in other estuaries on the Brazilian coast

(Eskinazi-Sant'Anna and Björnberg, 2006; Costa *et al*., 2009), reflecting the ample distribution of these species in the region.

In addition to the direct relationship found between salinity and the spatial and temporal distribution of the zooplankton, other factors, such as turbidity and tidal currents may influence the density of these organisms (McLusky and Elliot, 2004; Marques *et al*., 2009). The high concentrations of suspended material reduced the penetration of solar radiation into the water column, which has a direct effect on phytoplankton growth (Matos *et al*., 2011), resulting in indirect effects on the spatiotemporal variation of zooplanktonic organisms.

In the present study, turbidity was correlated positively with the density of most of the most common species recorded at stations S2 and S3. A number of different studies (Diodato and Hoffmeyer, 2008; Menéndez *et al*., 2012) have shown that suspended sediments and detritus constitute an excellent source of food for copepods. Roman *et al*. (2001) have also suggested that the ability of some copepod species to ingest suspended particles allows them to prosper in environments with high turbidity.

CONCLUSIONS

The spatial and temporal (among tidal phases and months) variability of the mesozooplankton in the Taperaçu Estuary was controlled by the variation in precipitation, salinity, turbidity and chlorophyll-a concentrations. The copepods were dominant throughout the study period. The densities of the omnivorous copepods *Acartia tonsa* and *A. lilljerborgi* were correlated negatively with the chlorophyll-a concentrations and positively with turbidity. This may reduce intraspecific competition for feeding resources, allowing for the coexistence of these species in the same estuary without alternating between seasons, as previously suggested for this same estuary. The reduction in precipitation during June 2012 led to a significant increase in salinity, making this environment favorable to the occurrence of typically marine species, such as *P. quasimodo* and *O. dioica*. The results of the present study indicate that oscillations in the climatic and hydrological conditions (especially salinity) of the estuarine ecosystem are responsible for modifications in the occurrence and distribution of zooplankton species, and that these processes are more accentuated in the estuaries of the Amazon region, where precipitation rates are higher than in many other tropical and subtropical regions around the world.

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CAPÍTULO III

Biomass and Secondary Production of A*cartia tonsa* and A*. lilljerborgi* in an Amazonian estuary (Bragança, Pará, Brazil)

Artigo a ser submetido para publicação no periódico ***Journal of Marine Systems*** ISSN: 0924-7963. Para fins de padronização do *layout* de apresentação desta tese foi utilizada a fonte ‘Arial’, tamanho 12, com espaçamento entre linhas de 1,5 e uma coluna. As normas de submissão para esta revista encontram-se nos anexos.

BIOMASS AND SECONDARY PRODUCTION OF A*cartia tonsa* and *A. lilljerborgi* IN AN AMAZONIAN ESTUARY (BRAGANÇA, PARÁ, BRAZIL).

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ABSTRACT

The dinamics of the *A. tonsa* and *A. lilljeborgi* were described for the first time in the Taperaçu Estuary. The acartiids were collected using plankton nets (200 µm) in June 2012, March 2013 (rainy season) and September 2012 and 2013 (dry season). The oscillations in rainfall and the fluctuations in hydrological variables influenced the abundance, biomass, and production of both *A. tonsa* (17.2±23 to 8500.9±13,248.1 ind.m^{-3}; 16,385.29 mg.C.m^{-3}; 0.09±0.21 to 355.17±590.84 mg.C.m^{-3}.d^{-1}) and *A. lilljeborgi* (14.3±10.8 to 1470.4±1590.6 ind.m^{-3}; 22,398.40 mg.C.m^{-3}; 177.99±263.13 mg.C.m^{-3}.d^{-1}) with clear monthly, seasonal, and spatial patterns. The high levels of production (independently of the analytical model) may have been related to the relative abundance of feeding resources and nutrients available in the estuary, given that acartiids are known to be omnivores, capable of surviving and reproducing on different types of diet. Given this, despite the possibility that the values were underestimated due to the size of the net mesh. This high productivity may be related to the constant high temperatures throughout the year, the presence of waters rich in particulate organic material derived from the adjacent mangrove forests, favoring the development and reproduction of the two species in the study estuary.

Key-Words: rainfall, Amazonian coast, environmental variables, Acartiidae

1. INTRODUCTION

In marine and estuarine ecosystems, copepods account for more than 80% of the mesozooplankton abundance and biomass (Leandro et al., 2007), and play an extremely important role in the transfer of material and energy to higher trophic levels (Valiela, 2015). Estimates of copepod biomass and secondary productivity represent one of the most important tools for the formulation of theories on the biological productivity of these environments, which are especially useful for the monitoring of environmental changes related to pollution or climate change (Primo et al., 2009; Muxagata et al., 2012).

The copepods of the genus *Acartia* are common and widely distributed around the world, and given their extreme tolerance to environmental oscillations (Cervetto et al., 1999), they can be found in both tropical (Ordóñez-López and Ornelas-Roa 2003, Álvarez-Cadena et al., 2007, Magalhães et al., 2015, Atique et al., 2016) and temperate environments (Pastorinho et al., 2003; Azeiteiro et al., 2005; Leandro, et al., 2006; Derisio et al., 2013). The species of this genus are often predominant in the pelagic environment (Lawrence et al., 2004; Marques et al., 2006), and are considered to be key species for studies of the productivity of coastal ecosystems. In pelagic estuarine environments, variables such as salinity and temperature, as well as the availability of feeding resources, are the principal factors influencing the distribution, biomass, and productivity of the Acartiidae (Ara, 2001; Muxagata et al., 2012), and are influenced directly by variations in climate (Marques et al., 2009), and in particular the instability of precipitation regimen (Lam-Hoai et al., 2006, Andrade et al., 2016).

The main *Acartia* species found in the Amazon region are *A. tonsa* and *A. lilljeborgi*, which are known to occur in a number of different estuarine and marine ecosystems (Marques et al., 2006; Leandro et al., 2006; Magalhães et al., 2015; Leite et al., 2016). These species are especially abundant in the Taperaçu Estuary, the present study area (Magalhães et al., 2012, Palma et al., 2013), where a clear ecological succession can be observed over the course of the year, with a mean annual abundance of 512.4±1,740.2 in *A. tonsa* and

730.1±1,066.9 in *A. lilljeborgi*, and the highest values observed during the rainy and dry seasons, respectively (Magalhães et al., 2013; 2015).

While the relationship between the abundance of *A. tonsa* and *A. lilljeborgi* and environmental variables has been well documented in the estuaries of northern Brazil (Leite, et al., 2009; Costa et al., 2008; Magalhães et al., 2011; 2013; Leite et al., 2013; Palma et al., 2013), few data are available on the biomass and secondary production of these species in the Amazon region, although a number of studies have described patterns based on empirical models derived from other estuarine environments on the Brazilian coast (Ara, 2001; Muxagata et al., 2012).

Given this paucity of data, the present study aimed to provide the first description of the temporal and spacial patterns in the abundance, biomass, and production of *A. tonsa* and *A. lilljeborgi* in the Taperaçu Estuary, considering not only the adults, but also the different developmental stages (copepodites: C1-C5 and adults: C6). This permits the comparison of rates of secondary production with the data available for other tropical estuaries, in particular those of the Amazon region, based on the empirical models used exclusively for the adults thus revealing the important role of juvenile stages of both species on the productivity of these ecosystems.

2. MATERIALS AND METHODS

2.1. Study area

The Taperaçu Estuary (46º42'–46º45' W, 00º50'–00º57" S) is located 200 km southeast of the mouth of the Amazon River, in the municipality of Bragança, in northeastern Pará, Brazil. This estuary is limited to the north by the Atlantic Ocean, and to the west, by Maiaú Bay, with 21 km^2 of surface water and a drainage basin of approximately 40 km^2 (Asp et al., 2012), although it does not have a continuous effective source of freshwater. The Taperaçu is classified as a shallow (mean depth = 4.2 m), permanently open estuary, with strong currents, of up to 2.04 $m.s^{-1}$ and the presence of sandbanks in its central portion (Magalhães et al., 2012; Asp et al., 2012). The estuary is dominated by semidiurnal, meso/macrotides, with a tidal range of around 5 m, often reaching 6 m during equinoctial spring tides (DHN, 2015).

The local climate is hot humid equatorial, with a rainy season from January to July and a dry (or less rainy) season from August to December (Moraes et al., 2005). Considerable variation can be observed in this pattern among years, however. This marked seasonality is determined primarily by the seasonal shifts in the position of the Inter-Tropical Convergence Zone (ITCZ), which is found at latitudes of around 14°N in August and September, migrating southward to around 2°N in March and April, right over the Amazon region (Souza-Filho et al., 2009). Temperature averages range from 25.2ºC to 26.7ºC, ranging between 20.4ºC and 32.8ºC during the day (Schories and Mehlig, 2000). Mean annual precipitation is 2500 mm, 75% of which is recorded during the rainy season (INMET, 2015).

The drainage area of the Taperaçu Estuary is bordered by extensive mangrove forests, with trees of up to 20 m in height, dominated by *Rhizophora mangle* L*, Avicennia germinans* (L). Stearn and *Lacuncularia racemosa* and *Avicennia schaueriana* are less abundant (Menezes et al., 2008). The mangroves also extend along a number of tidal channels that link the Taperaçu with the neighboring Caeté Estuary (Asp et al., 2012).

2.2. Climatology and fieldwork

Precipitation data were obtained from the National Meteorological Institute’s (INMET) Tracuateua station, 17 km from the municipality of Bragança.

Data were collected in the Taperaçu Estuary in June 2012 and March 2013 (rainy season), and September 2012 and 2013 (dry season) through simultaneous hauling of the subsurface water at three fixed stations, located in the lower (S3: 00°50'30.9" S, 46º43'02.4" W), middle (S2: 00°55'06.8" S, 46º44'0" W) and upper (S1: 00°56'58.4" S, 46º46'26.9" W) sectors of the estuary (Fig. 1). The samples were collected during neap tides at 3-hour intervals over a 25-hour period, encompassing both the flood and ebb tides.

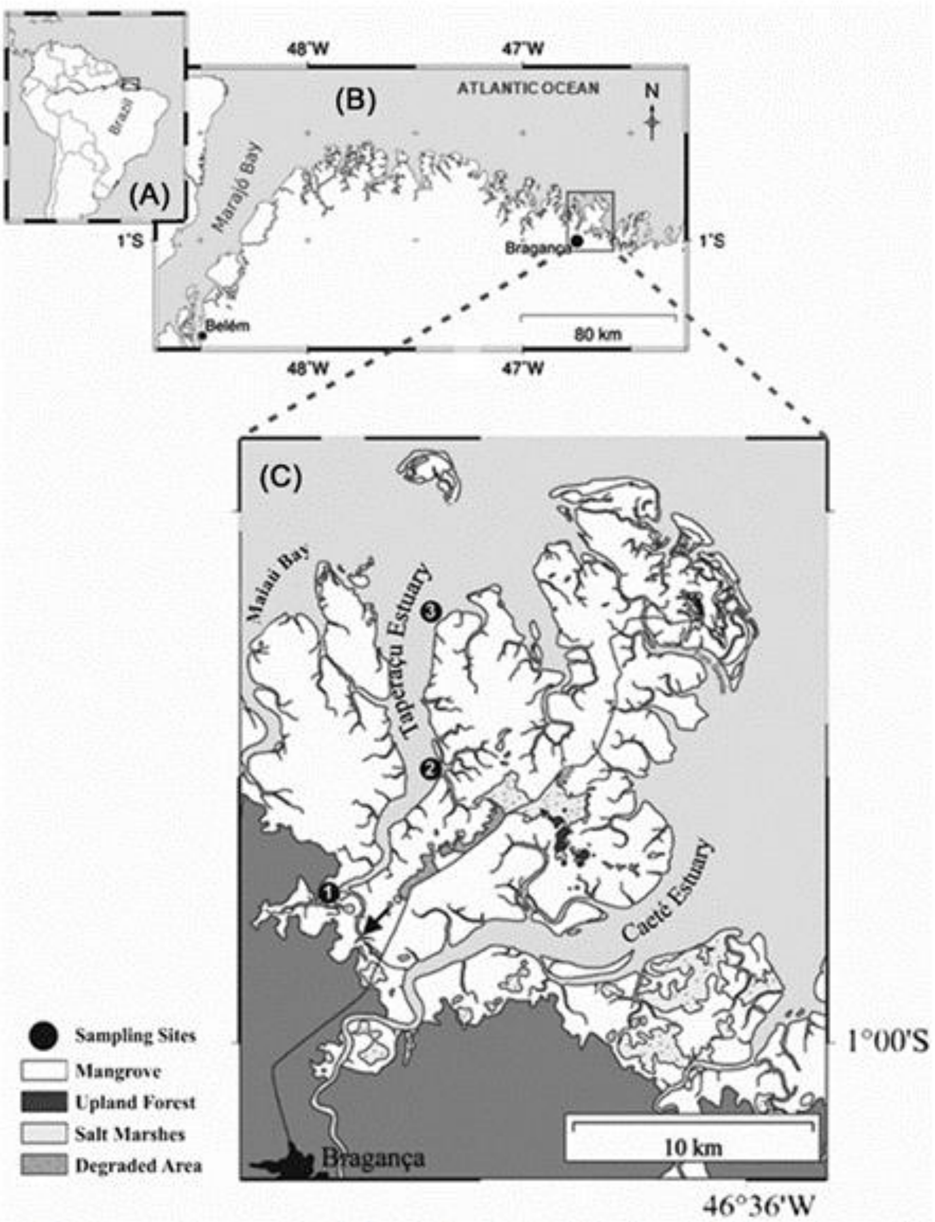

Fig. 1. Study area: (a) South America; (b) Taperaçu Estuary (00º50’–00º57” S, 46º42’–46º45’ W) located on the Amazon Coast in northern Brazil; (c) location of the three sampling stations in the (1) upper, (2) middle, and (3) lower sectors of the estuary (Source: Magalhães, 2015, modified from Mehlig, 2001).

2.3. Environmental variables

The physical and chemical variables of the water (temperature, salinity, and turbidity) were measured *in situ* using CTDs (RBR) with turbidity sensors. Subsurface water samples were also collected for the measurement of the concentrations of chlorophyll-a and dissolved nutrients (nitrite, nitrate, phosphate, and silicate), which were determined by spectrophotometry, following Parsons and Strickland (1963) and UNESCO (1966), and Grasshoff et al. (1983), respectively.

2.4. Abundance, biomass and production of acartiids

The samples were obtained using conical plankton nets with a 200 µm mesh, 2 m in length and a mouth of 50 cm, which were equipped with a mechanical flowmeter to estimate the volume of water filtered by the nets. The samples were transferred to 600 ml plastic containers and fixed in a 4% formalin solution (final concentration) neutralized with sodium tetraborate.

In the laboratory, the samples were subdivided using a Folsom-type subsampler, and all the specimens of *A. tonsa* and *A. lilljeborgi* were identified and counted (Björnberg, 1981). The copepodites (C1-C5) and adults (C6) were identified based on Sabatini (1990) and Björnberg (1972), respectively, and classified by sex (male and female). The prosome of each specimen was measured using a stereoscopic microscope equipped with a micrometric scale. In the case of the adult (C6) *A. lilljeborgii*, the spines on the posterior portion of the cephalothorax were not included in the measurement, given that the length and angle of these structures vary among individuals (Ara, 1998).

The mean carbon biomass of each development stage of the two study species was estimated by multiplying the abundance of each stage by the individual dry weight (*DW*) estimated for the size of the prosome, using species-specific weight-length regression equations (Ara, 2001). The dry weight was converted into carbon (C), assuming a carbon content of 50.6% dry weight for *A. tonsa*, and 47.0% for *A. lilljerborgi* (Leite et al., unpublished data). The organic carbon content was obtained using an automatic carbon, hydrogen and nitrogen (CHN) analyzer, using a protocol modified from Ribeiro (2006).

The daily production rate (Pc, $mg.C.m^{-3}.d^{-1}$) was calculated by:

$$Pc = \Sigma\, D.Wc.g$$

where D = density ($ind.m^{-3}$), Wc = individual carbon weight (mg.C), and g = weight-specific individual growth rate (d^{-1}).

The growth rates (*g*) of *A. tonsa* and *A. lilljerborgi* were obtained using two different general growth models:

$\mathbf{\log_{10} g = -1.1355 + [0.0246 * (\mathit{T})] - [0.2962 * \log_{10}(\mathit{DW})}$ (Hirst and Sheader, 1997)

and

$\mathbf{\log_{10} g = 0.0186(\mathit{T}) - 0.288 \log_{10}(\mathit{DW}) + 0.417 \log_{10}(\mathit{Cl}) - 1.209}$ (Hirst and Bunker, 2003),

where, *g* = the growth rate (d^{-1}), *T* = the temperature (°C), *DW* = carbon weight (mgC), and *Cl* = chlorophyll concentration ($mg.m^{-3}$). The Hirst and Bunker (2003) model used in the present study describes the individual growth rate in the juveniles and adults for both broadcasters and sac spawners species.

2.5. Statistical analyses

The effects of the sampling station, study month, tide (flood/ebb) and season (rainy/dry) on the environmental variables, and the abundance, biomass, and different models of acartiid production were analyzed using a one-way and two-way ANOVA (Zar, 2010). The data were log-transformed (log x+1) prior to the analyses and the homoscedasticity of variances was verified using the Cochran test (Sokal and Rolf, 1981). The Spearman correlation was used to investigate the relationship between the environmental variables and the density of *A. tonsa* and *A. lilljerborgi*.

For each of the study variables, the values were grouped (mean±SD) and analyzed in relation to the variation among months and sampling stations, and between tides and seasons. All the statistical analyses were run in Statistica 8.0, with a 5% significance level ($\alpha = 0.05$).

3. RESULTS

3.1. Environmental variables

The salinity, temperature and turbidity of the water, and the chlorophyll-a concentrations varied significantly among months ($F = 116.95$; $p < 0.000$), between seasons ($F = 120.21$; $p < 0.00$), and sampling stations ($F = 19.42$; $p < 0.000$), but not between tides. Mean salinity varied from 22.96±14.76 in March 2013 to 40.20±1.37 in September 2012, in station S1 and, respectively (Fig. 2). While lower levels of precipitation were recorded in September 2012 (monthly mean of 2 mm) in comparison with September 2013 (mean = 78 mm), no significant differences were found in the salinity between 2012 and 2013 (Fig. 2).

The mean temperature of the water varied from 27.64±0.68ºC in March 2013 to 29.29±0.60ºC in September 2013, both at station S1 (Fig. 2). While only a discreet level of temporal (seasonal/monthly) variation was observed during the study period, water temperatures were significantly higher ($F = 26.2$; $p < 0.000$) during the periods of lowest precipitation.

Mean turbidity varied from 10.73±11.27 UNT at station S3 in March 2013 to 681.76±73.00 UNT at station S2 in June 2012 (Fig 2), with significant monthly ($F = 117.44$; $p < 0.000$), seasonal ($F = 109.55$; $p < 0.000$) and spatial ($F = 137.07$; $p < 0.000$) differences, with the highest values being recorded at stations S1 and S2 during the rainy season.

The mean chlorophyll-a concentration was lowest in March 2013, at station S3 (1.61±2.36 $mg.m^{-3}$). A much higher concentration (54.25±40.26 $mg.m^{-3}$) was recorded at station S1 in September, however, when precipitation levels were extremely low (Fig. 2). Marked seasonal differences were recorded at station S1, with significantly higher values ($F = 18.51$; $p < 0.000$) being recorded during the dry season.

The mean nitrite (NO_2^-) concentration was significantly ($F = 4.76$; $p < 0.0002$) higher at station S1 in March 2013 (0.09±0.07 $µm.L^{-1}$), while nitrate (NO_3^-) concentrations varied from 0.77±1.43 $µm.L^{-1}$ to 2.71±2.63 $µm.L^{-1}$, with both values being recorded in March 2013, at stations S3 and S2, respectively (Fig. 2). No statistically significant variation was found, however.

In the Taperaçu Estuary, the concentrations of phosphate (PO_4^{-3}) and silicate (SiO_2) varied significantly between months and sampling stations (PO_4^{-3}: $F = 5.20$, $p < 0.001$; SiO_2: $F = 17.21$, $p < 0.000$), with the highest concentrations of both phosphate (1.31±0.61 $µm.L^{-1}$) and silicate (196.72±92.66 $µm.L^{-1}$) being observed at station S1 in September 2012.

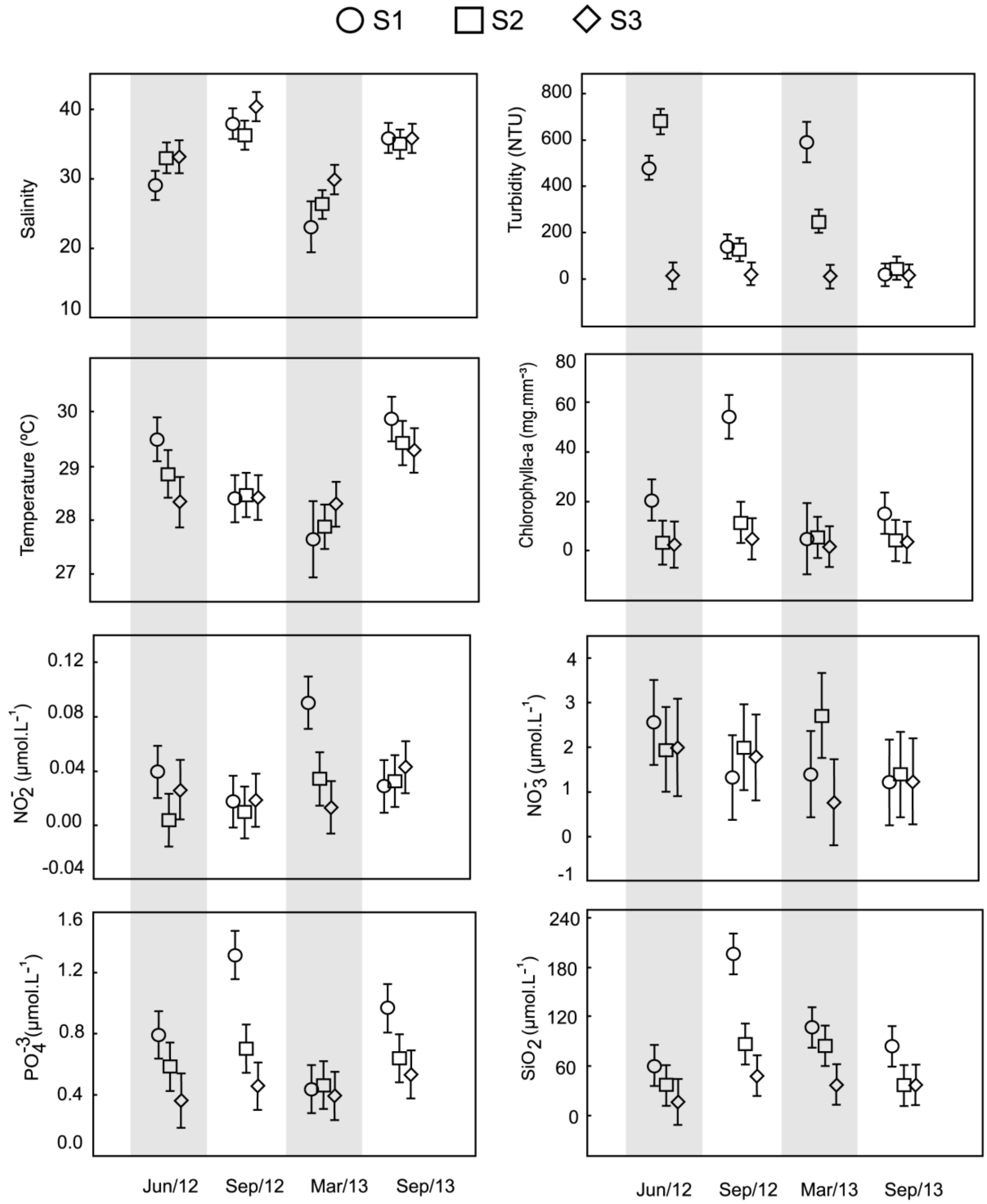

Fig. 2. Mean (±SD) variation in the environmental variables and nutrients in the Taperaçu Estuary during the study period. The gray shading indicates the months of the rainy season.

3.2. Abundance of Acartiidae

In the present study, the abundance of *A. tonsa* and *A. liljerborgi* varied significantly among months (F = 3.37; $p < 0.05$), and between seasons (F =

5.33; $p < 0.05$) and sampling stations (F = 3.08; $p < 0.05$), although no significant variation was observed between tides. The species *A. tonsa* predominated (75% of abundance) throughout the study period, reaching 85.3% of total acartiid abundance at S1 and 81.7% at S2 in June 2012.

The mean abundance of *A. tonsa* varied from 17.15±23.00 ind. m^{-3} at station S3 in June 2013, to 8,500.93±13,248.06 ind. m^{-3} at station S1 in the same month. All six developmental stages of *A. tonsa* (C1-C6) were recorded throughout the study period, with the copepodites (C1-C5) predominating over the adults in all months and at all sampling stations (Table 1), principally S1, in June 2012, when a mean abundance of 7,276.14±1,098.34 ind.m^{-3} was recorded. There was a significant increase (F = 12.05; $p < 0.000$) in the abundance of *A. tonsa* copepodites (C1-C5) at station S1 during the rainy season. During this period, these developmental stages contributed 66.1% of total abundance, while at the other two stations (S2 and S3), abundance was highest during the dry season.

In the case of the adults (C6), the female *A. tonsa* were significantly more abundant (F = 11.26; $p < 0.000$) at station S1 in June 2012 (1,194.86±2,338.96 ind.m^{-3}). A significant increase in abundance (F = 6.14; $p < 0.014$) was also observed during the rainy season, with a mean of 597.75±1,718.13 ind.m^{-3}. In September 2012 and March 2013, however, the abundance of the males of this species increased, with means of 16.01±35.65 and 34.48±67.40 ind.m^{-3}, respectively. In September 2013, the opposite pattern was recorded, with the females being more abundant.

The abundance of *A. lilljerborgi* oscillated significantly among months and stations (F = 8.78; $p < 0.000$), with mean values ranging from 14.28±10.83 ind.m^{-3} at station S2 to 1,470.37±1,590.65 at S1, both in June 2012. As for *A. tonsa*, significant seasonal variation (F = 6.19; $p < 0.002$) was observed, with higher values being recorded during the rainy season (1,116.13±1,500.51 ind. m^{-3}). In contrast with *A. tonsa*, however, the adult *A. lilljeborgi* predominated over the copepodites (C1-C5; Table 1), with the females being dominant throughout the study period, but with higher values being recorded in June 2012, at station S1 (1,039.93±992.31 ind.m^{-3}). The abundance of the females varied significantly between seasons, with higher values being recorded during the dry season at stations S2 (1.92±0.70 ind.m^{-3}) and S3 (1.49±0.58 ind.m^{-3}) (Table 1).

The comparative analyses of the environmental variables indicated that the abundance of *A. tonsa* copepodites and adults was correlated negatively with salinity (r = -0.17; $p < 0.05$), and positively with temperature (rs = 0.25; $p > 0.05$), even though the correlation was not significant in the latter case. The abundance of *A. lilljeborgi* copepodites and adults was correlated positively with salinity (r = 0.22; $p < 0.05$) and chlorophyll–a concentrations (rs = 0.23; $p < 0.05$). No significant correlations were observed between the abundance of either species and turbidity, nor with chlorophyll-a, in the case of *A. tonsa*.

Table 1

Two-way ANOVA for the effects of the months, sampling stations and seasons on the abundance of the copepodites and adults (male and female) *A. tonsa* and *A. lilljeborgi*. *p < 0.05; **p < 0.01; ***p < 0.001.

	Copepodites		Adults (Female)		Adults (Male)	
	A. tonsa *F*	*A. lilljeborgi* *F*	*A. tonsa* *F*	*A. lilljeborgi* *F*	*A. tonsa* *F*	*A. lilljeborgi* *F*
Month	4,07**	9.24***	16.49***	3.20**	4.88**	10.25***
Station	5.95**	2.38	2.72	1.53	3.01	0.18
Month x Station	7.41***	2.96**	11.26***	13.04***	4.77***	2.01
Season	0.00	19.87***	6.24**	3.74	2.88	14.16***
Station	9,57***	2.54	1.48	0.94	2.31	0.16
Season x Station	12.05***	4.38**	3.99**	3.37**	1.05	3.63**

3.3. Size of the prosome

During the study period, the mean (±SD) length of the prosome of both *A. tonsa* and *A. lilljerborgi* varied considerably between seasons (Table 2). While stages C1–C3 of *A. tonsa* were longer during the dry season, significant ($p < 0.05$) seasonal differences were recorded only for C1 (Table 2). Stages C4 and C5 presented significant ($p < 0.05$) spatial and seasonal variation, although in this case, the greatest lengths were recorded during the rainy season. Whereas the adult female *A. tonsa* were longer during the rainy season, the males were longer during the dry season (Table 2).

The C1 and C2 stages of *A. lilljeborgi* were not captured during the rainy season, while C3 and C4 were longer during the dry season, with significant ($p < 0.05$) spatial and seasonal differences. Both male and female *A. lilljeborgi* were significantly longer, on average, during the rainy season (Table 2).

Table 2

Minimum, maximum and mean (±SD) length of the prosome (µm) of the different development stages of *A. tonsa* and *A. lilljeborgii* during the rainy and dry seasons. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

	Acartia tonsa		*Acartia lilljeborgi*	
Stage	**Rainy** Min – Máx (Mean±SD)	**Dry** Min – Máx (Mean±SD)	**Rainy** Min – Máx (Mean±SD)	**Dry** Min – Máx (Mean±SD)
C1	260 – 380 (330.6 ±33.3	300 – 440 (373.3±40.8)***	–	300 – 420 (347.4±33)***
C2	400 – 580 (432.6±36.9)	320 – 800 (438.9±51)	–	400 – 520 (431.7±30)***
C3	460 – 660 (522.5±25.9)	420 – 740 (532±33.7)	460 – 740 (540±75.4)***	420 – 940 (551.6±100.6)***
C4	560 – 800 (645.8±41.2)***	500 – 800 (627±30.4)***	460 – 680 (590±75.6)**	500 – 920 (638.7±57.3)**
C5	600 – 960 (748.5±24.8)*	600 – 820 (735.7±26.3)*	620 – 1000 (814±35.6)	620 – 1020 (814.7±33.7)
C6 – female	780 – 960 (821.22±27.78)	760 – 960 (827.29±48.17)	760 – 1200 (939.26±34.31)***	880 – 1020 (923.80±23.90)***
C6 – male	620 – 820 (775.56±26.27)	660 – 920 (764.93±30.12)	800 – 1000 (882.55±54.15)	720 – 900 (853.95±33)

3.4. Biomass and secondary production

The biomass of both species varied considerably over the course of the study period (Fig 3).

The *A. tonsa* copepodites (C1–C5) presented clear monthly and spatial differences ($p < 0.05$), in particular stage C4, for which the highest values were recorded at station S1 in June 2012 (839.88±1518.80 $mgC.m^{-3}$), reflecting the abundance of the stage at this station. High mean biomass values were also recorded for the other copepodite stages at this station in June 2012 (C1: 0.08±0.30 $mgC.m^{-3}$; C2: 1.17±6.58 $mgC.m^{-3}$; C3: 9.76±45.54 $mgC.m^{-3}$, C5: 33.32±181.18 $mgC.m^{-3}$ and C6: 23.39±156.20 $mgC.m^{-3}$). The adult female *A. tonsa* also varied monthly and spatially ($F = 7.24$; $p < 0.000$) with significantly higher values being recorded in June 2012 and September 2013 at stations S1 (223.20±517.89 $mgC.m^{-3}$) and S2 (14.41±25.77 $mgC.m^{-3}$), while the biomass of the adult males was highest ($F = 2.39$; $p < 0.03$) at station S3 in June 2012 (2.22±3.89 $mgC.m^{-3}$). The carbon biomass varied seasonally in stages C1–C4 (C1: $F = 4.79$, $p < 0.01$; C2: $F = 6.88$, $p < 0.001$; C3: $F = 4.70$, $p < 0.011$; C4: $F = 3.63$, $p < 0.030$) and the adult females ($F = 3.17$; $p < 0.046$), significantly higher values being recorded during the rainy season, at station S1, while no significant variation was observed in the males.

In *A. lilljeborgi*, temporal (monthly) and spatial (among stations) fluctuations were observed in the biomass, with the highest values being recorded for stages C4 (1.19±1.62 $mgC.m^{-3}$, $F = 2.64$; $p < 0.02$) in September 2012 and C5 (165.83±191.67 $mgC.m^{-3}$, $F = 4.29$; $p < 0.0007$) in September 2013, both at station S2. In contrast with the pattern observed in *A. tonsa*, the biomass of the *A. lilljerborgi* females was higher than that of the males (Fig 3), when the combined effect of the months and sampling stations is taken into account ($F = 9.13$; $p < 0.000$), in September 2012 (499.95±1,347.84 $mgC.m^{-3}$) at station S2. In the males, a peak of biomass was observed in September 2012 (83.23±163.40 $mgC.m^{-3}$), also at S2. Significant seasonal differences were observed in stage C5 ($F = 3.66$; $p < 0.029$) and both the adult males ($F = 3.79$; $p < 0.025$) and females ($F = 7.84$; $p < 0.0006$), with biomass increasing during the dry season.

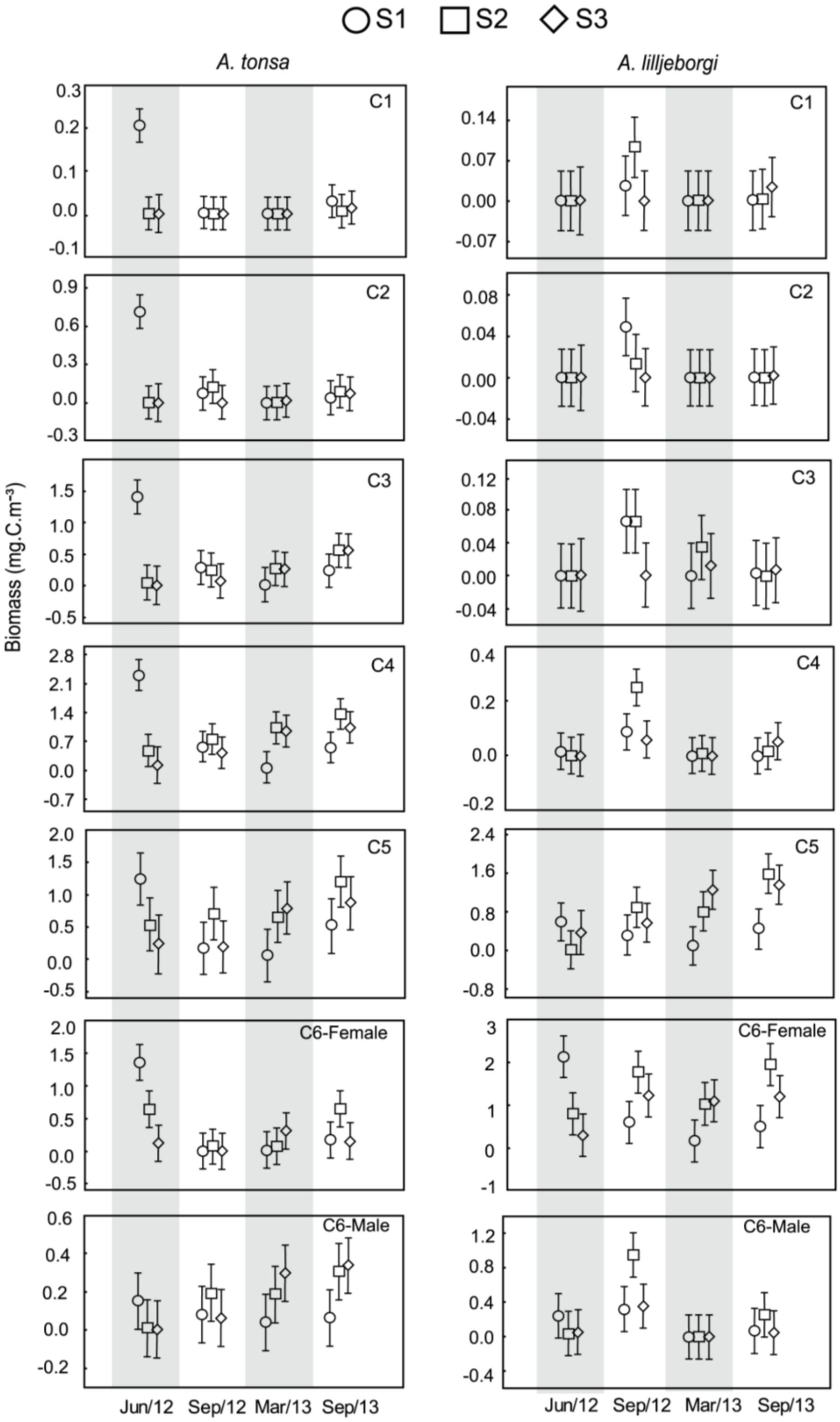

Fig. 3. Mean (±SD) variation in the carbon biomass (mg C m^{-3}) of *A. tonsa* and *A. lilljeborgi* in the Taperaçu Estuary (Bragança, Brazil). The data were log transformed to facilitate visualization. The gray shading indicates the period of the rainy season. Please note the difference in scales.

In the case of the copepodites, daily production in the *A. tonsa* stage C4 ranged from 0.10±0.27 to 256.46±448.72 mgC.m^{-3}.d^{-1} according to the Hirst and Sheader model, and from 0.09±0.21 to 355.17±590.84 mgC.m^{-3}.d^{-1} in the Hirst and Bunker model, in March 2013 and June 2012, respectively, both at station S1 (Fig 4). The production of the female *A. tonsa* was significantly higher in June 2012 at station S1 (Hirst and Shaedar model: 54.56±123.63 mgC.m^{-3}.d^{-1}, F=3.39, $p < 0.000$; Hirst and Bunker model: 74.38±164.36 mgC.m^{-3}.d^{-1}, F = 8.00; $p < 0.000$), whereas higher values were recorded for the adult males in September 2013, at station S3 (Hirst and Sheader model: 0.61±1.02 mgC.m^{-3}.d^{-1}; Hirst and Bunker model: 0.46±0.69 mgC.m^{-3}.d^{-1}, F = 2.76; $p < 0.046$) (Fig 4). In the combined analyses of seasons and stations, production was significantly higher in the adult female *A. tonsa* during the rainy season at station S1 (F = 3.97; $p < 0.021$).

In *A. lilljerborgi*, the highest secondary production was recorded for the adult copepods. The females presented significantly higher mean production values in June 2012 at station S1 (Hirst and Sheader model: 110.41±167.13 mgC.m^{-3}.d^{-1}, F = 9.07, $p < 0.000$; Hirst and Bunker model: 177.99±263.13 mgC.m^{-3}.d^{-1}, F = 9.56, $p < 0.000$) (Fig 5), while the highest values for the males were recorded in September 2012, at station S2 (Hirst and Shaedar model: 11.63±32.75 mgC.m^{-3}.d^{-1}; Hirst and Bunker model: 16.22±45.12 mgC.m^{-3}.d^{-1}), although the differences were not significant.

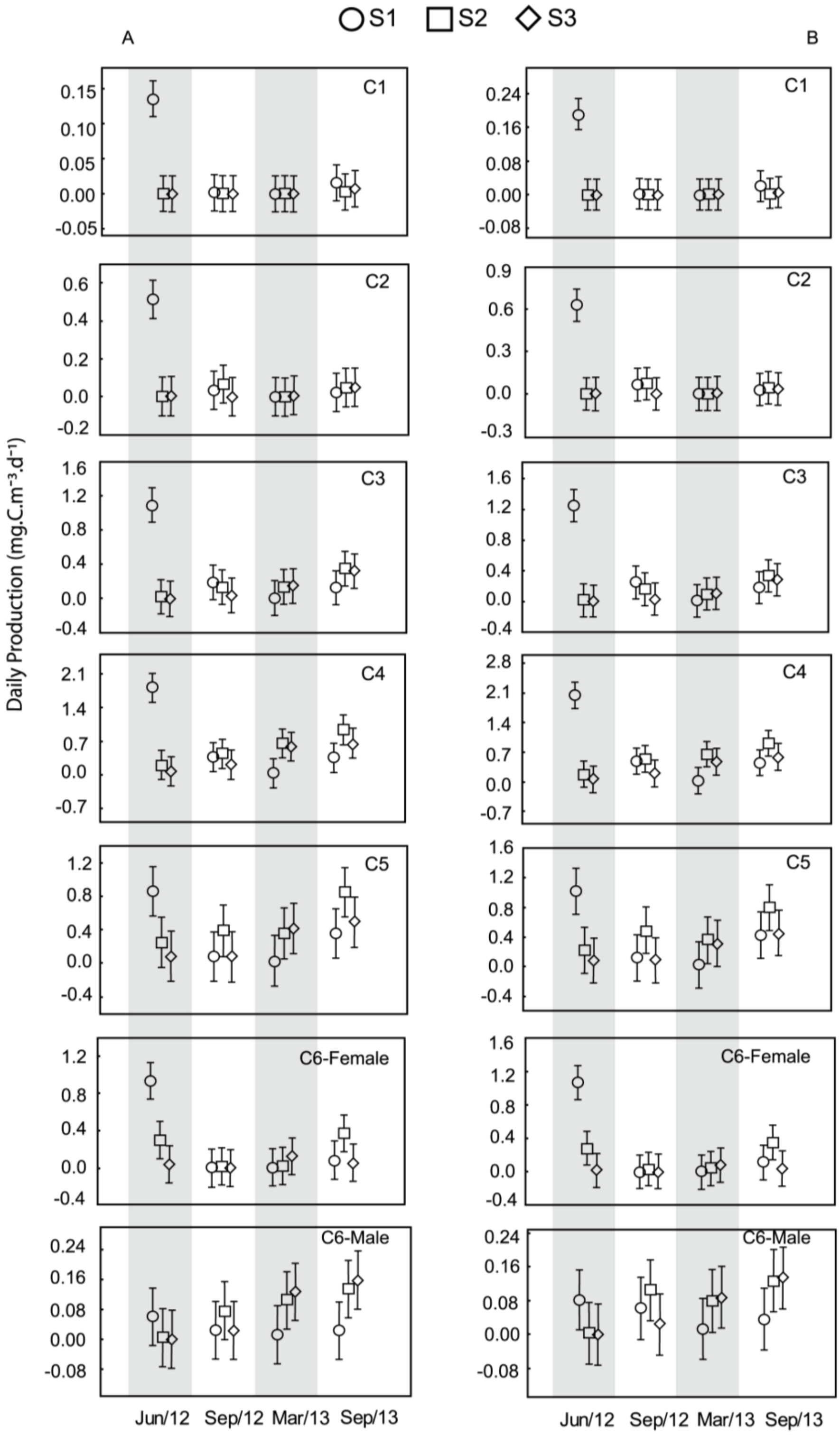

Fig. 4. Mean (±SD) variation in the secondary production (mg C m^{-3}) of *A. tonsa* in the Taperaçu Estuary (Bragança, Pará, Brazil) using the Hirst and Sheader (A) and Hirst and Bunker (B) models. The data were log transformed to facilitate visualization. The gray shading indicates the period of the rainy season. Please note the difference in scales.

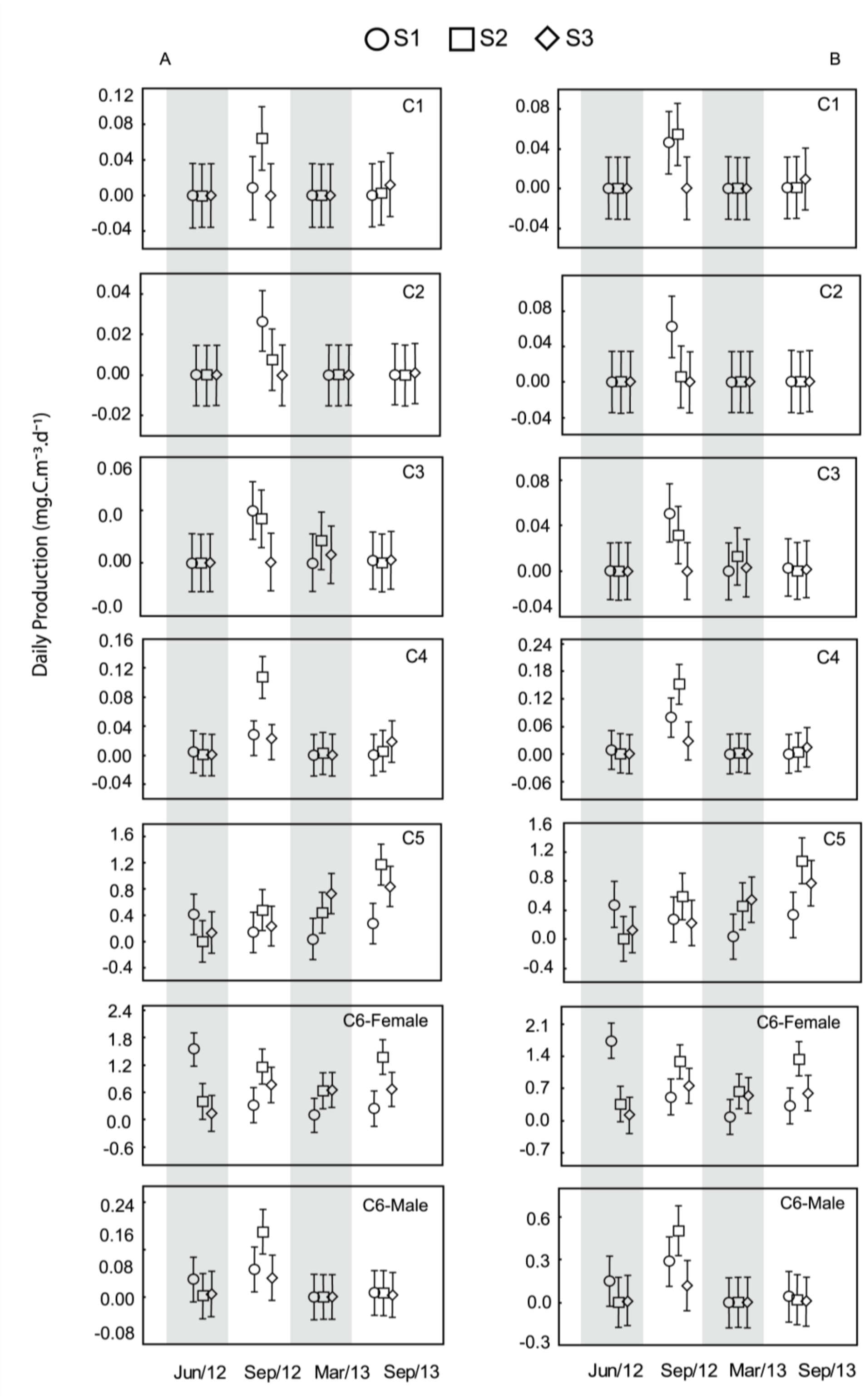

Fig. 5. Mean (±SD) variation in the secondary production (mg C m^{-3}) of *A. lilljeborgi* in the Taperaçu Estuary (Bragança, Pará, Brazil) using the Hirst and Sheader (A) and Hirst and Bunker (B) models. The data were log transformed to facilitate visualization. The gray shading indicates the period of the rainy season. Please note the difference in scales.

4. DISCUSSION

The seasonal variation in the environmental variables of the Taperaçu Estuary was influenced strongly by local precipitation rates (see Souza Junior et al., 2013; Leite et al., 2013; Costa et al., 2013; Magalhães et al., 2015), which are, in turn, determined by the seasonal migration of the ITCZ over the Amazon region. This results in growing precipitation levels during the first half of the year, which results in an increase in fluvial discharge, while during the second half of the year, the opposite pattern is observed (Marengo, 1995) being this seasonal variation typical of the estuaries in the Amazon region.

During the rainy season of 2012 (January–June), there was a substantial reduction in rainfall rates in the study area (INMET, 2015), even though large-scale climatic events such as El Niño, La Niña or severe droughts were not recorded during the period. The decline in rainfall rates appears to have been linked to abnormal surface sea temperatures in the Pacific and Atlantic oceans (Marengo et al., 2013), which provoked higher than normal atmospheric temperatures that, in turn, affected local precipitation levels. The World Meteorological Organization (WMO, 2013) recorded a deficit of 300 mm in 2012 in comparison with the region’s typical precipitation levels.

This reduction in precipitation rates observed in the region in 2012 had a major effect on the environmental variables of the Taperaçu Estuary. This, together with the morphology of the estuary and local hydrodynamics contributed to the high salinity, and chlorophyll-a and dissolved nutrient concentrations observed in September 2012 at station S1.

In previous studies (Costa et al., 2008; Palma et al., 2013; Magalhães et al., 2015), a predominance of marine conditions was observed during the dry season in the Taperaçu Estuary, due primarily to the absence of any effective fluvial discharge (Asp et al., 2012). Low levels of salinity are associated with the rainy season, due to the input of freshwater of the mangroves and wetlands associated with the upper portion of the estuary, as well as the oligohaline waters from the neighboring Caeté Estuary, which reach the Taperaçu through the Taici Creek during high tides. Even so, while June 2012 was considered to be a rainy season month for the purpose of the present study, precipitation (31.42 mm) was inconsistent with that recorded in previous studies in the study region (Souza et al., 2008; Magalhães et al., 2009), due to the reduction in rainfall levels.

Overall, the waters of the Amazon coast are often seen as having high levels of phytoplankton biomass, with high concentrations of chlorophyll-a being recorded during the periods of high levels of pluvial discharge (rainy season), which contribute to the availability of dissolved nutrients in the water column through the washing out of the mangroves located on higher terrain, and the lixiviation of inland areas (see Pereira et al., 2010).

Acartia tonsa and *A. lilljeborgi* have a cosmopolitan distribution, being found in the Atlantic, Pacific, and Indian oceans, as well as the Baltic, Black, Caspian, and Mediterranean seas (Brodskii, 1967; Björnberg, 1981). These species are also found in tropical estuaries and are common in Brazilian estuaries (Schwamborn et al., 2004; Costa et al., 2008; Dias et al., 2010; Magalhães et al., 2015). In coastal regions and estuaries, the spatial and temporal distribution of abundance of these two species tend to show a successional pattern (Marques et al., 2006: Magalhães et al., 2015), which results from differences in their ecophysiological characteristics (Gaudy et al., 2000; Calliari et al., 2006) or to intra- and inter-specific interactions, such as predation (Tiselius et al., 1997) or competition (Tester and Turner, 1991).

In the Taperaçu Estuary, the oscillations in local rainfall levels, together with the variation in environmental variables had a profound influence on the abundance and distribution of *A. tonsa* and *A. lilljeborgi*. In September 2013 (dry season), the abundance of *A. tonsa* was higher than that observed in the same month of 2012, possibly resulting from the increase in rainfall observed in the dry season of the second year, even though no global climatic phenomenon was recorded during this year (NOAA, 2014). This level of abundance for *A. tonsa* contradicts the previous data from the study area (Costa et al., 2008; Magalhães et al., 2012; 2015, Andrade et al., 2016), which show that an increase in abundance is typical during the rainy season. For *A. lilljeborgi*, on the other hand, an increase in abundance is typically observed during the dry season in the Taperaçu Estuary (Magalhães et al., 2015; Leite et al., 2016; Souza Junior et al., 2013), as observed during the present study.

In the present study, the copepodites of *A. tonsa* were more abundant than the adults, reflecting the capacity of this species to the prevailing environmental conditions found in the Taperaçu Estuary. *Acartia tonsa* is considered to be euryhaline and eurythermal, being capable of surviving in salinities of 0–31 (Muxagata et al., 2012; Magalhães et al., 2015), although its reproductive potential is reduced at salinities lower than 5 (Muelbert et al., 2010), given that, under these conditions, the nauplii are unable to complete their development. This pattern was confirmed in March 2013 at station S1, when *A. tonsa* was absent (0.00 ind.m^{-3}) from 77.7% of the samples analyzed. The precipitation recorded during the sampling period (March 19th and 20th 2013), were the highest (15.1 and 75.8 mm, respectively) recorded for this month (March 2013), which probably contributed to the marked reduction in salinity (8.23–2.92) and the reduction in the abundance of *A. tonsa* in the samples collected.

The absence of *A. tonsa* associated with a reduction in salinity has been observed in other regions of Brazil, in particular, in association with El Niño events (Kaminski, 2009; Muxagata et al., 2012), which are typically responsible for major peaks in rainfall. With the exception of station S1 in March 2013, *A. tonsa* was recorded throughout the whole study period, which may have been related to the osmoregulatory capacity of the species (Svetlichny and Hubareva, 2014) and its adaptability to the poly/euhaline conditions of the Taperaçu Estuary (Leite et al., 2009; Magalhães et al., 2009; 2015; Costa et al., 2011). The adaptability of *A. tonsa* to seasonal and spatial fluctuations in the hydrological conditions of the Taperaçu Estuary indicates that the production of resistant eggs by this species may be a strategy to compensate for the high mortality rates of the adults (Kiørbe, 2006). In this case, the remnant population is able to recuperate growth rates rapidly when favorable conditions are restored (Castro-Longoria, 2001; Hoffmeyer et al., 2009; Magalhães et al., 2015). This reproductive strategy may be one of the principal factors guaranteeing the recruitment of the species in the study region.

Acartia lilljeborgi was found in the Taperaçu Estuary within an ample range of salinity (17–37). This species, which is typically estuarine, has been observed in a number of estuaries on the coast of Pará, where it is found preferentially during the dry season (Leite et al., 2009; Costa et al., 2009; Magalhães et al., 2013). This species has estuarine-marine characteristics, and is an indicator of coastal waters (Björnberg, 1981) and is a dominant species in many tropical Brazilian estuaries (Schwamborn et al., 2004; Dias et al., 2010), together with *A. tonsa* (Sterza and Fernandes, 2006).

The abundance of adult female of *A. lilljeborgii* observed in the Taperaçu Estuary during the present study was directly linked to the polyhaline conditions of the estuary, indicating that the optimal salinity for the production of eggs in this species would be between 18 and 30, as previously reported by Magalhães et al. (2015). The differences observed between males and females may be related to both the sensitivity of the males to reduced salinity (Ara, 2001) and the increase in the production of eggs by the females, which may constitute one of the principal environmental mechanisms of population control in this species (Sabatini, 1990; Zaballa and Gaudy, 1996). Ara (2001) also observed a significant reduction in the production of eggs under reduced salinity, verifying that, during periods of low salinity (<17), the populations of this species were incapable of recuperating their numbers through the production of eggs. Temporal fluctuations in the abundance of *A. lilljeborgii* may thus be derived not only from its reproductive performance, but also the effects of local hydrological conditions, such as variations in salinity, on the physiological processes of these organisms.

The juvenile (C1–C5) and adult (C6) stages of *A. tonsa* and *A. lilljeborgi* presented seasonal and spatial variation driven by the development stage and local conditions (physical and chemical). In general, the dimensional variation of adult copepods depends on the effects of a number of different environmental factors on the development of the juvenile forms, mainly temperature, salinity and the availability of food (Gaudy and Verriopoulos, 2004). Geographical variation in body size may also result from varying hydrographic conditions (Pessoti et al., 1986) or the effects of latitude on local temperatures (Marques et al., 2006; Leandro et al., 2014). In the Taperaçu Estuary, the variation in the mean length of the prosome of *A. tonsa* and *A. lilljeborgi* was greater than that recorded by Ara (2001) in the Cananéia lagoon-estuarine system and by Muxagata et al. (2012) in the Patos Lagoon, both located on the coast of southern Brazil, as well as the value reported by Leandro et al. (2006), from the temperate estuary of the Aveiro River in Portugal.

The variation in the body size of *Acartia* copepodites and adults observed in the present study were related intimately to the availability of feeding resources in the study area (reflecting the high concentrations of chlorophyll-a, suspended material/turbidity, and nutrients) during both the dry and rainy seasons. In general, the chlorophyll-a concentrations were over 0.047 $mg.m^{-3}$, which is considered to be a minimum threshold for the development of *Acartia* (Landry, 1978). In addition, *Acartia* are able to feed heterotrophically on micro- and nano-plankton (Wiadnyana and Rassoulzadegan, 1989; White and Roman, 1992; Gasparini and Castel, 1997; Rollwagen Bollens and Penry, 2003). Given this, the results of the present study strongly indicate that in the Taperaçu, like in most other estuaries on the Amazon Coast, which are rich in autotrophic or heterotrophic sources of food, the availability of feeding resources is not a limiting factor for the growth of *A. tonsa* and *A. lillijeborgi*, thus favoring their development.

Relatively high mean levels of acartiid biomass ($mC.m^{-3}$) and production ($mgC.m^{-3}.d^{-1}$) were recorded in the Taperaçu Estuary in comparison with other tropical and subtropical ecosystem in different regions around the world (Weber and Roff, 1995; Roman et al., 2002; Satapoomin et al., 2004; Miyashita et al., 2009; Muxagata et al., 2012). During the present study period, clear differences were found in the rates of production observed in the adults and copepodites of the two acartiid species. Extremely high rates of production were recorded in C4 *A. tonsa* copepodites, although the 200 µm mesh used in the present study may be relatively ineffective for the capture of the juvenile stages (principally C1–C3). Meshes of less than 100 µm may be necessary for the efficient sampling of these initial stages (C1–C3) of *Acartia* species. Given this, the use of a 200 µm mesh in the present study may have contributed to underestimates of the biomass of the initial development stages.

Hopcroft et al*.* (1998) concluded that nets with meshes of 64 µm or 200 µm are efficient for the capture of individuals with prosomes longer than approximately 450 µm, which is consistent with the mean lengths recorded in the present study. Many studies, in a variety of species, have shown that a large proportion of the biomass and secondary production is provided by immature copepodites (Chisholm and Roff, 1990; Weber and Roff, 1995, Hopcroft et al., 1998). This pattern has been observed not only in tropical and subtropical regions (Hopcroft et al., 1998; Ara, 2004), but also at higher latitudes (Hopcroft et al., 2001). In oligotrophic waters, the predominance of small-bodied copepods may be accounted for by their greater efficiency in the capture of picoplankton and nanoplankton when compared with larger individuals (Dias et al., 2015). Even so, as mentioned above, the availability of feeding resources does not appear to be a limiting factor for the development of the study organisms. In this case, even if the abundance of these development stages has been underestimated, the data obtained in the present study can still provide important insights into the role of the copepodites and adults of the study species in the estuaries of the Amazon region, and in particular the Taperaçu Estuary. The initial copepod stages are usually the most abundant component of the mesozooplankton, as observed in *A. tonsa* in the present study, and form the principal link between the microbial trophic network and other zooplankton and nektonic species, which together represented the principal source of food for fish larvae (Fryer, 1986; McKinnon and Duggan, 2003).

In the Taperaçu Estuary, considerable differences were found between males and females in the biomass and production rates of both study species. Whereas in most studies, the secondary production rates of the females are derived primarily from the production of eggs (Kiørboe and Nielsen, 1994; Hay, 1995; Nielsen and Sabatini, 1996), *in situ* observations demonstrate that the production of the females may be less than that of their juvenile equivalents (Hirst and Bunker, 2003). A similar pattern was observed in the Taperaçu, where the C4 copepodites reached a mean production of 256.45 $mgC.m^{-3}.d^{-1}$, a value higher than those recorded for the adults, and this value would be even higher if the initial development stages (C1–C3) were included.

In most cases, estimates of the copepod biomass and secondary production rates have derived from growth rates determined from preserved samples (Landry, 1978; McLaren et al., 1989) through direct measures of somatic growth or reproductive rates. Even so, empirical models are used widely to determine secondary production from physiological rates (Huntley and Boyd, 1984), temperature (Huntley and Lopez, 1992), temperature and body weight (Hirst and Sheader, 1997; Hirst and Lampitt, 1998), and temperature, body weight, and chlorophyll-a concentrations (Hirst and Bunker, 2003).

The estimates of production obtained from the two models used in the present study were not significantly different, although the production rates calculated using the Hirst and Bunker (2003) model were slightly higher than those obtained using the global Hirst and Sheader (1997) model. The latter empirical model is derived from body weight and temperature, and does not assume copepod growth is limited by food availability (e.g., phytoplankton or chlorophyll-a concentrations) at different times of year. While temperature may be one of the principal abiotic factors limiting copepod development (given their ectothermal characteristics) in subtropical estuaries, where temperatures are high throughout the year, models that consider only this variable may overestimate growth rates (Calbet and Agustí, 1999).

Variables such as temperature, body weight, and feeding adaptations have been increasingly considered to be the most important factors in the regulation of secondary production, as well as the production of eggs by female copepods (Hirst and Bunker, 2003; Bunker and Hirst, 2004), in tropical oligotrophic ecosystems (Satapoomin et al., 2004) and few studies have tested the Hirst and Bunker (2003) model in tropical or subtropical environments. In the present study, the rates of growth and secondary production estimated for *A. tonsa* and *A. lilljeborgi* were relatively high in comparison with other studies in tropical, subtropical, and temperate environments, based on different models (e.g., Ara, 2001; 2004; Leandro et al., 2007; Muxagata et al., 2012; Magalhães et al., 2013). This high productivity may be related to the constant temperature, availability of food typical of Amazon estuaries, even though seasonal variation is often found.

Acartia tonsa is considered to be omnivorous, and thus capable of surviving and reproducing on different diets (Saiz et al., 2007). In a laboratory experiment, Teixeira et al. (2010) recorded a higher production of eggs by *A. tonsa* when fed on *Thalassiosira weissflogii* than with other species of microalga. The relative abundance of food (phytoplankton, suspended organic matter, microzooplankton, etc.) in the Taperaçu Estuary may account for the high production observed in stage C4 of *A. tonsa* throughout the study period, given that, given the dimensions of this stage, the dimensional trophic spectrum may be more ample than that observed in the adults. While no significant correlation was found between the production rates of either *A. tonsa* or *A. lilljeborgi* and the chlorophyll-a concentrations, the highest values were obtained from the model that includes this variable (Hirst and Bunker, 2003). This emphasizes the importance of feeding resources for the rates of growth and secondary production in the study acartiids, despite their being recognized as omnivores.

The production rates recorded in the Taperaçu Estuary in the present study were similar to or higher than those recorded in the port of Kingston, Jamaica (22.1 mg.Dw.m^{-3}.d^{-1} and 14.74 mg mg.Dw.m^{-3}.d^{-1}, Hopcroft et al., 1998), in the temperate ria of Aveiro, in Portugal (minimum: 0.96 and maximum: 5.65 mgC.m^{-3}.d^{-1}, Leandro et al., 2006) and the lagoon-estuarine system of Cananéia, Brazil (minimum: 1.76 and maximum: 2.31 mgCm^{-3} .d^{-1}). The values were also higher than those recorded in previous studies in the Taperaçu it self (Magalhães et al., 2012), which focused only on the adults of the two study species.

In most cases, the considerable differences in the procedures used in studies of the production of *Acartia* species tend to limit or impede reliable comparisons. These differences include the geographic region, sampling frequency, mesh size, and type of plankton net, as well as the analytical approaches used to define estimates of biomass and production. In this context, the present study is the first to estimate the role of the different copepodite juvenile stages (C1-C5) and the male and female adults (C6) of Amazonian acartiids. This approach revealed that the highest abundance, biomass, and production in *A. tonsa* were found in the immature stages (C1-C5), whereas in *A. lilljeborgi*, the highest values were recorded for the adults, even using plankton nets with a 200 µm mesh. The biomass and production of copepods in tropical and subtropical have traditionally been considered to be lower than those of temperate and sub-boreal waters during the summer (Durbin and Durbin, 1981; Uye and Liang, 1998).

5. CONCLUSIONS

The present study nevertheless indicates that, even taking into account the possibility that biological variables, such as abundance, biomass, and production, may be underestimated due to the mesh size of the nets used to collect samples, the biomass and productivity in equatorial mangrove estuaries may be relatively high in comparison with the levels observed in other lagoon, estuarine and neritic systems around the world. This high productivity can be attributed to the relatively high temperatures observed in the study area throughout the year (Magalhães et al., 2015), as well as the presence of waters rich in particulate organic material derived from the mangroves adjacent to the study estuary. This material is consumed by a number of copepod species, in particular *A. tonsa* and *A. lilljeborgi*, which are characterized by high rates of productivity in the study estuary.

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CONSIDERAÇÕES FINAIS

1. CONCLUSÕES GERAIS

Esta tese enfocou questões importantes relacionados a dinâmica da comunidade zooplanctônica (abundância, diversidade e equitabilidade) e biomassa e produção secundária das principais espécies de copépodos no estuário do Taperaçu. A primeira questão levantada foi: ***como o ciclo circadiano e os períodos de maré afetam a dinâmica da comunidade zooplanctônica no estuário do Taperaçu?***

Com base nos resultados apresentados no Capítulo II, observou-se que as características morfológicas e morfodinâmicas do estuário do Taperaçu, tais como as baixas profundidades, as fortes correntes de maré e a ausência de descarga fluvial influenciaram as oscilações das variáveis hidrológicas e a dinâmica do zooplâncton, principalmente a população de copépodos. De forma geral, a comunidade zooplanctônica esteve caracterizada por uma relativa homogeneidade, muito embora, a abundância das principais espécies registradas (*Acartia tonsa*, *Paracalanus quasimodo*, *Labidocera fluviatilis* e *Pseudodiaptmus marshi*) tenha variado sistematicamente com relação aos períodos de maré enchente e vazante. Estas variações estiveram diretamente relacionadas as variações da salinidade, associadas ao recrutamento de organismos do estuário Caeté para o Taperaçu, através do canal do Taici.

No que concerne a abordagem relacionada ***aos efeitos da precipitação sobre a abundância, diversidade específica e a equitabilidade das espécies zooplanctônicas no estuário do Taperaçu e as correlações destas com as variáveis ambientais*** (segundo tópico estudado na tese), os resultados apresentados no Capítulo III demonstraram que a variabilidade do mesozooplâncton nas escalas espacial e temporal estiveram diretamente relacionadas aos períodos sazonais (seco/chuvoso) e as variações da salinidade, turbidez e concentrações de clorofila-a.

Durante todo o período de estudo os copépodos constituíram os organismos mais abundantes dentro da comunidade zooplanctônica. Os resultados também demonstraram que as espécies onívoras *A. tonsa* e *A. lilljeborgi* se correlacionaram negativamente com as concentrações de clorofila-a e positivamente com a turbidez, permitindo a coexistência destas espécies e diminuindo a competição intraespecífica por recursos alimentares, uma vez que estas espécies não apresentaram uma sucessão ecológica evidente, como sugerido em estudos anteriores.

A redução das chuvas no ano de estudo (2012) ocasionou um aumento significativo da salinidade, tornando o ecossistema em estudo favorável a ocorrência de espécies tipicamente marinhas, tais como *P. quasimodo* e *Oikopleura dioica*. Os resultados obtidos indicam que a influência das variações climáticas sobre as variáveis hidrológicas, em especial a salinidade, foram responsáveis pela ocorrência e distribuição das espécies mesozooplanctônicas identificadas no estuário do Taperaçu.

Considerando a aplicação de modelos empíricos de crescimento das principais espécies de copépodes do estuário do Taperaçu, terceiro aspecto abordado no presente estudo, foram avaliados ***os efeitos, em escala temporal e espacial, das variáveis ambientais sobre a abundância, biomassa e produção secundária de copepoditos e adultos (machos e fêmeas) de*** *Acartia tonsa* ***e*** *A. lilljeborgi*. Com base nos resultados apresentados no capítulo IV, constatou-se que *A. tonsa* apresentou elevadas abundâncias durante todo o período de estudo, muito embora esta espécie tenha sido previamente registrada para o ecossistema em questão durante o período chuvoso. As abundâncias de *A. lilljeborgi*, por sua vez, seguiram os padrões outrora observados para o referido estuário, com maiores abundâncias obtidas durante os períodos de menor pluviosidade (período seco).

A partir dos resultados obtidos neste trabalho, foi possível evidenciar elevados valores de abundância, biomassa e produção dos estágios imaturos de *A. tonsa,* e dos adultos de *A. lilljeborgi*. As taxas de produção registrados no presente estudo foram semelhantes ou mais elevadas que àquelas descritas na literatura para as mesmas espécies em outros estuários do mundo. Os elevados valores de biomassa e produção obtidos devem estar relacionados às elevadas temperaturas observadas durante todo o ano, e as elevadas concentrações de matéria orgânica (particulada e dissolvida) observadas no Taperaçu, os quais são em sua maioria originários das florestas de mangue adjacentes a estuário e servem de alimento para ambas as espécies.

As estimativas de produtividade secundária podem também diferir de acordo com o método utilizado nos cálculos da taxa instantânea de crescimento (*g*). No presente estudo, estas estimativas foram calculadas utilizando-se o modelo global de Hirst e Sheader (1997) e de Hirst e Bunker (2003), nos quais as taxas de crescimento são dependentes do peso do corpo e da temperatura; e da temperatura, peso corporal e concentrações de clorofila-a, respectivamente

As estimativas de produção para os copepoditos e adultos de *A. tonsa* e *A. lilljeborgi* apresentadas neste estudo foram as primeiras a serem realizadas para ambientes estuarinos da costa norte do Brasil e evidenciou o importante papel destas espécies na transferência de carbono e energia dos produtores primários aos níveis tróficos superiores.

Com base no conjunto dos resultados obtidos, chegamos as seguintes conclusões:

1. O estuário do Taperaçu apresenta um conjunto de características morfológicas e morfodinâmicas que influenciaram a distribuição espacial e temporal (em diferentes escalas) das espécies zooplanctônicas locais;

2. Não foram evidenciadas a influência dos períodos do dia e noite sobre a comunidade zooplanctônica, devido as baixas profundidades e hidrodinâmica local;

3. Os períodos de maré (enchente/vazante), associados às variações de salinidade influenciaram a distribuição e a ocorrência de espécies de copépodos no estuário do Taperaçu;

4. As oscilações na precipitação pluviométrica, em conjunto com as oscilações da salinidade, turbidez e as concentrações de clorofila-a, controlaram a variabilidade do mesozooplâncton no estuário do Taperaçu;

5. No que concerne às variáveis ambientais e a dinâmica da comunidade zooplanctônica, o estuário do Taperaçu apresenta uma considerável diferença entre as estações amostradas (S1, S2 e S3) no presente estudo;

6. Os comprimentos dos prossomas de *A. tonsa* e *A. lilljeborgi* registrados no presente estudo foram maiores que àqueles observados em outros ecossistemas estuarinos do mundo, estando tal fato, possivelmente

relacionados à elevada disponibilidade de alimento observada tanto durante o período seco quanto durante o período chuvoso.

7. As estimativas de produção das formas imaturas (C1-C5) de *A. tonsa*, registradas nesta tese foram superiores às obtidas para as formas adultas, muito embora a abertura de malha de rede utilizada não seja a mais propícia para estimativas de biomassa e produção dos estágios iniciais de desenvolvimento das espécies estudadas.

8. As taxas de biomassa e produção encontradas no estuário do Taperaçu, foram mais elevadas que às descritas para outros estuários do mundo, sendo os elevados valores observados atribuídos, possivelmente, às altas temperaturas e às elevadas concetraçnoes de material particulado em suspensão.

9. No estuário do Taperaçu, a variabilidade espacial, mensal e sazonal observada na estrutura e dinâmica populacional do zooplâncton esteve principalmente relacionada às flutuações nas taxas de precipitação, as quais afetaram diretamente a salinidade da água, e consequentemente, a abundância, biomassa e produção destes organismos.