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DEPARTAMENTO DE OCEANOGRAFIA  
PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA

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**DIVERSIDADE E VARIAÇÃO ESPACIAL DE DECÁPODES PLANCTÔNICOS  
DA RETROFLEXÃO E PLUMA DO RIO AMAZONAS, BRASIL**

Recife  
2019

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Dissertação apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de mestre em oceanografia.

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**Orientador:** Prof<sup>o</sup>. Dr. Ralf Schwamborn

**Coorientadora:** Dr<sup>a</sup>. Simone Maria de Albuquerque Lira

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Aprovada em 27 de fevereiro de 2019.

**BANCA EXAMINADORA**

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## RESUMO

No presente estudo o efeito dos fatores espacial e turno, foram testados com o objetivo de descrever o gradiente costa-oceano para a abundância, diversidade e composição da comunidade de decápodes planctônicos ao longo da Pluma do Rio Amazonas (ARP) e retroflexão da Corrente Norte do Brasil (CNB). Para isso, 33 amostras planctônicas foram obtidas através de arrastos oblíquos, em rede Bongô (300 µm), durante o cruzeiro oceanográfico Camadas Finas III (outubro/novembro, 2012), em três transectos definidos de acordo com a influência da ARP: Região costeira influenciada pela ARP (**Coastal IARP**); Região oceânica influenciada pela ARP (**Ocean IARP**) e Região oceânica sem a influência da ARP (**Ocean**). Um total de 13.117 espécimes, pertencentes a 33 táxons, foram registrados. Os táxons mais abundantes foram: Brachyura (zoeae), Luciferidae (larvas e adultos), Callianassidae (zoeae) e Palaemonidae (zoeae). A análise total das amostras planctônicas propiciou o registro de táxons considerados raros: Enoplometopidae; *Anphionides reynaudii*; Aristeidae, ampliando a ocorrência desses táxons no Atlântico tropical. A diversidade, abundância e composição da comunidade de decápodes planctônicos foram fortemente influenciadas pela descarga do rio Amazonas, distância da costa e por processos hidrográficos relacionados à retroflexão da CNB e ARP. O gradiente costa-oceano para a abundância e diversidade apresentou uma tendência similar a outras regiões costeiras, da parte oriental da América do Sul. Porém, as proporções de abundância na área oceânica adjacente a costa foi maior do que em outras áreas oceânicas tropicais devido ao transporte *offshore* de organismos e enriquecimento planctônico causado pela retroflexão da CNB e ARP. Devido a isso, uma maior contribuição de decápodes meroplanctônicos originados do suprimento larval de organismos bentônicos e holopelágicos associados a ambientes da costa, plataforma continental e talude, principalmente zoeas de Brachyura e larvas e adultos de camarões Luciferidae, foram registrados para os transectos sob a influência da pluma. Como esperado, áreas oceânicas sem a influência da ARP, foram predominantemente dominadas por táxons holopelágicos caracteristicamente oceânicos. Dessa forma, a presente dissertação confirma a importância de ambientes costeiros e da plataforma continental como áreas de estoques parentais de decápodes planctônicos para ecossistemas pelágicos da Plataforma Norte do Brasil e área oceânica adjacente.

Palavras chave: Larvas de crustáceos. Distribuição em mesoescala. Camadas finas III. Ambientes tropicais. Oceano Atlântico ocidental.

## ABSTRACT

In the present study the effect of the spatial factors (coastal and oceanic areas influenced by Amazon River Plume and oceanic area without this influence) and time of day factor (day vs. night) were tested to describe the coastal-oceanic gradient in abundance, diversity and composition of planktonic decapods assemblages along the Amazon River Plume (ARP) continuum and North Brazil Current (NBC) retroflection. In this regard, 33 planktonic samples were obtained through oblique hauls, with bongo net (300  $\mu\text{m}$ ), during the “Camadas Finas III” oceanographic cruise (October/November, 2012), on three sampling transects according the ARP influence: Coastal and shelf areas influenced by the ARP (**Coastal IARP**); Oceanic waters influenced by the ARP (**Ocean IARP**) and Oceanic waters without ARP influence (**Ocean**). A total of 13,117 specimens belonging to 33 taxa were recorded. The most abundant taxa were: Brachyura (zoeae), Luciferidae (larvae and adults), Callinassidae (zoeae) and Palaemonidae (zoeae). The total analyses of the planktonic samples allowed the record of rare oceanic larvae taxa: Enoplometopidae; *Anphionides reynaudii* and Aristeidae, increasing the occurrence of these taxa within the tropical Atlantic. The composition, diversity and abundance of planktonic decapods community were strongly influenced by the Amazon River runoff, coast distance and oceanographic processes related to the retroflection of NBC and ARP. The coastal-oceanic gradient of abundance and diversity presented a similar trend to other coastal regions in Eastern South America shelf. However, due to ARP influence offshore, higher abundance proportions were found in the oceanic adjacent area when compared to others shelves adjacent to oceanic areas in Tropical Atlantic. A great abundance of meroplanktonic decapods from larval supply of benthic and holopelagic organisms related to coastal, continental shelf and slope environments, were recorded to the transects under the ARP influence (mainly Brachyura zoeae and larvae and adults of Luciferidae shrimps), as a result of the coast-related organisms transport along the ARP. Oceanic areas without the ARP influence predominantly dominated by holopelagic organisms. Furthermore, this M. Sc. thesis highlights the importance of coastal and shelf environments as a parental stock of planktonic decapods for pelagic ecosystems at the North Brazilian shelf and adjacent oceanic areas.

Keywords: Crustacean larvae. mesoscale distribution. “Camadas finas III” project. Tropical environments. Western Tropical Atlantic.

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## LISTA DE ABREVIATURAS E SIGLAS

|              |                                                                                                  |
|--------------|--------------------------------------------------------------------------------------------------|
| Af           | fully humid                                                                                      |
| Am           | equatorial monsoon                                                                               |
| ARP          | Amazon River Plume                                                                               |
| CCNE         | Contracorrente Norte Equatorial                                                                  |
| CNB          | Corrente Norte do Brasil                                                                         |
| COADS        | Comprehensive Ocean Atmosphere Dataset 2005                                                      |
| Coastal IARP | Região costeira influenciada pela ARP - <i>coastal area influenced by the Amazon River Plume</i> |
| $d$          | Margalef species richness index                                                                  |
| DCN          | chlorophyll maximum layer                                                                        |
| DOC          | Dissolved Organic Carbon                                                                         |
| FO           | Frequency of occurrence                                                                          |
| $H'$         | Shannon diversity index                                                                          |
| IndVal       | Indicator Value                                                                                  |
| ITCZ         | Intertropical Convergence Zone                                                                   |
| $J'$         | Pielou evenness                                                                                  |
| Max          | maximum abundance                                                                                |
| MDS          | multi-dimensional scaling                                                                        |
| MN           | milhas náuticas                                                                                  |
| N            | Norte                                                                                            |
| NBC          | North Brazil Current                                                                             |
| NECC         | North Equatorial Countercurrent                                                                  |
| nMDS         | Non-metric multidimensional scaling ordination                                                   |

|            |                                                                                                        |
|------------|--------------------------------------------------------------------------------------------------------|
| Ocean IARP | Região Oceânica influenciada pela ARP - <i>oceanic area influenced by the Amazon River Plume</i>       |
| Ocean      | Região oceânica sem a influência da ARP - <i>oceanic area not influenced by the Amazon River Plume</i> |
| AP         | Amapá                                                                                                  |
| PERMANOVA  | Anova Permutacional                                                                                    |
| RA         | Relative abundance                                                                                     |
| RDA        | Redundancy Analyses                                                                                    |
| ROMS       | Regional Ocean Modeling System                                                                         |
| SD         | Standard Deviation                                                                                     |
| SSS        | Sea Surface Salinity                                                                                   |
| SST        | Sea Surface temperature                                                                                |
| WOA        | World Ocean Atlas                                                                                      |
| WTA        | Western Tropical Atlantic                                                                              |
| WTNA       | Western Tropical North Atlantic                                                                        |
| ZCI        | Zona de Convergência Intertropical                                                                     |
| ZEE        | Zona Econômica Exclusiva                                                                               |

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## 1 INTRODUÇÃO

O zooplâncton corresponde à parcela animal do plâncton (equinodermos, briozoários, ctenóforos, cnidários, rotíferos, anelídeos, moluscos, quetognatos, crustáceos, cordados, entre outros), seres heterótrofos, de pouca capacidade de locomoção, que desempenham um importante papel no transporte de energia, sendo relevantes na transferência de carbono por servirem como elo trófico entre os produtores primários e consumidores ao longo da cadeia alimentar marinha (BOLTOVSKOY, 1981; BRANDINI et al., 1997; BOLTOVSKOY et al., 1999; SCHWAMBORN et al., 1999b). De acordo com o ciclo de vida, pode-se classificar o zooplâncton em holoplâncton e meroplâncton. O holoplâncton corresponde aos organismos que permanecem no plâncton durante todo seu desenvolvimento, enquanto que são classificados como meroplâncton, aqueles que passam apenas parte do seu ciclo no plâncton, a exemplo das larvas e juvenis de organismos do bentos e pélagos (BRANDINI et al., 1997). Ainda pode-se classificar o plâncton de acordo com seu tamanho em Microplâncton (20-200 µm), Mesoplâncton (0,2-20 mm), Macroplâncton (2-20 cm) e Megaloplâncton (20-200 cm) (SIEBURTH et al., 1978).

A ordem Decapoda é um dos grupos mais diversos dentre os crustáceos, sendo constituído por 10 infraordens, 233 famílias e mais de 18 mil espécies descritas (DE GRAVE et al., 2009; MARTIN et al., 2014). Seus integrantes são popularmente conhecidos em sua forma adulta (lagostas, camarões e caranguejos), devido à importância econômica que apresentam (DE GRAVE et al., 2009). A grande maioria dos decápodes estuarinos e marinhos apresenta um desenvolvimento larval planctônico, constituindo uma parcela importante do mesozooplâncton, o que possibilita uma maior dispersão, e permite um maior fluxo gênico entre as populações da mesma espécie, diminuindo a competição de espaço e a taxa de predação dos jovens (MCCONAUGHA, 1992; KOETTKER & FREIRE, 2006; LANDEIRA et al., 2009). Em ambientes costeiros tropicais, a contribuição de decápodes meroplanctônicos é expressiva, em decorrência de organismos bentônicos que liberam seus ovos/larvas durante todo o ano (SCHWAMBORN et al., 1999), enquanto que em regiões oceânicas ocorre uma maior representatividade de decápodes holoplanctônicos (BOLTOVSKOY, 1981; JUDKINS, 2014).

Devido às diferenças na estrutura da cadeia trófica marinha entre os ambientes costeiros e oceânicos, é observado um padrão típico no gradiente nerítico-oceano para a

diversidade e abundância do zooplâncton (LOPES et al., 2006). As águas superficiais (0-100m) do Oceano Atlântico Tropical são categorizadas como oligotróficas por apresentarem uma baixa quantidade de nutrientes, em consequência disso, apresentam uma baixa biomassa de organismos planctônicos e uma maior diversidade, devido a maior complexidade da teia trófica, quando comparadas à região costeira, ambientes tipicamente mesotróficos, com uma maior biomassa e menor diversidade zooplanctônica (BOLTOVSKOY et al., 1999; SCHWAMBORN et al., 1999b; LOPES et al., 2006).

Padrões nos gradientes de diversidade e abundância podem ser alterados por fenômenos que modifiquem a dinâmica físico-químicas local (temperatura, salinidade, disponibilidade de luz e nutrientes), como ressurgências e grandes descargas fluviais, tal qual a do rio Amazonas (VALENTIN, 1984; GONZALEZ-RODRIGUEZ et al., 1992; CONROY et al., 2016b; NEUMANN-LEITÃO et al., 2018). Entender esses padrões é de extrema importância para se compreender a dinâmica larval dos decápodes planctônicos, uma vez que esses processos influenciam diretamente na sua distribuição (TEMPLEMAN, 1936; ANGER, 2001; LANDEIRA et al., 2009; LANDEIRA et al., 2010; MARTIN et al., 2014; CASTEJÓN et al., 2018).

O rio Amazonas apresenta uma grande pluma que se estende a partir de sua foz, durante a primeira parte do ano (janeiro a maio) suas águas são dispersadas para noroeste, em direção ao Mar do Caribe. Essas regiões sob a influência da pluma são descritas como áreas que possuem águas turvas e lençóis *offshore* de baixa salinidade (menores que 35) (MULLER-KARGER et al., 1988; LENTZ, 1995; MULLER-KARGER et al., 1995; LENTZ, 1995b). No segundo semestre do ano, de junho a dezembro, a influência do rio Amazonas na região oceânica é aumentada significativamente, devido à retroflexão oceânica da Corrente Norte do Brasil (CNB), que leva a pluma para leste, em direção à África (MULLER-KARGER et al., 1988; LENTZ, 1995b). Essa retroflexão está situada entre 5 e 10°N, sendo caracterizada por uma curvatura acentuada descendo para sudeste e depois seguindo para leste. Essa curvatura ocorre devido o fluxo da CNB se direcionar além da latitude de fluxo da Contracorrente Norte Equatorial (CCNE), que está situada um pouco mais ao sul (MULLER-KARGER et al., 1988; MULLER-KARGER et al., 1995).

A maior parte dos estudos desenvolvidos na região da foz da Bacia Amazônica e área oceânica adjacente visam à questão da produtividade, sobretudo primária do plâncton, por exemplo, os estudos realizados por: Carpenter et al. (1999), Subramaniam

et al. (2008), Goes et al. (2014) e Santos et al. (2008). Estudos com ênfase na comunidade zooplanctônica ainda são escassos (e.g. DAHL, 1891; JACOB et al., 1966; BJÖRNBERG & CAMPANER, 1990; COSTA et al., 2008; PALMA et al., 2013; CONROY et al., 2016a; CONROY et al., 2016b; ARAUJO et al., 2017; NEUMANN-LEITÃO et al., 2018), sobretudo aqueles com ênfase em decápodes planctônicos (e.g. MARQUES, 2009; CAVALCANTE et al., 2012; DE OLIVEIRA et al., 2012; CARVALHO et al., 2013; NÓBREGA et al., 2014), restringindo-se a região costeira e estuarina, sendo poucos voltados para a região oceânica próxima ao talude (CALEF & GRICE, 1967; MELO, 2004; MELO et al., 2014; CONROY, 2016). Estudos sobre decápodes planctônicos na região da foz do rio Amazonas indicaram que o gradiente costa-oceano, em termos de abundância, diminui significativamente em direção a região oceânica, com as maiores valores registradas na região nerítica, como verificado para *Belzebub faxoni* (MELO et al., 2014), que assim como outros decápodes planctônicos, apresentam grandes abundâncias para regiões de baixa salinidade da plataforma norte do Brasil e região oceânica adjacente (JACOB et al., 1966; CALEF & GRICE, 1967; CONROY, 2016).

Por vezes, a contribuição de decápodes no plâncton é maior que a de Copepoda (MCCONAUGHA, 1992; SCHWAMBORN et al., 1999b; DÍAZ et al., 2009; CONROY et al., 2016a), demonstrando o potencial desses organismos na transferência de carbono na teia trófica marinha. Como a pluma do rio Amazonas se apresenta como uma das maiores bombas de carbono marinha do planeta (TERNON et al., 2000; HU et al., 2004), entender a estrutura dessa comunidade biológica se torna uma necessidade primária para a compreensão da dinâmica zooplanctônica na região ocidental do Atlântico tropical.

Nesse estudo foi realizada a primeira descrição detalhada para a comunidade de decápodes planctônicos, abordando a composição e variação espacial desses organismos na região costeira, margem continental e região oceânica influenciadas pela retroflexão da CNB e pluma do rio Amazonas.

### **Hipóteses da dissertação**

- Existe uma maior abundância e diversidade de decápodes planctônicos na região costeira e oceânica influenciada pela pluma do rio Amazonas em relação à área não influenciada pela mesma;
- Existe uma maior contribuição, em termos de abundância, da parcela de decápodes meroplanctônicos (Brachyura, Achelata, Caridea e Anomura) para a comunidade

zooplancônica da plataforma continental devido à contribuição de organismos bentônicos locais e larvas exportadas de ambientes costeiros;

- Existe uma maior contribuição, em termos de composição taxonômica, da parcela de decápodes holopelágicos (Sergestidae, Penaeidae) para a região oceânica;

## 2 OBJETIVO

Verificar os gradientes neríticos-oceânicos para a abundância, composição e diversidade dos decápodes planctônicos ao longo da retroflexão da Corrente Norte do Brasil e pluma do rio Amazonas.

### 2.1 OBJETIVOS ESPECÍFICOS

- Identificar e quantificar os decápodes planctônicos da região costeira, talude continental e região oceânica sob a influência da retroflexão e pluma do rio Amazonas
- Identificar e quantificar os decápodes planctônicos da região oceânica sem a influência direta da pluma do Rio Amazonas
- Verificar a estrutura da comunidade de Decapoda planctônicos da região costeira e região oceânica influenciada e não influenciada pela pluma do rio Amazonas
- Comparar e analisar a distribuição da comunidade de Decapoda planctônicos entre a região influenciada pela pluma do rio Amazonas (transecto Costal IARP e Ocean IARP) e a região que não sofre a influência direta da pluma (transecto Ocean)
- Verificar a influência de processos em hidrológicos em mesoescala (vórtices e correntes superficiais), na comunidade de decápodes planctônicos

### 3 DESCRIÇÃO DA ÁREA DE ESTUDO

A área de estudo está localizada nas regiões Norte (Pará e Amapá) e Nordeste (Ceará) do Brasil, em parte contida na Zona Econômica Exclusiva (ZEE) que abrange a coluna d'água da plataforma, talude continental e a parte oceânica, desde o limite das 12 milhas náuticas (MN) do mar territorial brasileiro até o contorno, distando 200 MN da linha de costa do Brasil. A partir deste limite, os pontos de amostragem se localizam em águas internacionais. As coletas iniciaram-se na baía do Marajó, na região central em frente da foz do rio Pará, se direcionando a norte até as proximidades do Cabo Orange-AP (extremo norte do Brasil), seguindo para região oceânica e por fim retornando a costa brasileira na cidade de Fortaleza-CE (Figura 1). A área de estudo é influenciada pela pluma do rio Amazonas, que é uma camada hipossalina considera rasa, que possui entre cinco e vinte e cinco metros de profundidade, e se desloca em direção norte por influência de ventos sazonais e correntes superficiais.

O rio Amazonas possui umas das maiores bacias hidrográficas do mundo. Sua descarga de água doce no mar é consideravelmente maior do que a de qualquer outro rio do planeta e apresenta cerca de  $206\,000\text{ m}^3\text{ s}^{-1}$  de descarga para a parte ocidental do Oceano Atlântico Tropical (CALLÈDE et al., 2010; GOES et al., 2014). Esse *input* equivale a mais de 17% de toda a entrada de água doce nos oceanos, descarregando no mar grandes quantidades de sedimento, nutrientes, partículas e matéria orgânica dissolvida colorida (DEL VECCHIO & SUBRAMANIAM, 2004; SUBRAMANIAM et al., 2008; MILOSLAVICH et al., 2011).

As águas do rio Amazonas são transportadas por milhares de quilômetros da região costeira por plumas de superfície, que no segundo semestre do ano (julho a novembro), sofre uma imensa retroflexão oceânica, na qual nutrientes inorgânicos transportados (especialmente fósforo e silicato) facilitam a ocorrência de florações de fitoplâncton, principalmente diatomáceas e cianobactérias diazotróficas simbiotes. Esses organismos, por sua vez, apresentam-se como principais responsáveis pela fixação de carbono e nitrogênio atmosférico numa área de aproximadamente um milhão de quilômetros quadrados, criando assim, a maior bomba marinha de carbono do planeta (DEL VECCHIO & SUBRAMANIAM, 2004; SUBRAMANIAM et al., 2008; CHONG et al., 2014).

A plataforma norte do Brasil é considerada um ambiente marinho único, segundo Fontes et al. (2008), por estar sujeita a uma série de processos hidrodinâmicos complexos relacionados a sua enorme descarga fluvial, influência de marés e ventos alísios, juntamente com a presença da Corrente Norte do Brasil. A CNB é uma forte corrente de

limite ocidental de baixa latitude, que sofre uma retroflexão entre 5-10°N durante o verão e outono do hemisfério norte em decorrência principalmente da mudança no padrão de ventos. Na primavera existe a predominância de ventos alísios de nordeste enquanto que no outono predominam os ventos alísios de sudeste (FRATANTONI & RICHARDSON, 2006).

A mudança no padrão de ventos ocorre em decorrência da migração sazonal da zona de convergência intertropical (ZCIT). Quando a ZCIT se localiza mais ao norte de 3°N (agosto e setembro), ocorre uma predominância dos ventos alísios de sudeste, como as correntes locais são correntes de giros geostroficos, a água se movimenta contra o gradiente de pressão e também devido ao transporte de Ekman que a direciona para a direita em relação à posição dos ventos. Assim, a água é defletida para nordeste, alimentando a Contra Corrente Norte Equatorial que flui para leste (PHILANDER & PACANOWSKI, 1986; LENTZ, 1995; 1995b; STRAMMA et al., 2005; GARRISON, 2012).

Nos meses de março e abril a ZCIT está localizada mais próxima ao equador, e na região da Foz do Amazonas e parte norte da plataforma norte do Brasil, predominam os ventos de noroeste (PHILANDER & PACANOWSKI, 1986). Com o enfraquecimento da retroflexão, durante o inverno e primavera boreal, o fluxo da pluma do rio Amazonas em direção ao Mar do Caribe ganha mais força (LENTZ, 1995; 1995b).

Vale salientar que a retroflexão oceânica da CNB e consequentemente da pluma do rio Amazonas, é um processo complexo e outros fatores como o aumento do fluxo de descarga do rio no final de maio e começo de março, bem como o maior fluxo da CNB nos meses de julho a dezembro (CSANADY, 1985); e, a presença de vórtices “de vida longa” na área, que se movem para noroeste (JOHNS et al., 1990; HU et al., 2004), influenciam diretamente nesse fenômeno oceanográfico. Além disso, todos os mecanismos que o causam, ainda não são completamente esclarecidos.

#### 4 PLANKTONIC DECAPODS OF THE AMAZON RIVER PLUME AND RETROFLECTION

##### ABSTRACT

The Western Tropical Atlantic is strongly influenced by the Amazon, receiving all the discharge from the largest hydrographic basin of the world. The oceanic retroflection of the Amazon River Plume (ARP) enhances planktonic productivity in offshore oligotrophic waters through the input of nutrients, but may also convey zooplankton from coastal areas, such as decapod crustacean larvae and holoplanktonic shrimps. In order to ascertain the coastal-oceanic gradient in abundance, diversity and composition of planktonic decapod communities along the ARP and retroflection, 33 plankton samples were obtained through oblique hauls with a Bongo net (300 µm mesh size) along three sampling transects: Coastal and shelf areas influenced by the ARP (**Coastal IARP**); Oceanic waters influenced by the ARP (**Ocean IARP**) and Oceanic waters without ARP influence (**Ocean**). Sampling occurred during the ‘Camadas Finas III’ cruise, from October to November 2012, when the ARP extends far eastward. A total of 13,117 specimens, belonging to 33 taxa, were registered. The most abundant taxa were: *Brachyura* (zoeae), *Luciferidae* (larvae and adults), *Callinassidae* (zoeae) and *Palaemonidae* (zoeae). The distribution of planktonic decapod communities was strongly influenced by the Amazon discharge, showing the following patterns: (1) The coastal-oceanic gradients in decapod abundance and diversity are similar to other shelf areas of South America, but the proportions of abundance are much larger in the ARP influence area; (2) Meroplanktonic decapods dominate in abundance in coastal and some oceanic areas due to the transport of coast-related organisms along the ARP; and (3) The ARP is clearly responsible for the differences in community structure between the three transects. Furthermore, greater abundances of planktonic decapods were related to meso-scale processes (eddies and CNB retroflection). This study highlights the importance of coastal and shelf environments as sources of planktonic decapods for pelagic ecosystems at the North Brazilian shelf and adjacent oceanic areas.

**Key words:** Crustacean larvae; Mesoscale distribution; “Camadas Finas III” project; Amazon River-Ocean Continuum, Tropical environments.

## INTRODUCTION

The discharges of large tropical rivers have a great influence on adjacent coastal waters due to the transference of sediments from the continent, changes in nutrient dynamics and input of organic matter and freshwater. All these mechanisms together can change the physical-chemical parameters and consequently the biological community of coastal marine environments (NIXON et al., 1986; MEADE, 1996; DAGG et al., 2004; WU et al., 2017).

The Amazon River basin, world's largest hydrographic basin, enriches not only the coastal area, but also the adjacent oceanic region of the retroflexion of the North Brazilian Current (NBC) through complex interrelated hydrological processes that transport the Amazon buoyant riverine plume. The NBC retroflexion is associated with changes in trade wind patterns (dominance of southeastward trades), migration of the Intertropical Convergence Zone (ITCZ) and geostrophic gyres, jointly with the period of major discharge in Amazon River mouth and more intense flow of NBC (CSANADY, 1985; LENTZ, 1995; 1995b). As the wind stress changes, it can reduce or revert the northwestward Amazon River Plume (ARP) waters flow, creating an eastward water flow that feeds the North Equatorial Countercurrent (NECC) along the Western Tropical Atlantic (WTA) (BUSALACCHI & PICAUT, 1983; PHILANDER & PACANOWSKI, 1986).

These complex current dynamics generate a series of anticyclonic eddies ranging from 400 to 500 km diameter which are displaced northwestwards and are responsible for part of the water mass transport between South and North Atlantic Ocean (JOHNS et al., 1990; HU et al., 2004). Upwelling events associated with anticyclonic eddies as well inshore area of the retroflexion (MULLER-KARGER et al., 1988; WOODS, 1988), can increment the nutrient supply in the ARP, favoring the occurrence of phytoplankton blooms and consequently the increase in the productivity of the zooplankton community (MULLER-KARGER et al., 1995; CARPENTER et al., 1999; SUBRAMANIAM et al., 2008; GOES et al., 2014; CONROY et al., 2016b).

One of the planktonic assemblages that deserves prominence in regions with estuarine influence are the decapods. This group of organisms are component of a significant portion of the zooplankton community in tropical marine environments, mostly in coastal areas with the presence of large mangrove forests, such as on the north Brazilian shelf. In these environments the exportation of decapod larvae from

mangroves to open shelf is significant, since these habitats act as nurseries for larvae of several species of brachyuran and anomuran crabs, shrimps and mud shrimps (SCHWAMBORN et al., 1999b; KATHIRESAN & BINGHAM, 2001). Thus, contributing to a greater abundance of meroplanktonic decapods in the shelf area. However, previous studies at the north Brazilian shelf influenced by the ARP, and NBC retroflection indicated a dominance on abundance of holoplanktonic decapods, mainly represented by shrimps of the families Luciferidae and Sergestidae (MELO et al., 2014; CONROY et al., 2016b; NEUMANN-LEITÃO et al., 2018). However, the dominance of holoplanktonic decapods is commonly related to oceanic areas (JUDKINS, 2014).

Hydrological process in micro and mesoscale such as eddies and fronts, are described by many studies as important events influencing the abundance enhance, dispersion and retention of decapods larvae (MCCONAUGHA, 1992; EPIFANIO & GARVINE, 2001; QUEIROGA & BLANTON, 2005; LANDEIRA et al., 2009; LANDEIRA et al., 2010). These hydrological processes act directly on abundance and distribution of planktonic community and are potential factors to cause disturbances on coastal-oceanic gradient of plankton distribution, which are typical of tropical Western Atlantic regions. Usually, these gradients in distribution show higher abundance values and lower diversity values in coastal mesotrophic areas, while the opposite occur in oligotrophic oceanic area (BOLTOVSKOY et al., 1999; LOPES et al., 2006).

The coastal-oceanic gradient of planktonic decapods abundance at the area influenced by the ARP decrease substantially towards the oceanic area, as observed by Melo et al. (2014) for luciferid shrimps. Other surveys about this group were performed in the study area by Marques (2009), Cavalcante et al. (2012), De Oliveira et al. (2012), Carvalho et al. (2013) and Nóbrega et al. (2014). Nevertheless, the majority of these studies were carried out on the continental shelf close to the Amazon River mouth, and just few studies in oceanic areas near the shelf break and slope (MELO et al., 2014) or following the ARP across the NBC retroflection (CONROY, 2016). Therefore, possible spatial fluctuations on abundance and diversity of planktonic decapods in the western tropical Atlantic Ocean influenced by ARP remain undescribed.

The present study intends to provide, for the first time, a detailed description of the composition and spatial variability of the planktonic Decapoda assemblage along the coastal and oceanic areas influenced by the ARP and its retroflection. The main objective was to answer the following question: does the coastal-oceanic gradient in diversity and abundance of planktonic decapods differ from the typical plankton

gradient off tropical environments due to the influence of the NBC retroflection and plume of the Amazon River?

## MATERIAL AND METHODS

### Study area

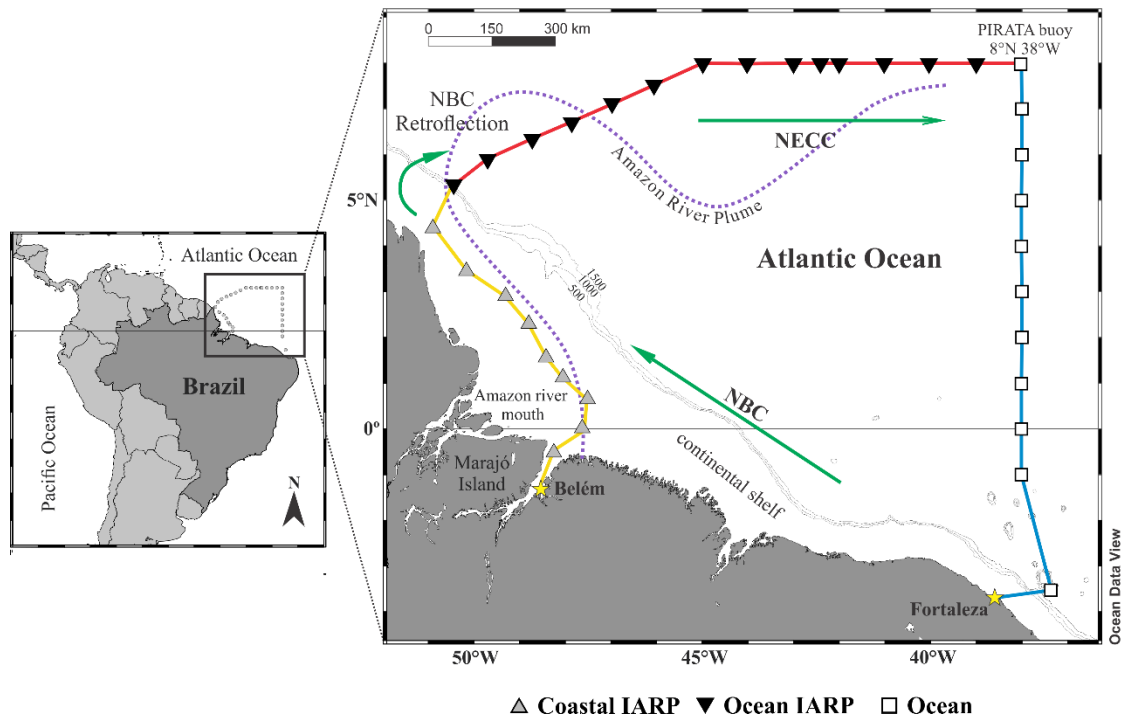
This study was conducted in the North (Pará and Amapá states) and Northeast (Ceará state) coast and oceanic region of Brazil. The North continental Brazilian shelf and oceanic adjacent area are under the influence of the large Amazon and Tocantins river basins, corresponding to the discharge of the Amazon and Pará rivers to the Western Tropical Atlantic (WTA), respectively.

The Amazon River basin is considered the largest of the world, with a input of  $206\,000\text{ m}^3\text{ s}^{-1}$  equivalent to 17% of all freshwater discharge in oceans (CALLÈDE et al., 2010). The dominant climates are equatorial rainforest, fully humid (Af) and equatorial monsoon (Am) (Köppen-Geiger classification system) with precipitation along all months and absence of dry season well defined (KOTTEK et al., 2006; PEEL et al., 2007).

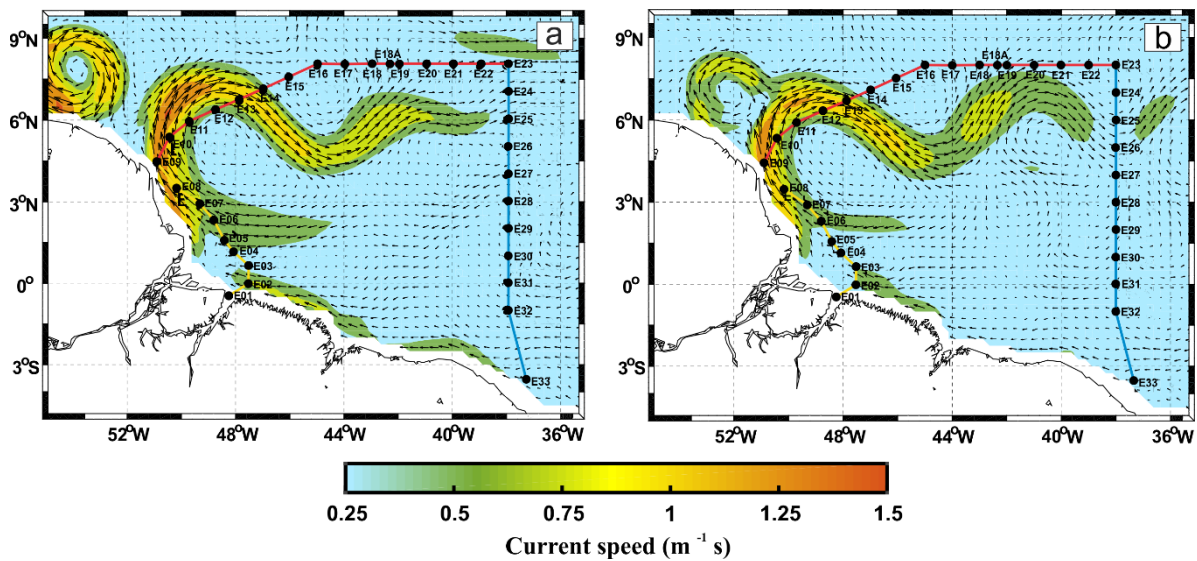
Due to the difference of density between the continental and oceanic waters a superficial plume is formed. The plume carries a large amount of sediments, nutrients and organic matter, that are transported mainly by currents dynamics mechanism thousand kilometers away from rivers mouths, exceeding distances of 3000 km in the open ocean (HU et al., 2004). These plume waters are characterized, in the oceanic province, by salinities lower than 35 and tides are an important factor acting in the mixing between plume and oceanic waters (MULLER-KARGER et al., 1988; VARONA et al., 2019). The Amazon River discharge showed a seasonal effect in consequence of variation on rainfall over the basin, showing a maximum in discharge between late May to early June and a minimum in mid-November (LENTZ, 1995b).

The NBC flows northwestward intercept the Amazon and Pará waters transporting the ARP along the Brazilian continental north shelf, however due to the NBC retroflection (July to November) and consequent NECC intensification, the ARP is drag out to shelf from eastward in oligotrophic Tropical North Atlantic. Therefore, it improves the planktonic production due to all the transported material (CARPENTER et al., 1999; DEL VECCHIO & SUBRAMANIAM, 2004; SUBRAMANIAM et al., 2008; CHONG et al., 2014) (Figure 1 and 2). The influence of the Pará River on the oceanic plume is

little, due to its volume compared to the Amazon River, in this study we will treat only as Amazon River Plume.



**Figure 1.** Cruise route showing the sampling station transects: Coastal area influenced by the Amazon River Plume (yellow line); Oceanic area influenced by Amazon River Plume (red line); and Oceanic area without influence of Amazon River Plume. Green setae indicating the current flow direction: North Brazil Current (NBC); NBC Retroflection and North Equatorial Countercurrent (NECC).



**Figure 2.** Monthly variability of surface current dynamics at Western Tropical Atlantic during October (a) and November (b). Coastal area influenced by ARP (yellow line); Oceanic area influenced by ARP (red line); and Oceanic area without ARP influence (blue line). Source: Varona et al. (2019).

## Sampling strategy

Zooplankton sampling was carried out in context of the “*Camadas Finas III/ Amadeu II Belém–Fortaleza*” project, from October 13 to November 01, 2012, on board NHO Cruzeiro do Sul (H-38, Brazilian Navy). Sampling stations were previously defined from a satellite image showing the chlorophyll-a distribution along the Amazon River Plume. The course of *Camadas Finas III*, leg 2, followed the NBC, along the northern border of the North Brazilian shelf, then leading offshore towards Northeast until reaching 8°N latitude (Figure 1). From this latitude, the cruise followed the NECC along 8°N until reaching the PIRATA buoy station at 8°N38°W. From there, the cruise followed straight southwards, towards the city of Fortaleza.

Samples were collected along three transects: Coastal transect influenced by the Amazon River Plume (**Coastal IARP**), with 9 stations; Oceanic transect influenced by the Amazon River Plume (**Ocean IARP**) with 14 stations; and Oceanic transect without influence of the Amazon River Plume (**Ocean**), with a total of 11 stations. Local depth at stations ranged from 9.2 to 65 meters on the shelf and 1,830 to 4,816 meters in the oceanic area.

At each station, oblique tows were carried out down to 200 m or 90% of local depth (in shallow stations), during 20 minutes, using Bongo nets with 60 cm diameter and 300 µm mesh size, equipped with a Hydro-Bios (Kiel, Germany) flowmeter. At the first shallow station, a sub-surface horizontal tow was conducted with a standard plankton net of the same mesh size, because of the extremely shallow depth in Marajó Bay. All samples were fixed with 4% formaldehyde buffered with sodium tetraborate (0.5 g L<sup>-1</sup>).

## Laboratory work

The majority of samples were analyzed *in toto*. Some coastal samples with grater decapod abundance were analyzed in fractions containing ~300 decapods using a Motoda Splitter (OMORI & IKEDA, 1984). Planktonic decapods were identified to the lowest taxonomic level possible, except for the infraorder Brachyura, using the standard literature and larval descriptions, mainly by Kurata (1970); Calazans (1993), Dos Santos et al. (2004); Fernandes (2006) and Martin et al. (2014).

## Environmental data

In order to analyze the behavior of enhancing the planktonic production was taken from Varona et al. (2019) the result of hydrodynamics simulation using Regional Ocean Modeling System model (ROMS) (SHCHEPETKIN & MCWILLIAMS, 2005). In which the monthly and seasonal climatological patterns of the marine currents, temperature and salinity were simulated. The region was spatially discretized with a spatial resolution of  $0.25^\circ$  and 32 vertical levels from a bathymetry of 2 min resolution and concentrating the 20 higher levels in the first 500 m. The surface forcings were taken from monthly climatology of Comprehensive Ocean Atmosphere Dataset 2005 (COADS) and the initial conditions and lateral boundary were obtained from World Ocean Atlas 2009 (WOA).

## Data analyses

Decapod abundance was expressed in individuals (organisms) per 100 cubic meters ( $\text{ind.}100 \text{ m}^{-3}$ ) of filtered water. The abundance data of all taxa were used to calculate the relative abundance (RA) and frequency of occurrence (FO) of each taxon, as well as the following ecological indexes: Shannon diversity ( $H'$ ) (SHANNON, 1948), evenness ( $J'$ ) (PIELOU, 1966), and Margalef's richness index ( $d$ ) (MARGALEF, 1958). Percentages of abundance were used to calculate the meroplankton/holoplankton ratio.

The biological data were classified for each sampling transects (spatial factor: Coastal IARP vs Ocean IARP vs Ocean) and periods of the day (day vs night). Total abundances were  $\log(x + 1)$ -transformed to improve the normality and homoscedasticity of the data. Normality was tested by means of a Kolmogorov-Smirnov test and homoscedasticity was tested by Levene's test (ZAR, 1999).

ANOVA one-way or Kruskal-Wallis ANOVA was used with post-hoc comparisons (Tukey or Mann-Whitney tests, respectively), to test possible differences between factors (spatial and day/night) in total abundance, main taxa (with more than 2% of relative abundance), ecological indexes and meroplankton:holoplankton ratios. These tests were conducted using STATISTICA v 8.0 (StatSoft, Tulsa, OK, USA), at  $\alpha=0.05$  (ZAR, 1996).

The data were square-root transformed and the similarity matrix between samples was calculated using the Bray-Curtis index (BRAY & CURTIS, 1957). The

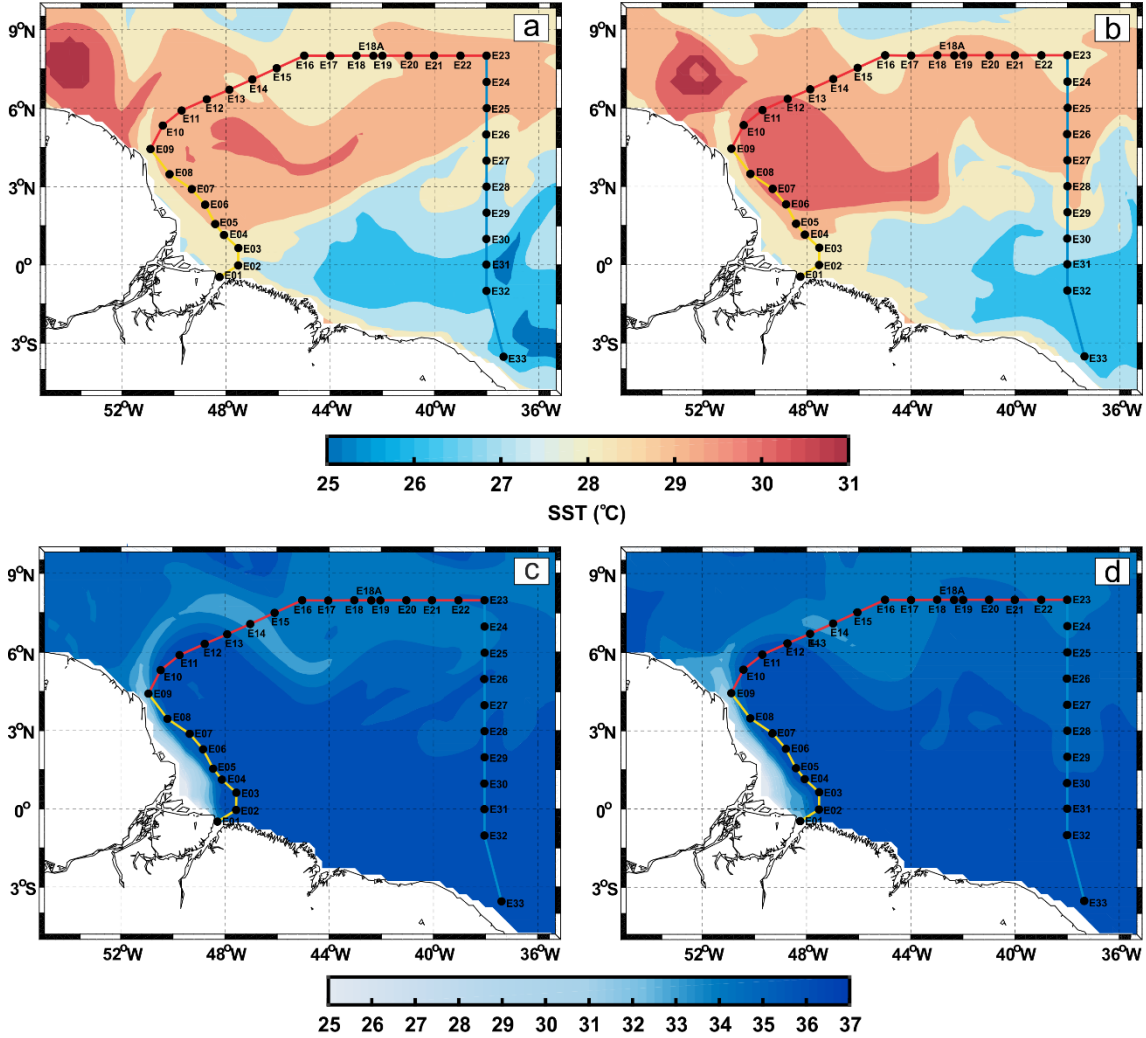
dissimilarity matrix was used to create the Non-metric multidimensional scaling (nMDS) ordination (CLARKE & WARWICK, 2001), and the PERMANOVA to test differences in community structure between factors (ANDERSON, 2001). SIMPER (CLARKE & WARWICK, 2001) was carried out to identify the taxa responsible for differences between groups. All multivariate analyses were performed based on abundance of all taxonomic groups using PRIMER with PERMANOVA (ANDERSON et al., 2008). Redundancy Analysis (RDA) was used to evaluate how factors may impact the planktonic decapod community structure (CANOCO). The Hellinger transformation was applied to process the biological data in CANOCO (LEGENDRE & GALLAGHER, 2001). To identify the characteristic (or bioindicator) species for each sampling transect and to ARP influence area the Indicator Value (IndVal) index (DUFRÊNE & LEGENDRE, 1997) was performed based on specificity and fidelity of each species in relation to the spatial factor. The IndVal index was calculated using the R (v. 3.2.5) statistical environment (available at <https://cran.r-project.org/>) through the RStudio (v. 0.99) user interface (available at <http://www.rstudio.com/>).

## RESULTS

### Environmental conditions

The surface currents, during the boreal mid-autumn, showed a well defined anticyclonic meandering ring in the NBC retroflection region, that deflects the Amazon River Plume towards the open ocean (Figure 2 a, b). The retroflection water flow presented higher values in October (Figure 2a). Anticyclonic eddies originated from the retroflection are dislocated northwestwards towards the Caribbean Sea. The Amazon mouth area was mainly under the influence of high-speed coastal waters from Brazilian Current and oceanic currents flowing westward contributing to the maintenance of Amazon waters close along the coast until the retroflection latitude. In oceanic areas the surface water flow is more intense in NECC meandering transport and cyclonic and anticyclonic eddies of smaller size are present along all NECC pathway stream (Figure 2). Sea Surface temperature (SST) varied little, from a minimum of 26.46°C at 33 station to maximum of 28.68°C at 22 station (Table 1). In the deep chlorophyll maximum layer (DCM) the mean temperature varied from a minimum of 17.53°C at 20 station to maximum of 28.17° at 02 station. Since the DCM deepens at

most oceanic stations, its temperature decreases towards the oceanic transects influenced and without influence of the ARP (Table 1). A warm pool of SST was observed concentrated in the region of NBC retroflection and inside of retroflection-



**Figure 3.** Monthly variability of SST (°C) during October (a) and November (b); SSS (psu) during October (c) and November (d) in the Western Tropical Atlantic. Sampling transects indicated by colored lines: Coastal IARP (yellow); Oceanic IARP (red); and Oceanic area without ARP influence (blue).

originated eddies (Figure 3a, b).

**Table 1.** Variation (mean $\pm$ SD) of environmental parameters (temperature and salinity) in the superficial layer (Surface) and deep chlorophyll maximum layer (DCN), during the sampling period.

|                | Temperature (°C) |                  |                  | Salinity (psu)   |                  |                  |
|----------------|------------------|------------------|------------------|------------------|------------------|------------------|
|                | Costal IARP      | Ocean IARP       | Ocean            | Costal IARP      | Ocean IARP       | Ocean            |
| <b>Surface</b> | 28.02 $\pm$ 0.21 | 28.87 $\pm$ 0.74 | 28.15 $\pm$ 0.82 | 33.36 $\pm$ 6.14 | 34.68 $\pm$ 1.45 | 35.71 $\pm$ 0.73 |

|            |            |            |            |            |            |            |
|------------|------------|------------|------------|------------|------------|------------|
| <b>DCM</b> | 27.07±1.31 | 25.28±2.73 | 26.15±1.23 | 36.42±0.30 | 36.20±0.18 | 36.28±0.12 |
|------------|------------|------------|------------|------------|------------|------------|

Sea Surface Salinity (SSS) varied from estuarine plume conditions with a minimum of 18.18 psu at the mouth of the Pará River (station 1) to typically oceanic salinities, generally found at most oceanic stations (maximum of 37.03 psu at station 2). In the DCM salinity varied from a minimum of 35.79 psu at 17 station to maximum of 37.03 psu at 2 station. Generally, the variation of salinity was greater in the Costal IARP and Ocean IARP area due to the major Amazon River Plume influence (Figure 3c, d). Note that the WTNA is an area with great variability in surface temperature and salinity within a short time period, due to the complex distribution of ARP influence and current dynamics (Figure 3).

### **Taxonomic composition and abundance**

In this study, 13,117 specimens of planktonic decapods belonging to 33 taxa were analyzed. The Dendobranchiata were represented by 8 taxa: Penaeoidea (protozoa, mysis and post-larval stages), Solenoceridae (protozoa and mysis stages), Benthescymidae (mysis stages), Sicyonidae (mysis stages), Aristeidae (mysis stages), Sergestidae (protozoa, mysis and post-larval stages), the sergestid shrimps *Acetes* sp. (H. Milne Edwards, 1930) (protozoae) and Luciferidae (protozoa, mysis, post-larvae and adult stages). The Pleocyemata were represented by 25 taxa: Spongicolidae (zoeae), Stenopodidae (zoeae), Caridea (others) (zoea and decapodid stages), Caridea morphotype 1 (zoea stages), *Amphionides reynaudii* (H. Milne Edwards, 1833) (zoeae), Oplophoroidea (zoeae), Bresiliidae (zoeae), Palaemonidae (zoeae), Pasiphaeidae (zoea and decapodid stages), Alphaeidae (zoeae), Lysmatidae (zoeae), Hippolytidae (zoeae), Processidae (zoeae), Axiidae (zoeae), Callianassidae (zoeae), Upogebiidae (zoeae), Achelata (phyllosoma stages), Enoplometopidae (zoeae), Anomura others (zoeae), Galathaeidae (zoeae), Porcellanidae (zoeae), Hippoidea (zoeae), Diogenidae (zoeae), Paguridae (zoeae) and Brachyura (zoeae and megalopae).

Seventeen of the 33 taxa were present in all transects, 3 taxa were exclusive from neritic stations (Penaeoidea nauplii; Upogebiidae and Porcellanidae) and 11 were exclusive from oceanic stations (Aristeidae; Sergestidae protozoae; Caridae morpho I; Spongicolidae; Stenopodidae; *Amphionides reynaudii*; Oplophoroidea; Lysmatidae; Axiidae; Enoplometopidae and Galatheidae). The coastal and oceanic area influenced by ARP present 4 exclusive taxa (Solenoceridae protozoae; *Acetes* protozoae;

Anomura and Paguridae) and just 1 taxon (Bresillidae) was exclusive from oceanic area without the ARP influence (table 2). Total abundance of planktonic decapods in present study showed a mean of  $4,445.16 \pm 12,444.26 \text{ ind.}100 \text{ m}^{-3}$ , varied between a minimum of  $765.24 \text{ ind.}100 \text{ m}^{-3}$ , at the station 28 to  $66,527.35 \text{ ind.}100 \text{ m}^{-3}$  at station 10. The most abundant groups among decapods were Brachyura (zoeae) with  $1,067.14 \pm 2,956.24 \text{ ind.}100 \text{ m}^{-3}$  (24.01%), Luciferidae with  $876.92 \pm 2,895.87 \text{ ind.}100 \text{ m}^{-3}$  (19.73%), Luciferidae (protozoeae) with  $651.20 \pm 2,091.11 \text{ ind.}100 \text{ m}^{-3}$  (14.65%), Callianassidae  $387.32 \pm 1,415.20 \text{ ind.}100 \text{ m}^{-3}$  (8.71%) and Palaemonidae with  $380.75 \pm 1,187.17 \text{ ind.}100 \text{ m}^{-3}$  (8.57%).

At **Transect 1**, the total abundance of decapods presented a mean of  $9,137.75 \pm 8,691.11 \text{ ind.}100 \text{ m}^{-3}$ , ranging from a minimum of  $765.24 \text{ ind.}100 \text{ m}^{-3}$  (station 4) to a maximum of  $28,986.87 \text{ ind.}100 \text{ m}^{-3}$  (station 9) (Figure 4). The taxa that most contributed in abundance were: Brachyura (zoeae):  $2,307.15 \pm 2,292.06 \text{ ind.}100 \text{ m}^{-3}$  (25.25%), Luciferidae (protozoeae):  $1,825.43 \pm 3,490.21 \text{ ind.}100 \text{ m}^{-3}$  (19.98%); Luciferidae:  $1,534.03 \pm 2,084.90 \text{ ind.}100 \text{ m}^{-3}$  (16.79%); Palaemonidae:  $869.61 \pm 1,579.45 \text{ ind.}100 \text{ m}^{-3}$  (9.52%); and Callianassidae:  $625.17 \pm 1,279.64 \text{ ind.}100 \text{ m}^{-3}$  (6.84%) (Table 2).

In the **Transect 2**, the total abundance of decapods presented a mean of  $4,889.28 \pm 17,741.14 \text{ ind.}100 \text{ m}^{-3}$ , range from  $16.76 \text{ ind.}100 \text{ m}^{-3}$  (station 18) to  $66,527.35 \text{ ind.}100 \text{ m}^{-3}$  (station 10) (Figure 4). The taxa that most contributed in abundance were: Luciferidae:  $1,141.10 \pm 4,194.64 \text{ ind.}100 \text{ m}^{-3}$  (23.34%); Brachyura (zoeae):  $1,107.63 \pm 4,113.82 \text{ ind.}100 \text{ m}^{-3}$  (22.65%); Callianassidae:  $533.42 \pm 1,972.71 \text{ ind.}100 \text{ m}^{-3}$  (10.91%); Luciferidae (protozoeae):  $406.08 \pm 1,492.84 \text{ ind.}100 \text{ m}^{-3}$  (8.31%), and Palaemonidae:  $364.26 \pm 1,324.83 \text{ ind.}100 \text{ m}^{-3}$  (7.45%) (Table 2).

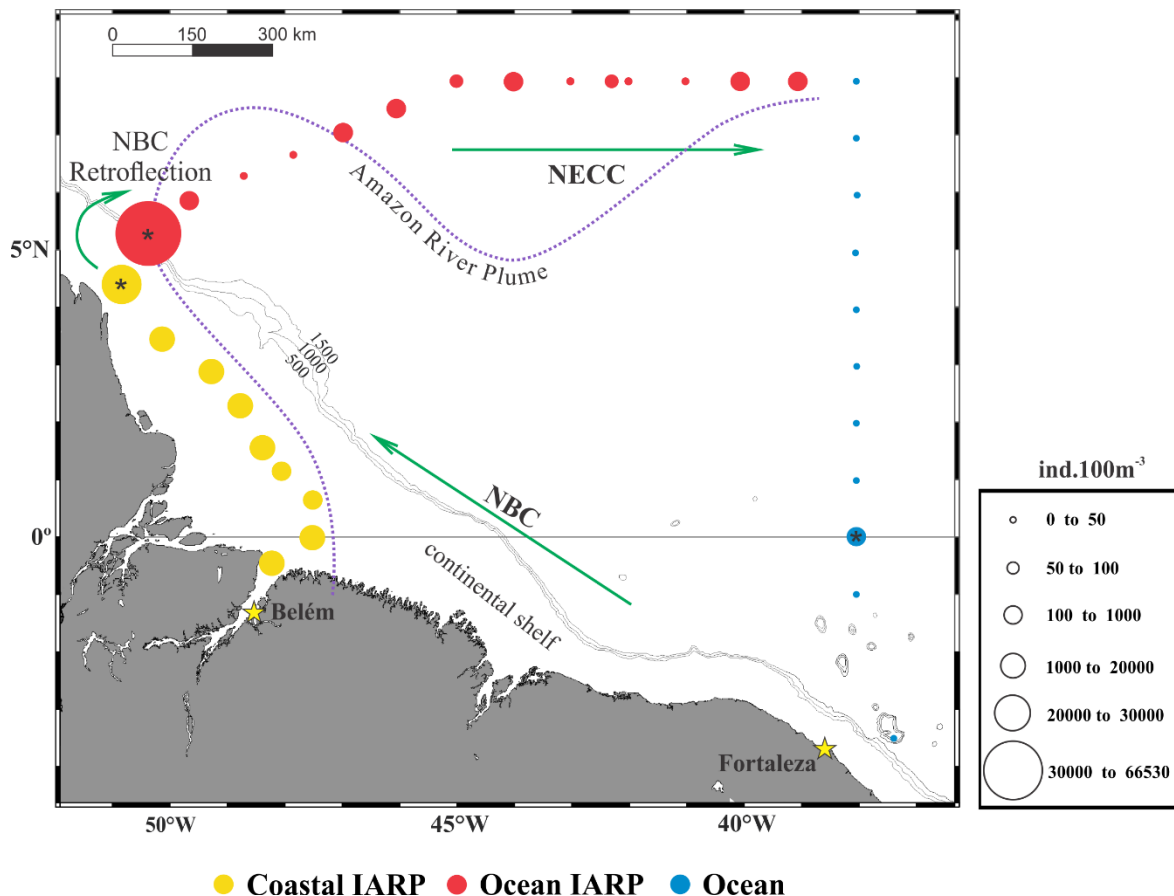
In the **Transect 3**, the total abundance of decapods presented a mean of  $74.28 \pm 22.83 \text{ ind.}100 \text{ m}^{-3}$ , range  $14.35 \text{ ind.}100 \text{ m}^{-3}$  (station 28) to  $100.68 \text{ ind.}100 \text{ m}^{-3}$  (station 31) (Figure 4). The taxa that most contributed in abundance were: Sergestidae (protozoeae):  $7.23 \pm 8.16 \text{ ind.}100 \text{ m}^{-3}$  (17.84%); Callianassidae:  $6.79 \pm 8.05 \text{ ind.}100 \text{ m}^{-3}$  (16.77% RA); Penaeoidea (protozoeae):  $3.23 \pm 4.20 \text{ ind.}100 \text{ m}^{-3}$  (7.96%); Luciferidae:  $3.07 \pm 1.54 \text{ ind.}100 \text{ m}^{-3}$  (7.58%), and Luciferidae (protozoeae):  $2.72 \pm 6.54 \text{ ind.}100 \text{ m}^{-3}$  (6.71%) (Table 2).

**Table 2.** Mean (ind.100 m<sup>-3</sup>), Standard Deviation (SD), maximum abundance (Max. ind. 100 m<sup>-3</sup>), relative abundance (RA%) and frequency of occurrence (FO%) of the community of planktonic decapods in the sampling transects: coastal area influenced by the Amazon River Plume (Coastal IARP); oceanic area influenced by the Amazon River Plume (Ocean IARP) and oceanic area not influenced by the Amazon River Plume (Ocean). Most abundant (RA >15%) and frequent decapods (FO >70%) on each transect are in bold font.

| Taxa                         | Coast IARP |         |          |              |              | Ocean IARP |         |          |              |              | Ocean |      |       |              |              |
|------------------------------|------------|---------|----------|--------------|--------------|------------|---------|----------|--------------|--------------|-------|------|-------|--------------|--------------|
|                              | Mean       | SD      | MAX      | RA           | FO           | Mean       | SD      | MAX      | RA           | FO           | Mean  | SD   | MAX   | RA           | FO           |
| Penaeoidea (nauplii)         | 2.91       | 8.47    | 25.48    | 0.03         | 22.22        | -          | -       | -        | -            | -            | -     | -    | -     | -            | -            |
| Penaeoidae (protozoa)        | 312.70     | 400.12  | 1101.88  | 3.42         | 66.67        | 182.31     | 650.29  | 2441.56  | 3.73         | <b>92.86</b> | 3.23  | 4.20 | 11.55 | 7.96         | <b>81.82</b> |
| Penaeidae                    | 2.90       | 6.61    | 20.32    | 0.03         | 44.44        | 11.16      | 23.73   | 82.48    | 0.23         | 50           | 0.75  | 1.09 | 3.71  | 1.85         | 63.64        |
| Solenoceridae (protozoa)     | 76.42      | 170.94  | 527.72   | 0.84         | 55.56        | 22.69      | 83.57   | 313.02   | 0.46         | 28.57        | -     | -    | -     | -            | -            |
| Solenoceridae (mysis)        | 11.07      | 31.65   | 95.41    | 0.12         | 33.33        | 11.14      | 24.26   | 70.86    | 0.23         | 28.57        | 1.56  | 3.87 | 13.07 | 3.84         | 45.45        |
| <i>Gennadas</i> sp.          | 0.10       | 0.31    | 0.92     | 0.001        | 11.11        | 1.75       | 2.82    | 7.65     | 0.04         | 42.86        | 0.70  | 1.11 | 3.09  | 1.72         | 54.55        |
| Sicyoniidae                  | 39.94      | 99.11   | 300.51   | 0.44         | 44.44        | 28.86      | 99.88   | 375.62   | 0.59         | 42.86        | 1.15  | 2.59 | 8.71  | 2.84         | 45.45        |
| Aristeidae                   | -          | -       | -        | -            | -            | 0.04       | 0.13    | 0.49     | 0.001        | 7.14         | 0.17  | 0.38 | 0.97  | 0.43         | 18.18        |
| Sergestidae (protozoa)       | -          | -       | -        | -            | -            | 19.80      | 22.44   | 66.28    | 0.40         | <b>100</b>   | 7.23  | 8.16 | 29.23 | <b>17.84</b> | <b>100</b>   |
| Sergestidae                  | 195.41     | 540.12  | 1633.04  | 2.14         | 33.33        | 131.48     | 472.80  | 1773.78  | 2.69         | <b>78.57</b> | 1.38  | 1.20 | 3.55  | 3.42         | <b>90.91</b> |
| <i>Acetes</i> (protozoa)*    | 307.60     | 673.84  | 2003.41  | 3.37         | 44.44        | 268.30     | 1003.90 | 3756.25  | 5.49         | 7.14         | -     | -    | -     | -            | -            |
| Luciferidae (protozoa)**     | 1825.43    | 3490.21 | 10805.91 | <b>19.98</b> | <b>77.78</b> | 406.08     | 1492.84 | 5592.64  | 8.31         | <b>85.71</b> | 2.72  | 6.54 | 21.77 | 6.71         | 27.27        |
| Luciferidae*                 | 1534.03    | 2084.90 | 5747.29  | <b>16.79</b> | <b>100</b>   | 1141.10    | 4194.35 | 15713.64 | <b>23.34</b> | <b>92.86</b> | 3.07  | 1.54 | 4.64  | 7.58         | 100          |
| Spongicolidae                | -          | -       | -        | -            | -            | 0.07       | 0.24    | 0.92     | 0.001        | 7.14         | 0.15  | 0.22 | 0.53  | 0.38         | 36.36        |
| Stenopodidae                 | -          | -       | -        | -            | -            | 0.19       | 0.47    | 1.69     | 0.004        | 21.43        | 0.25  | 0.38 | 0.97  | 0.63         | 36.36        |
| Caridea (others)*            | 533.65     | 1353.96 | 4129.27  | 5.84         | 66.67        | 13.39      | 44.24   | 166.94   | 0.27         | 57.14        | 0.46  | 1.31 | 4.36  | 1.13         | 18.18        |
| Caridea (morpho 1)           | -          | -       | -        | -            | -            | 6.72       | 23.13   | 86.97    | 0.14         | 28.57        | 0.53  | 0.63 | 1.90  | 1.32         | 54.55        |
| <i>Anphionides reynaudii</i> | -          | -       | -        | -            | -            | 0.11       | 0.22    | 0.60     | 0.002        | 21.43        | 0.08  | 0.27 | 0.89  | 0.20         | 9.09         |

| Continuation table 2 |                |                |         |              |              |                |                 |          |              |       |              |              |       |              |              |
|----------------------|----------------|----------------|---------|--------------|--------------|----------------|-----------------|----------|--------------|-------|--------------|--------------|-------|--------------|--------------|
| Oplophoroidea        | -              | -              | -       | -            | -            | 1.30           | 2.25            | 8.44     | 0.03         | 50    | 0.93         | 1.45         | 4.36  | 2.29         | 45.45        |
| Bresiliidae          | -              | -              | -       | -            | -            | -              | -               | -        | -            | -     | 0.41         | 0.80         | 2.09  | 1.00         | 27.27        |
| Palaemonidae**       | 869.61         | 1579.45        | 4908.44 | 9.52         | <b>88.89</b> | 364.26         | 1324.83         | 4966.60  | 7.45         | 64.29 | 1.75         | 2.17         | 6.78  | 4.32         | 72.73        |
| Pasiphaeidae         | 47.16          | 49.26          | 143.11  | 0.52         | <b>77.78</b> | 10.66          | 38.98           | 146.08   | 0.22         | 28.57 | 0.14         | 0.47         | 1.55  | 0.35         | 9.09         |
| Alpheidae            | 12.82          | 23.50          | 69.79   | 0.14         | 55.56        | 22.16          | 66.39           | 250.42   | 0.45         | 50    | 1.83         | 4.73         | 15.97 | 4.51         | 45.45        |
| Lysmatidae           | -              | -              | -       | -            | -            | 7.56           | 27.86           | 104.34   | 0.15         | 21.43 | 0.22         | 0.45         | 1.45  | 0.53         | 27.27        |
| Hippolytidae         | 169.90         | 481.69         | 1452.64 | 1.86         | 22.22        | 0.58           | 1.34            | 5.06     | 0.01         | 35.71 | 0.25         | 0.45         | 1.45  | 0.61         | 36.36        |
| Processidae          | 2.46           | 4.68           | 10.94   | 0.03         | 33.33        | 11.69          | 38.75           | 146.08   | 0.24         | 42.86 | 0.03         | 0.09         | 0.30  | 0.07         | 9.09         |
| Axiidae              | -              | -              | -       | -            | -            | 3.35           | 11.08           | 41.74    | 0.07         | 28.57 | 0.25         | 0.84         | 2.78  | 0.62         | 9.09         |
| Callianassidae       | 625.17         | 1279.64        | 3586.73 | 6.84         | <b>77.78</b> | 533.42         | 1972.71         | 7387.29  | 10.91        | 64.29 | 6.79         | 8.05         | 26.62 | <b>16.77</b> | <b>72.73</b> |
| Upogebiidae          | 38.55          | 97.53          | 297.02  | 0.42         | 33.33        | -              | -               | -        | -            | -     | -            | -            | -     | -            | -            |
| Achelata             | 0.39           | 1.16           | 3.49    | 0.004        | 11.11        | 0.36           | 0.65            | 1.83     | 0.007        | 28.57 | 0.05         | 0.16         | 0.53  | 0.12         | 9.09         |
| Enoplometopidae      | -              | -              | -       | -            | -            | 0.03           | 0.12            | 0.46     | 0.0007       | 7.14  | 0.04         | 0.12         | 0.39  | 0.09         | 9.09         |
| Anomura              | 32.06          | 59.06          | 182.78  | 0.35         | 66.67        | 0.32           | 0.62            | 1.97     | 0.007        | 28.57 | -            | -            | -     | -            | -            |
| Galatheididae        | -              | -              | -       | -            | -            | 3.38           | 8.63            | 31.15    | 0.07         | 21.43 | 1.01         | 3.36         | 11.13 | 2.50         | 9.09         |
| Porcellanidae        | 2.68           | 7.58           | 22.85   | 0.03         | 22.22        | -              | -               | -        | -            | -     | -            | -            | -     | -            | -            |
| Hipoidea             | 3.42           | 9.72           | 29.34   | 0.04         | 33.33        | 0.76           | 1.66            | 5.41     | 0.02         | 21.43 | 0.40         | 0.51         | 1.59  | 0.98         | 54.55        |
| Diogenidae**         | 117.26         | 233.07         | 701.19  | 1.28         | <b>77.78</b> | 249.29         | 931.29          | 3484.96  | 5.10         | 42.86 | 0.04         | 0.15         | 0.48  | 0.11         | 9.09         |
| Paguridae            | 0.52           | 1.56           | 4.69    | 0.006        | 11.11        | 6.15           | 22.26           | 83.47    | 0.13         | 21.43 | -            | -            | -     | -            | -            |
| Glaucothoe (Anomura) | 1.73           | 2.28           | 6.98    | 0.02         | 55.56        | 11.34          | 24.50           | 83.47    | 0.23         | 42.86 | 0.24         | 0.39         | 1.20  | 0.60         | 36.36        |
| Brachyura (zoea)     | 2307.15        | 2292.06        | 6974.38 | <b>25.25</b> | 100          | 1107.63        | 4113.82         | 15400.62 | <b>22.65</b> | 64.29 | 1.04         | 2.46         | 8.35  | 2.56         | 45.45        |
| Brachyura (megalopa) | 37.81          | 78.51          | 242.42  | 0.41         | 66.67        | 33.34          | 94.22           | 354.76   | 0.68         | 42.86 | 1.01         | 1.26         | 3.48  | 2.48         | 63.64        |
| Decapoda damaged     | 8.97           | 17.65          | 50.96   | 0.10         | 33.33        | 276.02         | 1025.71         | 3839.72  | 5.65         | 57.14 | 0.55         | 0.64         | 1.55  | 1.37         | 54.55        |
| Decapoda n.id        | 17.93          | 47.29          | 143.11  | 0.20         | 33.33        | 0.52           | 1.80            | 6.75     | 0.01         | 14.29 | 0.11         | 0.19         | 0.48  | 0.26         | 27.27        |
| <b>TOTAL</b>         | <b>9137.75</b> | <b>8691.11</b> |         | <b>100</b>   |              | <b>4889.28</b> | <b>17741.14</b> |          | <b>100</b>   |       | <b>74.28</b> | <b>22.83</b> |       | <b>100</b>   |              |

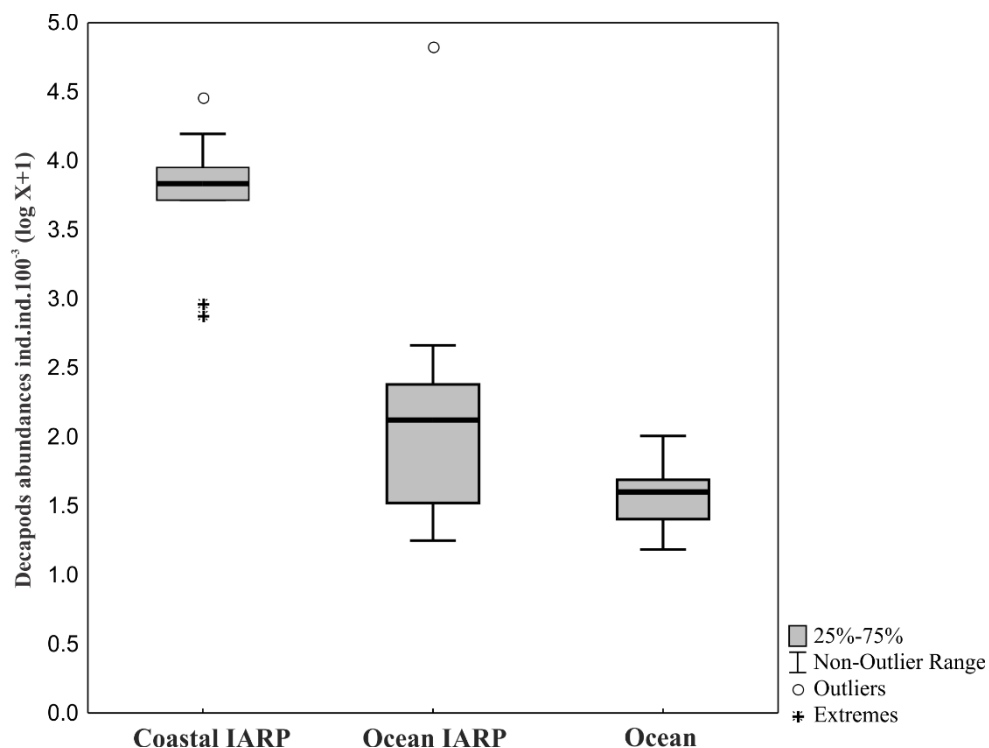
\* significant difference  $p < 0.05$ ; \*\* significant difference  $p < 0.01$



**Figure 4.** Spatial distribution of total planktonic decapods abundance in sampling stations on transects influenced and not influenced by the Amazon River Plume. Yellow circles: Coastal area influenced by Amazon River Plume (Coastal IARP); Red circles: Oceanic area influenced by Amazon River Plume (Ocean IARP); and Blue circles: Oceanic area without the Amazon River Plume influence (Ocean). Size circles are proportional to the value of each respective abundance interval. Surface currents indicated by green arrows. \*indication the station on each transect with the greatest abundance value.

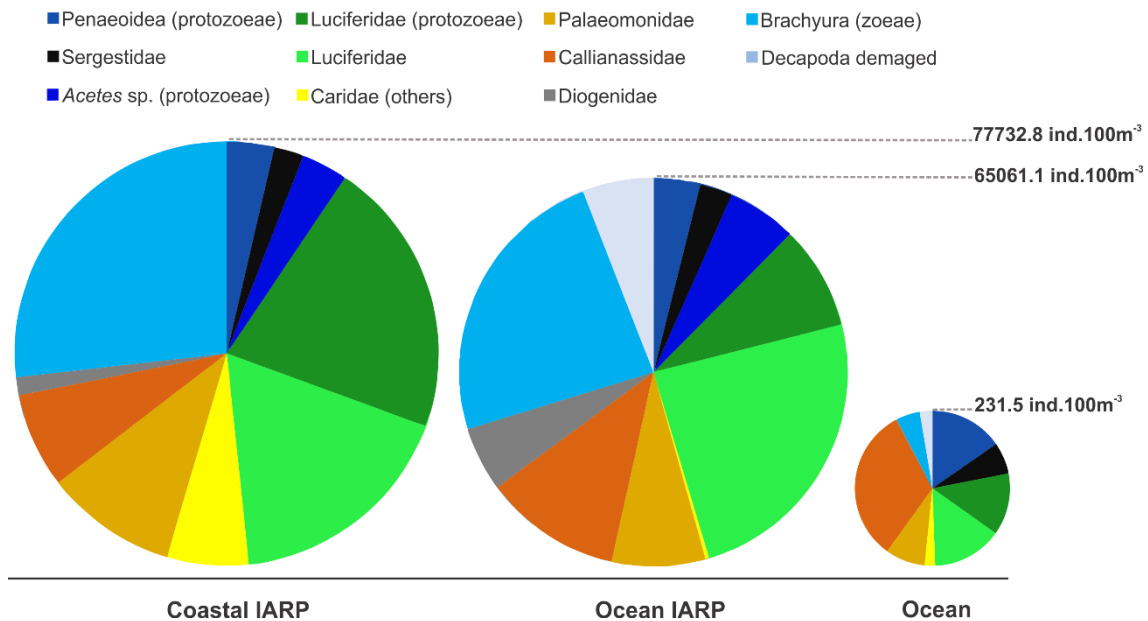
### Variability in Abundance

Total number of planktonic decapods showed differences in relation to the spatial factor ( $p < 0.001$ , ANOVA one-way) (figure 5). Higher abundances of planktonic decapods were found in the coastal area under ARP influence (Coastal IARP) when compared to oceanic stations influenced (Ocean IARP) and not influenced (Ocean) by the ARP (TUKEY,  $p = 0.001$ ), nevertheless, the station 10 in the Ocean IARP, showed the greatest abundance among all samples (figure 4, \*red circle). No differences in total abundance were recorded between the oceanic areas influenced and not influenced by the ARP. No differences were recorded between or inside the transects, in relation to the periods of day. Interactions between spatial and day/night factors were not recorded.



**Figure 5.** Box-Plot (median and quartiles) representing the spatial distribution of total abundance (ind.100 m<sup>-3</sup>) of planktonic decapods (log X+1) in the sampling transects: Coastal area influenced by Amazon River Plume (Coastal IARP); Oceanic area influenced by Amazon River Plume (Ocean IARP); and Oceanic area without the Amazon River Plume influence (Ocean).

Some taxa (with total RA >2%) showed differences in relation to transects: *Acetes* sp. (protozoaeae) (p=0.02), *Luciferidae* (p=0.0001), *Palaemonidae* (p=0.006) and *Brachyura* (zoeae) (p=0.0001) showed higher abundances at Coastal IARP when compared to both offshore areas. *Luciferidae* (protozoaeae) (p=0.01) and *Caridea* (others) (p=0.02) presented higher abundance values at transects influenced by ARP when compared to Ocean transect without ARP influence. *Diogenidae* showed differences in abundance between all the transects (p=0.002), presenting higher abundance values at coastal stations and lower values at oceanic stations, particularly at the Ocean transect (Figure 6, Table 2). The taxa tested did not display significant differences in relation to day/night.

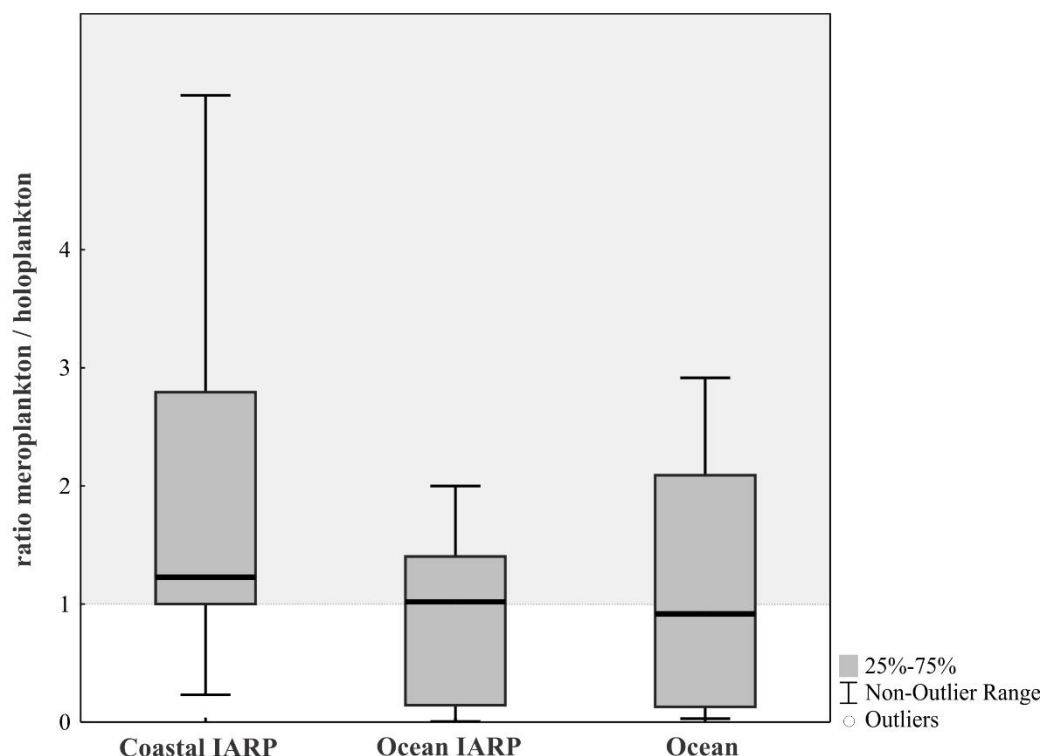


**Figure 6.** Relative abundance of main taxa (total RA >2%) on three sampling transects: Coastal area influenced by Amazon River Plume (Coastal IARP); Oceanic area influenced by Amazon River Plume (Ocean IARP); Oceanic area without the Amazon River Plume influence (Ocean). The total abundance of main taxa is indicated by dashed lines. Illustrative circle size ratio.

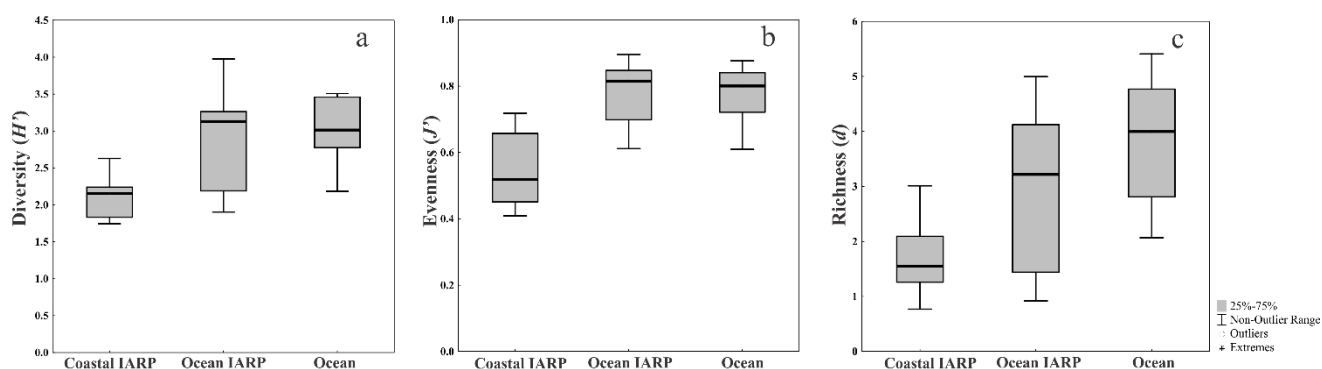
In both transects influenced by the ARP, the meroplankton:holoplankton ratio presented values greater than 1 (1.11 and 1.07 for the Coastal IARP and Ocean IARP respectively), indicating a major contribution of meroplanktonic decapods (e.g., larvae of brachyuran and anomuran crabs). The oceanic area without ARP influence showed values lower than 1 (mean 0.81 for the Ocean transect), indicating major contributions of holoplanktonic decapods (e.g., sergestid and penaeid shrimps) (Figure 7).

### Diversity Indexes

The ecological indexes showed a total mean of  $2.72 \pm 0.65$ ,  $0.72 \pm 0.14$  and  $2.90 \pm 1.39$  for diversity ( $H'$ ), Evenness ( $J'$ ) and richness ( $d$ ), respectively. The Coastal IARP transect showed the lowest values for all ecological indexes ( $2.10 \pm 0.30$   $H'$ ,  $0.56 \pm 0.12$   $J'$  and  $1.70 \pm 0.75$   $d$ ), when compared to oceanic transects influenced ( $2.90 \pm 0.69$   $H'$ ,  $0.78 \pm 0.09$   $J'$  and  $2.93 \pm 1.37$   $d$ ) and not influenced ( $3.0 \pm 0.45$   $H'$ ,  $0.79 \pm 0.08$   $J'$  and  $3.84 \pm 1.12$   $d$ ) by the Amazon River Plume (ANOVA,  $p < 0.01$ ). The oceanic transects (Ocean IARP and Ocean), did not display significant differences between each other (Figure 8).



**Figure 7.** Box-Plot (median and quartiles) representing the ratio meroplankton: holoplankton abundance of planktonic decapods ( $\log X+1$ ) in the sampling transects. Gray area (ratio  $\geq 1$ ) indicating samples with higher contribution of meroplankton. Coastal IARP: Coastal transect influenced by the Amazon River Plume; Ocean IARP: Ocean transect influenced by Amazon River Plume; and Ocean: Ocean transect without the plume influence.



**Figure 8.** Box-Plot (median and quartiles) representing the spatial distribution of ecological indexes of planktonic decapods in the sampling transects influenced (Coastal IARP and Ocean IARP) and not influenced (Ocean) by the Amazon River Plume: a. Shannon diversity index ( $H'$ ); b. Pielou evenness ( $J'$ ) and c. Margalef species richness index ( $d$ ).

## Community structure

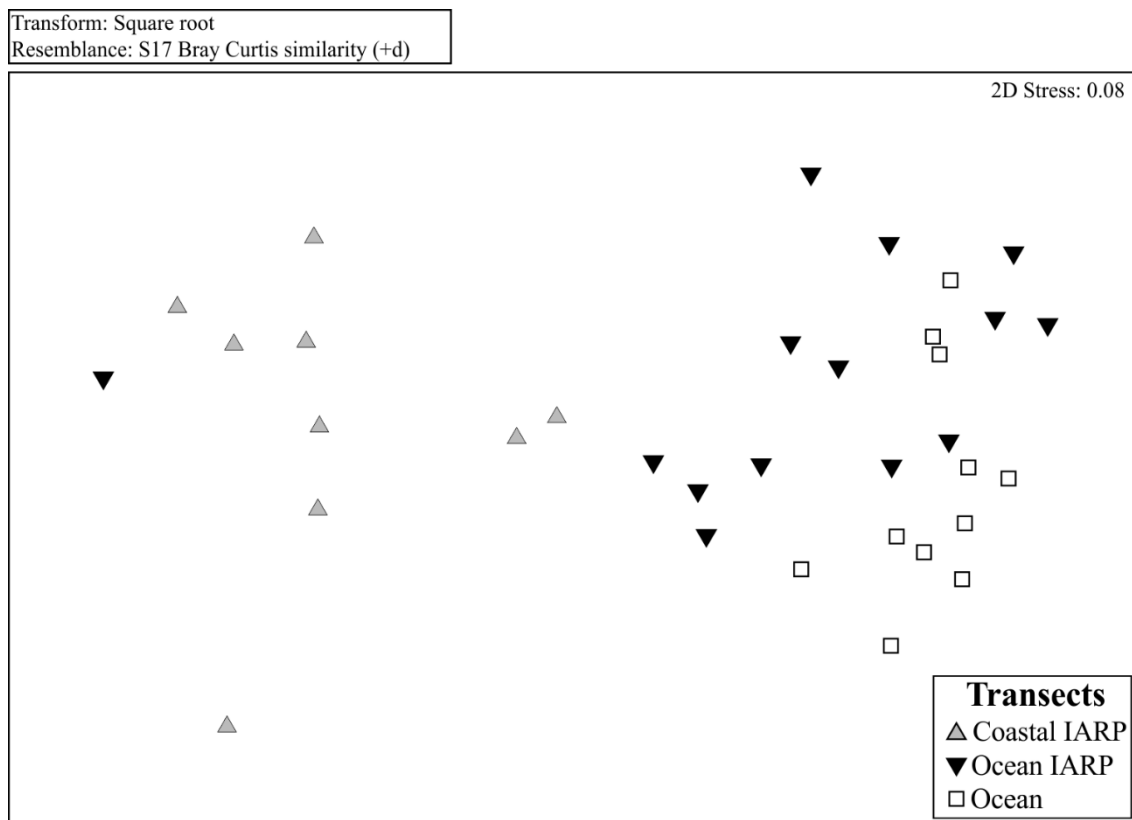
The nMDS ordination suggested considerable differences in community structure between transects (Figure 9). The samples of the coastal region influenced by the ARP showed a clear distinction from those collected in the oceanic transects, mainly the oceanic region without ARP influence. The three first stations of the Ocean transect are clearly grouped with the Ocean IARP transect, indicating an influence of ARP in these sampling stations. These differences in community structure of planktonic decapods in relation to spatial factor (transects) were confirmed by the PERMANOVA. All pairwise tests performed revealed differences between all sampling transects (Tables 3, 4).

**Table 3.** PERMANOVA results of the planktonic decapod community structure in relation to the spatial factor (sampling transects) and periods of day (day/night) along the Amazon River Plume.

| Factor              | df | MS     | Pseudo-F | <i>p</i> |
|---------------------|----|--------|----------|----------|
| Spatial             | 2  | 13048  | 6.9347   | 0.001    |
| Day/Night           | 1  | 1825.4 | 0.97014  | 0.468    |
| Spatial x Day/Night | 2  | 2976.9 | 1.5821   | 0.042    |

**Table 4.** Pairwise PERMANOVA of planktonic decapod community structure between sampling transects along the Amazon River Plume. Coastal IARP: Coastal transect influenced by the Amazon River Plume; Ocean IARP: Ocean transect influenced by Amazon River Plume; and Ocean: Ocean Transect without the plume influence.

| Groups                   | <i>t</i> | <i>p</i> |
|--------------------------|----------|----------|
| Coastal IARP, Ocean IARP | 2.7001   | 0.001    |
| Coastal IARP, Ocean      | 3.64     | 0.001    |
| Ocean IARP, Ocean        | 1.5541   | 0.013    |



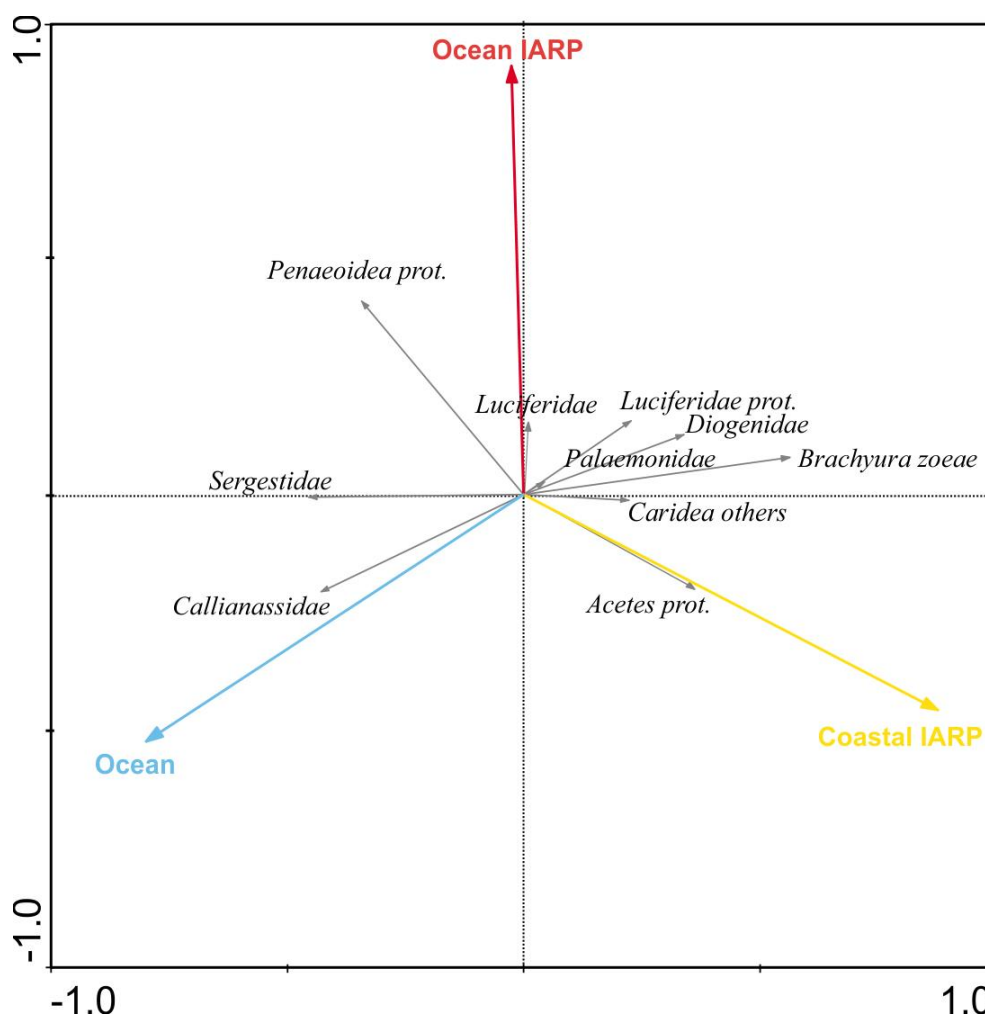
**Figure 9.** Non-metric multidimensional scaling ordination (nMDS) plotted from the similarity between samples based on the abundance of 33 planktonic decapods taxa from coastal transect influenced by the Amazon River Plume (Coastal IARP); ocean transect influenced by the Amazon River Plume (Ocean IARP) and ocean transect without Amazon River Plume influence (Ocean).

The SIMPER test showed an average of similarity of 39.75, 41.05 and 52.20 from transects Coastal IARP, Ocean IARP and Ocean, respectively. The main taxa responsible for the similarity were *Brachyura* (zoeae) (31.51%), *Luciferidae* (20.17%) and *Palaemonidae* (9.93) for the Coastal IARP; *Sergestidae* (protozoeae) (22.74%), *Penaeoidea* (protozoeae) (16.60%), *Luciferidae* (15.34%) for the Ocean IARP; and *Sergestidae* (protozoeae) (21.44%), *Luciferidae* (18.06%) and *Penaeoidea* (protozoeae) (11.69%) for the Ocean transect. The dissimilarity between the sampling transects were high (up to 60%), the main taxa responsible for the dissimilarity between the areas are summarized in the table 5.

**Table 5.** Planktonic decapods contribution (<70%) to the mean dissimilarity between the sampling transects: Coast area influenced by the ARP (Coastal IARP), Ocean area influenced by the ARP (Ocean IARP) and Ocean area without influence of ARP (Ocean).

| <b>Group/taxa</b>                    | <b>Mean<br/>Dissimilarity</b> | <b>Contribution<br/>(%)</b> | <b>Cumulative<br/>value (%)</b> |
|--------------------------------------|-------------------------------|-----------------------------|---------------------------------|
| <b>Coastal IARP &amp; Ocean IARP</b> | 84.17                         |                             |                                 |
| Brachyura (zoeae)                    |                               | 17.13                       | 17.13                           |
| Luciferidae                          |                               | 11.85                       | 28.98                           |
| Luciferidae (protozoeae)             |                               | 9.69                        | 38.67                           |
| Palaemonidae                         |                               | 8.68                        | 47.35                           |
| Callianassidae                       |                               | 6.07                        | 53.43                           |
| Caridea (others)                     |                               | 5.27                        | 58.7                            |
| Penaeoidea (protozoeae)              |                               | 4.50                        | 63.20                           |
| <i>Acetes</i> sp. (protozoeae)       |                               | 3.35                        | 66.55                           |
| Sergestidae                          |                               | 3.13                        | 69.68                           |
| <b>Coastal IARP &amp; Ocean</b>      | 90.72                         |                             |                                 |
| Brachyura (zoeae)                    |                               | 18.32                       | 18.32                           |
| Luciferidae                          |                               | 12.91                       | 31.22                           |
| Luciferidae (protozoeae)             |                               | 10.12                       | 41.34                           |
| Palaemonidae                         |                               | 9                           | 50.34                           |
| Callianassidae                       |                               | 5.74                        | 56.08                           |
| Caridea (others)                     |                               | 5.57                        | 61.65                           |
| Penaeoidea (protozoeae)              |                               | 4.39                        | 66.04                           |
| <i>Acetes</i> sp. (protozoeae)       |                               | 3.10                        | 69.14                           |
| <b>Ocean IARP &amp; Ocean</b>        | 64.97                         |                             |                                 |
| Luciferidae                          |                               | 7.83                        | 7.83                            |
| Callianassidae                       |                               | 6.54                        | 14.37                           |
| Luciferidae (protozoeae)             |                               | 6.48                        | 20.85                           |
| Sergestidae (protozoeae)             |                               | 5.99                        | 26.84                           |
| Brachyura (zoeae)                    |                               | 5.94                        | 32.78                           |
| Penaeoidea (protozoeae)              |                               | 5.58                        | 38.35                           |
| Palaemonidae                         |                               | 5.14                        | 43.5                            |
| Penaeidae                            |                               | 3.95                        | 47.45                           |
| Brachyura (megalopae)                |                               | 3.85                        | 51.3                            |
| Sergestidae                          |                               | 3.62                        | 54.92                           |
| Alpheidae                            |                               | 3.31                        | 58.23                           |
| Caridea sp1.                         |                               | 3.22                        | 61.45                           |
| Solenoceridae (mysis)                |                               | 2.99                        | 64.44                           |
| Deapoda damaged                      |                               | 2.98                        | 67.42                           |

Some groups were indicative of a specific transect: Anomura (IndVal=0.812,  $p=0.005$ ), Pasiphaeidae (IndVal=0.796,  $p=0.005$ ), Solenoceridae (protozoae) (IndVal=0.654,  $p=0.045$ ) and Upogebiidae (IndVal=0.577,  $p=0.020$ ) were the indicator taxa for the coastal transect influenced by the ARP. Spongiocolidae (IndVal=0.505,  $p=0.05$ ) was the only taxon detected as indicator of the Ocean transect without the ARP influence.



**Figure 10.** Redundancy Analyses (RDA) plot, showing the distribution of the identified taxa with relative abundance greater than 2%, from three sampling transects on area influenced (Coastal IARP; Ocean IARP) and without the influence (Ocean) of the Amazon River Plume in October/November 2012.

Despite the Ocean IARP transect not showing any singular indicator taxa, the group consisting of transects under the ARP influence together (Coastal IARP and Ocean IARP) included *Luciferidae* (protozoae) (IndVal=0.908,  $p<0.01$ ), *Brachyura* (zoeae) (IndVal=0.885,  $p<0.01$ ) and *Diogenidae* (IndVal=0.725,  $p<0.05$ ) as indicator

species. From the group of ocean transects together (Ocean IARP and Ocean), the indicator taxa were Sergestidae (protozoae) (IndVal=1.000,  $p<0.005$ ) and Oplophoroidea (IndVal=0.693,  $p<0.020$ ).

The Redundancy Analyses (RDA) explained the distribution of the taxa with relative abundance greater than 2% in relation to the spatial factors (transects). We observed two main groups: one most related with the transects influenced by ARP, composed in majority by coastal meroplanktonic decapods (Luciferidae protozoae; Diogenidae; Palaemonidae; Brachyura zoeae and Caridea others) and other most related with the ocean area under and out of the ARP influence, composed in majority by oceanic holopelagic decapods (Penaeidae protozoae; Sergestidae and Callianassidae). *Acetes* sp. (protozoae) was more related with Coastal IARP transect while Luciferidae (post-larvae and adults) were more related to the Ocean IARP transect. Although Callianassidae shows greater abundances in Coastal IARP and Ocean IARP transects (Table 2), this taxon was more related to the Ocean transect due to the dominance in abundance when compared to the other taxa in the area without ARP influence (Figure 10).

## DISCUSSION

This study brought new insights in relation to the community structure of planktonic decapods and their spatial variation in coastal, continental margin and oceanic waters influenced by the Amazon River Plume (ARP) during an oceanographic cruise in the retroflection period of the North Brazil Current in 2012. A great abundance of planktonic decapods was recorded in the coastal and oceanic region influenced by the Amazon River plume when compared to the oceanic region without the direct influence of the ARP. These abundance results corroborate with previous studies in the region that inferred the activity of the plume as a true fertilizer for the oligotrophic waters of the western equatorial tropical Atlantic Ocean, thus increasing planktonic productivity in this environment. In the region, published studies with emphasis on planktonic decapods that observed the coastal-oceanic gradient were previously performed by Melo et al. (2014) at stations near the Amazon River mouth, not contemplating the region of retroflection. Thus, this is the first study to investigate the distribution of planktonic Decapoda throughout the retroflection and oceanic region influenced by the ARP.

## **Taxonomy composition and variability in abundance**

Decapod abundance of coastal and oceanic areas influenced by the ARP were compared with other coastal and oceanic regions of the Atlantic Ocean that present plankton enrichment process (such as continental runoff, upwelling events, Island mass effect and the presence of eddies). Coastal abundance was lower than those recorded at the shelf areas in northwest Brazil (SCHWAMBORN et al., 1999b), and greater than that recorded in the Abrolhos Bank, eastern Brazilian shelf (KOETTKER & LOPES, 2013), south Brazilian shelf (BRANDÃO et al., 2015) and Balearic Sea, during autumn (TORRES et al., 2014). Oceanic abundances were greater than those recorded for oceanic regions in northeast Brazil (SCHWAMBORN et al., 1999b) and southern Brazil (BRANDÃO et al., 2015). When compared to oceanic islands, the abundance was greater than those registered for a coastal area of the Fernando de Noronha archipelago, open area of Saint Peter and Saint Paul Rock's (SPSP) and Canary Islands, being lower than the decapod abundance recorded in the inlet area of SPSP (BRANDAO et al., 2013; LANDEIRA et al., 2013; SANTANA et al., 2018).

The planktonic Decapoda community was dominated by meroplanktonic organisms present especially in transects directly influenced by the ARP. The Amazonian coastal region concentrates one of the largest and most developed mangrove forests in the world (HERZ, 1991; GIRI et al., 2011), as well as the largest muddy coast (stretching from the Amazon River mouth to Orinoco River mouth in Venezuela), due to the sedimentary material transported by the Amazon River dispersal system (KJERFVE et al., 2002). In addition to other complex habitats linked to the continental shelf, such as the extensive reef area recently recorded by Cordeiro et al. (2015) and Moura et al. (2016). These environments are potential habitats to the occurrence of different Decapoda taxa that exhibit meroplanktonic larvae, such as brachyuran and anomuran crabs, mud and reef shrimps, providing food and shelter for both adults and larvae (ROBERTSON & DUKE, 1987; SASEKUMAR et al., 1992; LONERAGAN et al., 1997; GIRALDES et al., 2015; DE CARVALHO et al., 2016). This huge abundance of adults decapods explains the greater dominance of meroplanktonic larvae in the Coastal region influenced by the ARP.

In this study, the Brachyura were the planktonic Decapoda that showed the highest abundances in the coastal regions influenced by the ARP, and one of the taxa with the greatest abundance of the planktonic community as observed by Araujo et al.

(2017), for the same study area. Schwamborn et al. (1999b; 2001) and Brandão et al. (2015) related high abundances of decapod larvae to estuarine plumes in northeastern and southern Brazil, where the abundance of brachyuran zoeae is concentrated in higher values within river plume areas than in adjacent habitats. The same pattern was recorded for the plume retroflexion of the Amazon River during the year of 2012 (present study), in which the abundance of brachyuran zoeae decreased drastically in the oceanic region without the ARP influence.

Despite the greater dominance of meroplanktonic larvae, the contribution of holoplanktonic organisms was also significant, mainly due to the great abundance of larvae and adults of luciferid and sergestid shrimps, both in the coastal and oceanic region influenced by the ARP. Low salinity coastal waters are preferable for reproduction of many of these organisms, in particular for the luciferid *Belzebub faxoni* (Borradaile, 1915) (Harper, 1968; Lee et al., 1992; Teodoro et al., 2012), and the sergestid *Acetes* sp. (Robertson & Duck, 1987; D’Incao & Martins, 2000). Thus, the low salinity recorded for the coastal and oceanic regions influenced by the ARP may be an explanation of the enormous abundance of these taxa.

The strong discharge of the Amazon River and Pará River play an important role in the export of planktonic larvae away from the coast towards the continental shelf (present study). Migrations of decapod larvae from more coastal regions to the shelf reduce mortality by planktivorous predators (mainly planktivorous fish and gelatinous plankton), but expose larvae to a greater risk of transport to the adjacent oceanic region (SCHWAMBORN et al., 1999b; LANDEIRA et al., 2009), which result in a lack of adequate habitat for development and settlement. Once on the shelf, this transport is carried by the North Brazil Current in the northwest direction following the Amazon River Plume. Along the NBC transport a large number of larvae exported from coastal habitats northmost of the Amazon River mouth are incorporated into the ARP and during the months of retroflexion these larvae are transported to oceanic region beyond the shelf break through the NBC retroflexion (present study).

Trends of an ontogenetic gradient can be observed for some groups of planktonic decapods in the study area. Coastal regions have concentrated higher abundances of early stages of development of holopelagic shrimps (sergestids, penaeids and carids) that reproduce in coastal regions of lower salinity. These regions offer a greater supply of food and shelter to the larvae (ROBERTSON & DUKE, 1987; LEE et al., 1992; KRUMME & LIANG, 2004; KRUMME, 2009). Something similar was observed for

the larvae of brachyuran crabs. Abundance values of *Brachyura* (zoeae) decreased significantly between the coastal and oceanic areas influenced by the ARP, being more associated with the coastal region. However, the values of abundance and relative abundance of the *Brachyura* (megalopae) did not vary greatly between the coastal and oceanic transect with ARP influence. Thus, the advanced stages of development may be more related to environments further from the coast, corroborating with the hypothesis that typically coastal planktonic decapods are dragged by the NBC to more distant oceanic regions. This explains the dominance of meroplanktonic organisms in transects influenced by the ARP.

Planktonic communities, including larvae of decapods (mainly brachyuran zoeae and megalopae), associated with estuarine substrates (Mangrove leaves) have already been related to the availability of Dissolved Organic Carbon (DOC) in the water, which is abundant in the ARP influence areas, probably used as food resource for these organisms (SCHWAMBORN & BONECKER, 1996). Another important factor is a high abundance of Appendicularia in the ARP-influenced oceanic regions (NEUMANN-LEITÃO et al., 2018). Some small copepods may use the aggregate of particles in the settling Appendicularia houses as a food source (TURNER, 2004; NEUMANN-LEITÃO et al., 2018). Planktonic decapods present different feeding strategies, and probably these Appendicularia and associated fauna serve as food resources for these organisms (GONZÁLEZ-GORDILLO & RODRÍGUEZ, 2003). This may be another explanation for the presence in large abundances of these groups in areas farther from the coast which are expected to be of oligotrophic nature.

### **Meso-scale processes influencing in decapod distribution and assemblage structure**

The peaks of planktonic decapods abundance in stations at the NBC retroflection and ARP (stations 9 and 10 respectively), provide a good evidence of meso-scale processes enriching the plankton abundance in this area. In particular, station 10, where was recorded an abundance 2 times larger than at station 9 and 28 times higher than station 31 (which presented the highest abundance of decapods in the oceanic transect not influenced by ARP).

The presence of strong surface currents with almost anticyclonic pattern and a warm pool in the region of the NBC retroflection (GLICKSON & FRATANTONI, 2001; NEWINGER & TOUMI, 2015; VARONA et al., 2019) may be related to these abundance

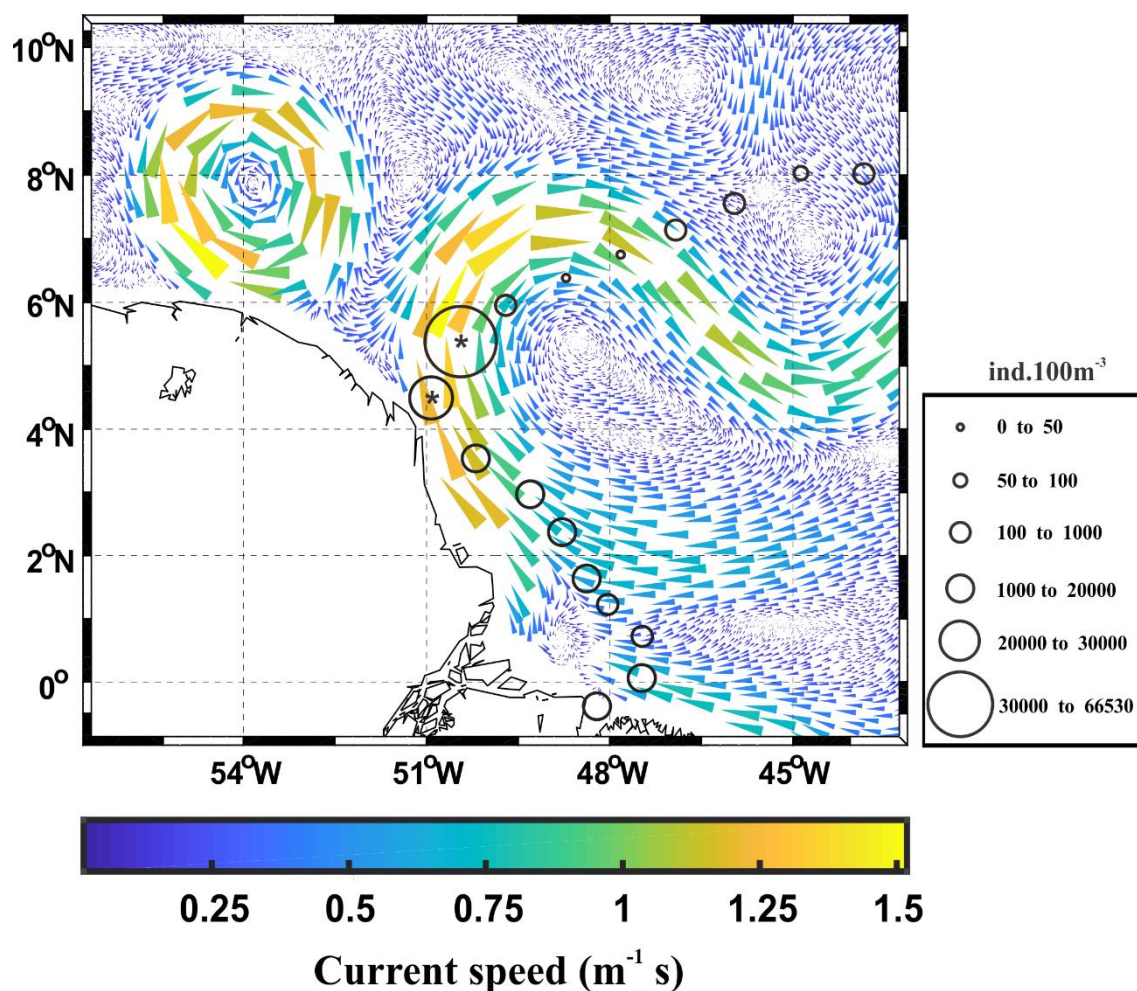
peaks (Figure 3a, b and Figure 11), once coastal and oceanic transported decapods were crowding over the shelf break and slope stations (Figure 11). Anticyclonic eddies are oceanographic phenomena known to cause disturbances that can increase productivity at its outer limits (MCWILLIAM & PHILLIPS, 1983). Larger abundances of planktonic decapods were recorded in waters surrounding warm-core eddies in southeastern coast Australia (MCWILLIAM & PHILLIPS, 1983) and Balearic Sea (TORRES et al., 2014). In addition, low chlorophyll concentrations were found in eddies cores originated from the NBC retroflection (GLICKSON & FRATANTONI, 2001).

Extensive values of phytoplankton and zooplankton biomass were recorded for stations 9 and 10 by Araujo et al. (2017). High phytoplankton productivity rates were also recorded for the same area of these stations during the retroflection period in 2014 by Otsuka et al. (2018), which related the high productivity of the retroflection region to the transition zone of the ARP, regions of abrupt variation of water transparency and large amounts of available nutrients, conditions that favor phytoplankton blooms. Huge numbers of diatoms and diazotrophic bacteria (such as *Trichodesmium* sp.) were recorded for the retroflection region, which may lead to greater abundance of planktonic organisms (ARAUJO et al., 2017; OTSUKA et al., 2018).

In relation to the composition and structure of the community found in these environments, stations influenced by the ARP were dominated by large abundances of Luciferidae at different stages of development, and brachyuran zoeae. These organisms are grazers and their abundances have already been related to diatom and *Trichodesmium* sp. blooms, including at the study area (LEE et al., 1992; SCHWAMBORN et al., 2002; ARAUJO et al., 2017). Mesozooplankton grazing is high in the retroflection region and decreases with increasing salinity (CONROY et al., 2016b). Therefore, the greater abundance of planktonic decapods in the retroflection area is also due to this greater availability of phytoplankton and micro/mesozooplankton as main food resources.

This cross-shelf gradient with assemblages of planktonic decapods associated with benthic organisms near the most coastal and neritic areas, while holopelagic species associated with more oceanic regions, is a common pattern and has been described in several tropical and subtropical areas of the Atlantic Ocean (SCHWAMBORN et al., 1999b; GONZÁLEZ-GORDILLO & RODRÍGUEZ, 2003; LOPES et al., 2006; YOSHINAGA et al., 2010; BRANDÃO et al., 2015). The community of decapods registered for the coastal region was similar to other neritic regions of the Brazilian shelf, such as:

Schwamborn et al. (1997; 1999b), for Itamaracá estuary, the largest estuarine system in northeastern Brazil; Koettker and Freire (2006), in the Arvoredo Archipelago; Fernandes et al. (2002) in the Guanabara Bay and Brandão et al. (2015) from the Cape of São Tomé to the Brazil / Uruguay border. The dominance in abundance of Brachyura zoeae in neritic regions, as well as large abundances of Luciferidae and Caridea shrimps appears to be a pattern in the eastern continental shelf of South America.



**Figure 11.** Monthly variability of surface current dynamic at Western Tropical Atlantic during October evidencing the presence of eddies along NBC retroflexion and NECC. Proportional spatial distribution of total decapods abundance in the sampling stations indicated by circles. \*stations presenting maximum peak of planktonic decapods abundance (stations 9 and 10).

Generally, in the oligotrophic Tropical Atlantic the planktonic decapod abundance is low, but we recorded a greater abundance at station 31 that was at least two times larger than the other sampling stations of the oceanic transect without the ARP influence. Callianassidae larvae, dominate in abundance in this station. Adults of

this taxa are more related to sand and mud bottoms in coastal and shelf slope, just scanty taxa living in ocean bottom under 2000 m depth (MANNING & FELDER, 1991; DWORSCHAK, 2000; BONECKER, 2006; FERNANDES, 2006). Decapods larvae related to continental shelf and slope have a wide distribution offshore (MILLER & MORGAN, 2013), and the presence of sea mounts as shallower points around the 31 station area are potential sites to shelter parental stocks.

### **Ecological and Indicator Indexes and Community structure**

The observed diversity is expected for the Tropical Atlantic region, with lower diversity values for the coastal region and higher values for the oceanic region. Araujo et al. (2017) showed the same trend for the planktonic community, with an emphasis on Copepoda, characterizing two distinct communities. These results in conjunction with the present study reinforce the abundance and diversity gradients for the various compartments and distinct communities in the coastal and oceanic areas influenced by the Amazon River discharge.

The lowest values of diversity recorded for the Coastal IARP occurred due to the high abundance of some taxa such as *Brachyura* zoeae, larvae, and adults of *Luciferidae* shrimps and some other taxa that exhibit habitats associated with the coastal environment at any moment of their development, which can be verified by the lower values of equitability and richness compared to both oceanic regions influenced and not influenced by ARP (Figure 6).

Despite the fact that the ARP-influenced oceanic transect allows the maintenance of high abundances of some typically coastal taxa, as a consequence of the hydrological mechanisms previously discussed, the approximate values of equitability and species richness among the oceanic transects show that the community does not suffer major fluctuations, and that abundance is relatively well distributed among taxa.

Since these environments are strongly connected, oceanic planktonic communities are present in both oceanic transects, which can be exemplified by the results of the analysis of indicator species, which did not categorize an indicator taxon for the transect Ocean IARP separately.

Thus, these distribution gradients, due to the influence of the ARP, may be responsible for the difference in community structure between the three transects, being possible to identify three assemblages of planktonic decapods: 1) Coastal ARP-

influenced environments with a dominance of benthic, shallow water and holopelagic coastal taxa; 2) Offshore ARP-influenced environments with a mixture of coastal and oceanic organisms with meroplankton predominance; and 3) Oceanic areas without the ARP influence predominantly dominated by holopelagic organisms.

The higher contribution of holoplanktonic decapods in oceanic areas is a commonly observed pattern in other Atlantic areas, as well as in coastal regions with high oceanic influence such as oceanic islands in the Tropical Atlantic (BRANDÃO et al., 2013), Subtropical Atlantic (LANDEIRA & LOZANO-SOLDEVILLA, 2018) and Western Mediterranean (TORRES et al., 2014), in addition to the Southernmost Brazilian shelf (BRANDÃO et al., 2015).

#### 4.1 CONCLUSION

The present study provides information on the abundance and diversity distribution, taxonomic composition and the relationship with oceanographic features of planktonic decapod communities in the Western Tropical Atlantic influenced by the Amazon River Plume. The coastal-oceanic gradient of abundance and diversity present a similar trend to other tropical coastal regions, but with considerably higher abundances. The planktonic decapod community in the study area were mainly composed by larvae of benthic organisms in the coastal and oceanic areas with ARP influence and holopelagic organisms at the oceanic area without the ARP influence. High abundances of brachyuran larvae and luciferid shrimps recorded in the present study are an indicative of the important contribution of planktonic decapods in the trophic transfer of energy to the macrozooplankton community of coastal and oceanic environments influenced by the ARP, a role mainly attributed for copepods along coastal and oceanic area of the tropical Atlantic. Our results showed that complex current dynamics and mesoscale events can lead to offshore mixing of coastal and oceanic communities. However, it is unlikely that these advected coastal organisms could encounter a suitable settlement environment at deep oceanic areas. Future studies covering the annual and seasonal of abundance and biomass variation shall clarify the distribution and biomass contribution of these organisms in the oceanic area during periods with and without the influence of the retroflection of the Amazon River Plume.

## ACKNOWLEDGEMENTS

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## 5 CONSIDERAÇÕES FINAIS

- Os resultados dessa pesquisa indicaram um impacto significativo da influência da pluma dos rios Amazonas e Pará na comunidade planctônica do Oceano Atlântico Tropical Ocidental, modificando o gradiente de abundância e composição taxonômica.
- A hipótese de que o gradiente nerítico-oceânico para abundância da comunidade de decápodes planctônicos se diferencia de outras regiões do Atlântico tropical, foi confirmada, uma vez que a região oceânica influenciada pela pluma apresentou grande abundância de decápodes, em oposição a área oceânica que não está sujeita a mesma influência da pluma.
- O padrão de distribuição de maiores abundâncias na região da plataforma e menores abundâncias para áreas oceânicas, característicos de ambientes tropicais, foi observado para a área de estudo.
- Os valores de diversidade seguiram a mesma tendência de distribuição observadas em estudos prévios na costa brasileira, apresentando maiores valores na região oceânica.
- Larvas de organismos costeiros dominaram em abundância nas regiões influenciadas pela pluma durante o período de amostragem. Em contrapartida, larvas e adultos de decápodes holopelágicos dominaram nas estações oceânicas sem influência da pluma do rio Amazonas.
- A alta abundância de larvas de decápodes na região costeira e oceânica influenciada pela pluma é indicativa da importante contribuição desses organismos na transferência de energia do mesozooplâncton, uma vez que os decápodes representam um abundante recurso alimentar para várias espécies macrozooplânctônicas, como larvas de peixes de grande importância econômica na região norte do Brasil.
- A necessidade de proteção aos ambientes costeiros e da plataforma continental foi evidenciada, uma vez que esses ambientes desempenham um importante papel no suprimento larval de decápodes. Desta forma, trabalhos futuros com o intuito de investigar a contribuição em biomassa desses organismos para as áreas influenciadas pela ARP são necessários.

- Mesmo com o conceito pré-estabelecido de que a região oceânica influenciada pela pluma é categorizada por salinidades  $<35$ , sua influência sobre a comunidade planctônica não se restringe a este parâmetro. Uma vez que o material transportado pela pluma permanece disponível para o fitoplâncton, gerando uma resposta no mesozooplâncton mesmo após uma mudança na salinidade superficial. Isso acontece devido a ação de ventos e marés, responsáveis pela mistura das águas da pluma e do oceano. Desta forma, uma estação com salinidade superficial de 37, pode estar sob influência da pluma do rio Amazonas, desde que esta seja comprovada a partir de análises físicas, químicas e/ou biológicas.
- A importância da análise de amostras planctônicas *in toto* foi evidenciada, já que muitos espécimes de decápodes que apresentam registros esparsos ou ausentes para o Atlântico Tropical, são negligenciados com o uso da metodologia de fracionamento (por exemplo: *Enoplometopidae*; *Anphionides reynaudii*; *Aristeidae*). Porém, fatores como a falta de disponibilidade de descrições taxonômicas para muitas fases larvais dos grupos analisados, assim como a grande abundância de organismos planctônicos, material em suspensão e amontoados de cascas de apendicularia; nas amostras planctônicas provenientes das regiões influenciadas pela pluma, dificultaram a triagem e identificação dos decápodes, aumentando em muitas vezes o tempo de esforço laboratorial.

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