Larval dispersal of Brachyura in the largest estuarine / marine system in the world

Francielly Alcântara de Lima¹, Davi Butturi-Gomes², Marcela Helena das Neves

Pantoja¹, Jussara Moretto Martinelli-Lemos¹

¹ Research Group on Amazon Crustacean Ecology (GPECA). Nucleus of Aquatic Science and Fisheries of Amazon (NEAP). Federal University of Pará (UFPA).

² Federal University of São João del-Rei, Campus Santo Antônio, Mathematics and Statistics Department.

^{#a}Current Address: UFPA, Avenida Perimetral 2651, Terra Firme, Belém-PA 66077-830, Brazil.

^{#b}Current Address: Praça Frei Orlando 170, Centro, São João del-Rei- MG, 36307-352, Brazil.

* Corresponding author: francielly@ufpa.br

Conceived and designed the experiments: JMML. Analyzed the data: FAL DBG MHNP JMML. Contributed reagents/materials/analysis tools: FAL DBG JMML. Wrote the manuscript: FAL. Designed the study: JMML. Analysis of the intensive multi-model approach: DBG. Performed the Brachyura taxonomy and morphology supervising and their identification: FAL MHNP. Drafted the manuscript: FAL DBG MHNP JMML. All authors read and approved the final manuscript.

Abstract

For the first time, this study monitored six sites in a wide transect with approximately 240 km radius on the Amazon Continental Shelf (ACS) every three months. The objective was to analyze the larval composition of Brachyura, its abundance in shallow/subsurface and oblique hauls, the extent of larval dispersion related to the estuary/plume, and to predict the probability of occurrence and abundance for the temperature, salinity, and chlorophyll-*a* profiles of the water column. A total of 17,759 identified larvae are distributed in 8 families and 25 taxa. The water salinity was the best predictor of larval distribution. The statistical models used indicated that Panopeidae and Portunidae larvae are more frequent and more likely to occur in shallow water layers, while Calappidae occur in deeper layers, and Grapsidae, Ocypodidae, Sesarmidae, Pinnotheridae and Leucosiidae occur similarly in both strata. The larval dispersion extent varies among families and throughout the year while the groups are distributed in different salinities along the platform. The probability of occurrence of Portunidae is higher in ocean water (≥ 33.5); Grapsidae, Panopeidae, and Pinnotheridae is higher in intermediate and ocean salinity waters (25.5 to 33.5); Ocypodidae, Sesarmidae and Calappidae is higher in estuarine and intermediate salinity waters (5 to 25.5), whereas Leucosiidae, euryhaline, occur in all salinities (5 to 33.5). Furthermore, the Amazon River seasonal flow and plume movement throughout the year not only regulate the larval distribution and dispersion of estuarine species but are fundamental for the ACS species, providing the necessary nutrient input for larval development in the region plankton.

Keywords: Amazon, Intensive multi-model approach, Decapoda, Larval export, vertical distribution, zooplankton.

Introduction

The various aspects of the Brachyura larval cycle, such as morphology, tolerance to environmental factors, and geographic distribution have been studied from the 1960s to the present day [1–3]. The larval dispersion strategies (retention and export) of estuarine crab species are known to be strongly correlated with vertical migration in the water column [4,5] since the speed and direction of horizontal currents vary with depth [6,7]. The changing vertical position of larvae, either by daily or ontogenetic migration, allows using the stratified currents for displacement in different distances and directions [8], the so-called Selective Tidal Stream Transport (STST) [9,10].

Dispersion strategies have been identified especially from laboratory experiments used to assess larva tolerance to varying abiotic factors and based on these results suggest the adopted migratory behavior. This type of study has already been carried out for crabs of the families Ocypodidae [11], Panopeidae [12], Varunidae [13], among several others. However, obtaining a successful experiment simulating environmental conditions and guaranteeing complete larval development, especially counting on obtaining ovigerous females whose eggs are in hatching conditions is not an easy task, which certainly contributes to the lack of data for most species. On the other hand, investigating larval distribution in a natural environment (estuary and continental shelf) and providing valuable information on the species life cycle and migratory behavior, also presents several difficulties especially in countries where research investment is low, justifying the low number of publications on this topic compared to studies developed with the adult population in the same environments [14–20].

This scenario is aggravated in the vast and complex Amazon region, which harbors one of the largest aquatic diversities on the planet so that a significant portion of species

is still unidentified and has unknown distribution limits [21–23], except for some relatively well documented commercial fish groups [24–26] and, recently, zooplankton [18], shrimps [27] and thalassinoids [28]. In estuarine and coastal Amazonian regions, data on the distribution of *Brachyura* larvae and their regulatory factors are extremely limited [29] and practically nonexistent for the extended continental shelf (≈ 240 km from the coast) [30], one of the widest in the world. This gap can be explained, mainly, by the high financial cost of sampling and strong currents, among others, which hinder the access to the area and limit the knowledge on the *Brachyura* fauna life history and geographical distribution.

This megadiverse and conspicuous environment of the Amazon Continental Shelf (ACS) [26] drains an average discharge of 5.7×10^2 m³/year from the Amazonas/Araguaia/Tocantins hydrographic system [31]. This freshwater mass from the continent forms a surface plume on the continental shelf, whose trajectory changes throughout the year due to the interaction of different factors, such as the Amazon River discharge, North Brazil Currents (NBC), North Equatorial Countercurrent (NECC) and Guyana Current (GC), the atmospheric Intertropical Convergence Zone (ITCZ), as well as winds and tides [32,33]. In addition to the enormous water discharge, a large supply of organic matter and sediment, approximately 900 to 1150×10^6 ton/year [34,35], greatly affects the planktonic dynamics and biomass of the adjacent coastal and Atlantic regions [36,37], making the Amazon estuary unique among estuaries worldwide [38].

To date, the occurrence of 194 species of adult *Brachyura* has been recorded in the ACS, of which only 74 have some larval stage described [39] while 34 species in their benthic phase are constantly captured as accompanying fauna by the industrial fishing fleet with emphasis to the pink shrimp *Farfantepenaeus subtilis* (Pérez-Farfante, 1967) [40]. In this study, the larval period of *Brachyura* was evaluated regarding species

composition, abundance in rare and deep environments, the larval dispersion extent related to the estuary/plume, frequency of occurrence (FO) in the plume categories, predicted probability of occurrence (PO) and abundance for the temperature, salinity, and chlorophyll-*a* profiles in the ACS. Our objective is to improve the knowledge on biodiversity of this important component of the aquatic food chain, as well as to characterize the group configuration in the plankton of the continental shelf, revealing possible larval dispersal strategies, distribution, and life cycle in the largest estuarine-marine region of the world. It was expected that all larval developmental stages of each species should be distributed on their parental populations over the ACS.

Material and Methods

Study area

The study was conducted on the Amazon Continental Shelf (ACS), specifically in the area affected by the plume of the Amazon and Tocantins/Araguaia Basins. We sampled in six different locations along the coastal area of Ilha do Marajó to near the slope, from 23 to 233 km away from the coast (Fig. 1), and every quarter from July/2013 to January/2015. The Amazon River discharge to the ACS has strong seasonality, with approximately 220,000 and 100,000 m³ s⁻¹ maximum and minimum flows in May and November, respectively [41,42]. Additionally, the Amazon plume that remains close to the continental margin in the winter in the Northern Hemisphere (January to March / April), begins to spread to the north during the peak discharge of the Amazon River in the spring (May) [33,43]. In the summer (June to July), the NBC retroflexion takes the plume to the east and, in the fall (September), 70% of the plume water is exported to the east via this route [33,43].

Fig 1. The Amazon continental shelf, northern Brazil, and the six sampling sites surveyed (23 km, 53 km, 83 km, 158 km, 198 km, and 233 km).

Data collection

Two sets of samples were collected, horizontal and oblique hauls in each site at different coastal distances (23, 53, 83, 158, 198, and 233 km). Two zooplankton hauls were conducted: one horizontal subsurface at 0.5 m from the surface and another oblique ('V'-shaped, covering up to 75 % of the local depth). Both hauls used a plankton trawl consisting of a 2 m long conical net with 200 µm mesh, 60 cm opening diameter, and a coupled flow meter. The hauls lasted five minutes at a speed of approximately 2 knots ($\approx$ 4 km / h). Simultaneously, water temperature (°C), salinity, and chlorophyll-*a* (µg / L) contents were measured, using a CTD probe (Hydrolab DS 5).

The obtained 84 samples (7 expeditions x 6 sites x 2 hauling methods), with an initial volume of 500 mL each, were preserved in formaldehyde buffered with sodium tetraborate, 4% final solution. In the laboratory, the samples were fractionated into 250 mL aliquots with a Folsom-type subsample. All Brachyura larvae in the aliquots were dissected and identified to the lowest taxonomic level possible by observing the morphological parameters, such as the arrangement and number of spines and setae in the antennae, antennules, maxilliped, maxilla, abdomen, and telson, under an Axioscope Zeiss A1 optical microscope (Carl Zeiss, Oberkochen, Germany) [44–60]. The recent taxonomy was checked in the World Register of Marine Species [<http://www.marinespecies.org>]. After identification, the non-dissected larvae were

deposited and registered in the Carcinological Collection of the Museu Paraense Emílio Goeldi (MPEG).

Data analyses

Density was estimated (larvae. m⁻³) by dividing this number by the water volume filtered through the plankton net. The volume was given by the number of rotations of the Hydrobios flowmeter attached to the net aperture, based on the difference between the initial and final numbers observed in each trawl, and calculated as $V = A \times R \times C$, where A = net aperture area ($A = \pi.r^2$), R = number of flowmeter rotations during the haul ($D_f - D_i$, final and initial numbers, respectively), and C = measurement factor (m rotations⁻¹ = 0.3) determined after device calibration.

The frequency of occurrence (FO %) of each species larvae was given as $FO = a \times 100/A$, where a = number of samples containing the species, and A = the total number of samples. The results were categorized as follows: very frequent ($FO \geq 70\%$), frequent ($30 \leq FO < 70\%$), infrequent ($10 < FO < 30\%$), and sporadic ($FO \leq 10\%$) [61].

The expected abundance of each species group (either family or genus, depending on the lowest taxonomic level identified) was predicted by an intensive multimodel approach [62]. We fit several different predictors to each dataset, corresponding to each group abundance data. Given the presence of many zeros in our datasets – some of which might simply be structural zeros – we conditionally predicted the expected abundance in the predicted probability of occurrence of each species group using the presence-absence data. The details of each step of the data analysis are given below.

To the presence-absence data, we fit binomial generalized linear models with logistic link-function [63] using different predictors. We computed the predictors by

taking the powerset (excluding, of course, the empty set; please check [64] for clarifications on this issue) of the available covariables (plankton net depth, temperature, chlorophyll-*a*, distance from the estuary, salinity, and their squared values) and used each element of the powerset to fit the models, which yields 511 different models. For each model, we computed the Akaike weights:

$$\omega_j = \frac{\exp\{-\Delta_j/2\}}{\sum_{i=1}^M \exp\{-\Delta_i/2\}}, \quad (1)$$

where ω_j is the Akaike weight for the j -th model and $\Delta_j = \text{AIC}_j - \min_{i \in M} \{\text{AIC}_i\}$ is the scaled AIC for the j -model in a set of M models. The value of M is the difference between the number of elements in the powerset of covariables (511) and the number of models that achieved convergence; thus, M may have varied greatly between any two species groups. Finally, the probability of occurrence (PO) was predicted based on all models weighted by their corresponding Akaike weights. We used, as a reference scenario for the predictions, the median values of temperature and chlorophyll-*a* and three different values of salinity (5, 23, and 33.5) for estuary distance varying between 23 and 233 km (respectively, the nearest and the farthest sites).

Given the predicted PO using the presence-absence data, we fit Poisson generalized linear models with log-link function to the observed abundance data using the previous rationale (several models, each one with one element of the powerset of covariables, weighted by the Akaike weights, discarding models that did not converge, computing the predictions on the reference scenario). Since the observed abundances largely depend on the water volume collected in the sample, we set the volume as an offset in all models.

The final prediction for the expected abundance of each group is given by the product between its predicted abundance and the PO in the reference scenario. It is noteworthy that our multimodel and information-theoretical approach does not allow (and meaningless) to report p-values of any kind [62,65], thus we used the total weight of each variable across plausible models (those were $\Delta_j < 2$, a widely used threshold), varying from 0 (never important) to 1 (always important), as a measure of influence on the predictions.

Results

Environmental variables

The water temperature amplitude in the ACS was 7°C (23 to 30°C), with the highest value recorded in January (begin of the more intense rain period) and the lowest in July (begin of the less rainy period). The lowest temperatures were recorded at high depths, from 200 km away from the continent. However, a temperature of about 28 °C was predominant in most of the shelf extension. The water salinity varied widely (amplitude of 36), with a minimum of 2 (May, rainy season) and a maximum of 38 (January), while increasing gradually away from the coast. The chlorophyll-*a* content ranged from 0.3 to 85.1 µg/L⁻¹, in January, decreasing as the coast-ocean distance increased (for detailed environmental variables in this region, see [27]). The Amazon River outflow was higher (291,900 m³.s⁻¹) in May and lower (≈110,000 m³.s⁻¹) in October / 2013-2014, with a water volume variation similar to the historical average from 1985 to 2015 (Fig 2).

Fig 2. Historical outflow variation of the Amazon River (Óbidos station, Pará) from 1985 to 2015 provided by the Brazilian National Water Agency (ANA) (<http://www.snirh.gov.br/hidroweb/>). Black circles indicate field sampling.

Larval species/family composition

A total of 17,759 identified larvae were distributed in eight families and 25 taxa (Table 1).

Table 1. Larval composition and frequency of occurrence of Brachyura on the Amazon Continental Shelf. Legend according to [66] that characterize the Amazon River plume depending on salinity (S): E = estuarine plume ($0 < S < 20$), IP = intermediate plume ($20 < S < 31$), OP = outer plume ($31 < S < 36$), OO = open ocean ($S > 36$).

Taxon	Stages	Month	Hauls	Plume			
				E	IP	OP	OO
Calappidae							
<i>Calappa</i> sp.	ZI–ZIV	Oct/14	O				
Grapsidae							
<i>Goniopsis cruentata</i>	ZI	Oct/13	O				
Grapsidae n. id.	ZII–ZIV	May/14	O				
<i>Pachygrapsus gracilis</i>	ZI–ZIII	Oct/13	O				
Leucosiidae							
Leucosiidae n. id.	ZII–ZIV	Jul/14	S				
<i>Persephona</i> spp.	ZI–ZIV	Oct/13	O				
Ocypodidae							
Gelasiminae 1	ZI	May/14	S				
Gelasiminae 2	ZI	May/14	S				
Gelasiminae 3	ZI	May/14	S				
Gelasiminae n. id.	ZII–ZVI	Jan/14	S				
<i>Leptuca cumulanta</i>	ZI, ZII	Oct/13	O				
Megalopa 1		Jan/14	O				

Megalopa 2		Jul/14	S	
<i>Minuca rapax</i>	ZI, ZIII, ZIV	May/14	S	
<i>Uca maracoani</i>	ZI, ZIII, ZIV	Jul/13	O	
<i>Ucides cordatus</i>	ZI	Jan/15	S	
Panopeidae				
<i>Hexapanopeus</i> spp.	ZI–ZIV	Jan/14	S	
Megalopa		Jan/15	S	
<i>Panopeus lacustris</i>	ZI–ZIV, M	Oct/13	S	
<i>Panopeus</i> sp.	ZI–ZIV	Oct/13	S	
Pinnotheridae				
<i>Austinixa</i> sp.	ZI–ZV	Jan/14	S	
<i>Dissodactylus crinitichelis</i>	ZI–ZIV	Jan/15	S	
<i>Pinnixa</i> sp.	ZI–ZV	Jan/14	S	
Megalopa		Jan/15	O	
Portunidae				
<i>Achelous</i> spp.	ZI–ZVII	Jul/13	S	
<i>Callinectes</i> spp.	ZI–ZVIII	Jul/13	S	
Megalopa 1		Jul/14	S	
Megalopa 2		Jan/14	O	
Portunidae n. id.	ZI–ZIII	May/14	S	
Sesarmidae				
<i>Armases rubripes</i>	ZI–ZIV, M	Jan/14	S	

233

234 ZI = zoea I; ZII = zoea II; ZIII = zoea III; ZIV = zoea IV; ZV = zoea V; ZVI = zoea VI; ZVII =
235 zoea VII; ZVIII = zoea VIII; M = megalopae; n. id. = not identified; S = sub-superficial; O =
236 oblique; Heat map = <10%; ≥10–30%; ≥30–70%; ≥70%

237

238 *Panopeus lacustris* Desbonne in Desbonne and Schramm, 1867 was the most
239 abundant species (67% FO, of which 57% megalopa), followed by *Achelous* spp. De
240 Hann, 1833 (12%) and *Armases rubripes* Rathbun, 1897 (9%). Both phases of larval
241 development (zoea and megalopa) of *P. lacustris*, *A. rubripes*, Gelasiminae Miers, 1886

and Portunidae Rafinesque, 1815 were found in the ACS. Also, the occasional occurrence of *Leptuca cumulanta* (Crane, 1943) ZI and ZII stages, and *Ucides cordatus* (Linnaeus, 1763) and *Goniopsis cruentata* (Latreille, 1803) ZI were also observed but not included in the mathematical models, whereas the other species larval stages occurred heterogeneously on the ACS (Table 1). *Achelous* spp., *A. rubripes*, *Calappa* sp. Weber, 1795, *Callinectes* spp. Stimpson, 1860, Gelasiminae 2, *Pachygrapsus gracilis* (de Saussure, 1857), *P. lacustris*, *Pinnixa* sp. White, 1846 larvae occurred over the entire study period. Whereas *Hexapanopeus* spp. Rathbun, 1898 zoea did not occur in May only and Portunidae did not occur during the lower outflow in October. Additionally, *Minuca rapax* (Smith, 1870), Gelasiminae 1, 2 and 3 larval density peaked during the higher river outflow in May (see supporting information S1 to S8).

Larval dispersal (depth strata, coastal distance, and estuarine plume)

The mathematical model results indicate different patterns of larval dispersion along the continental shelf. Regarding the disposition in the water column, Panopeidae Ortmann, 1863, Pinnotheridae De Haan, 1833, and Portunidae were more abundant and had a higher PO in subsurface waters while *A. rubripes* and Ocypodidae larval stages were more abundant in the water column. *Calappa* sp. larvae occurred almost exclusively in the water column, while Grapsidae MacLeay, 1938 and Leucosiidae Samouelle, 1819 abundances were similar in both strata, surface and water column (Fig 3, 4, 5).

Fig 3. Expected abundance/ probability of occurrence of Brachyura larvae. Grapsidae (A), Panopeidae (B) and Pinnotheridae (C).

Fig 4. Expected abundance/ probability of occurrence of Brachyura larvae. Portunidae (D), Ocypodidae (E) and *A. rubripes* (F).

Fig 5. Expected abundance/ probability of occurrence of Brachyura larvae. *Calappa* sp. (G) and Leucosiidae (H).

The occurrence of crabs was heterogeneous, varying according to the distance from the coast and water salinity. Portunidae larvae had a greater abundance and higher PO in waters with 33.5 salinity and furthest from the continent, from 83 km away from the coast (Fig 4D). On the other hand, Ocypodidae (Fig 4E) and *A. rubripes* (Fig 4F) abundance and PO were higher near the coast, up to 158 km, in estuarine and intermediate plume waters, with 5 and 25.5 salinity, respectively. Grapsidae (Fig 3A), Panopeidae (Fig 3B), and Pinnotheridae (Fig 3C) larval stages were also more abundant in coastal waters, however, with higher PO in waters with 25.5 and 33.5 salinity. *Calappa* sp. larvae occurred with especially higher density at 158 km (Fig 5G) between 83 and 233 km from the coast, mainly in waters with 5 and 25.5 salinity, while Leucosiidae larval distribution (Fig 5H) was similar throughout the continental shelf therefore, occurring in several salinities.

During the highest flow period, *Pinnixa* sp., Grapsidae, Panopeidae, Portunidae and Leucosiidae larvae were concentrated in the mid and outer continental shelf since the freshwater plume “pushes” the larvae to locations away from the coast. The opposite was observed during the lowest outflow, these larvae concentrated near coastal areas (23 and 53 km from the coast) due to the lower freshwater outflow entering the ACS (Fig. 6 and 7). On the other hand, Ocypodidae larval dispersal expanded up to 198 km in the highest flow and decreased to 23 km away from the coast in the lowest flow period, following the expansion and retraction of the freshwater plume, respectively. Furthermore, few taxa were not affected by the Amazon plume. The *A. rubripes* larvae occurred particularly in three sites closest to the coast (23, 53, and 83 km) with few variations in the period and

among months whereas *Calappa* sp. larvae occurred 158 km away from the coast, near reef areas, regardless of varying river flow, and *D. crinitichelis* Moreira, 1901, occurred only between 83 and 158 km away from the coast.

Discussion

The results indicate that the larval dispersal of Brachyura along the ACS is structured by the Amazon River plume, whose outflow reaches the highest and lowest volume in May and October, respectively. Larval species that hatch near the coast are subject to the same abiotic factors as light, temperature, pressure, and salinity [67], and biotic factors such as predators and food availability [68,69]. However, each taxon can adjust its vertical position up or down the water column according to the changing exogenous stimuli [10,70,71], affecting the direction and the distance that the larvae are horizontally transported [19,72]. These different responses are probably related to characteristics intrinsic to each species or family, such as adult habitat [73], osmoregulation [74], presence of predators [75], among other factors.

In the export process, Brachyura larvae are carried along the plume edge towards the ACS. In the maximum flow conditions, the Amazon plume can extend up to 300 km from the coast [76] and up to 10 meters deep [77], with salinity below 35 [78]. The plume edge is usually controlled by both, wind and Ekman flow, so that the balance of the wind mix (which undoes the vertical stratification) and the Ekman transport by buoyancy (which reinforces the vertical stratification) results in a plume edge with slowly increasing salinity as it moves into the sea carrying the larvae [79–81].

The pattern observed in other world regions suggests that temperature is one of the most important seasonal factors controlling the biological processes within plankton

populations and communities [82,83]. In this study, however, temperature and chlorophyll-*a* were not important dispersal predictors so that the different larval strategies seem to be mainly regulated by the strong influence of the Amazon River outflow on the water salinity and the Amazon plume expansion and retraction throughout the year. Increases in meroplankton abundance are likely to be ascribed to high nutrient input and primary production, e.g. chlorophyll-*a* between 4 and 5 (mg/m³) [15] and the fact that chlorophyll-*a* is widely available in PCA, this factor does not explain the variation in larval abundance. Although plume flow was not closely followed in this study, its influence on the salinity is notorious and, consequently, on the larval community of brachyurans on the continental shelf, diverging from other coastal regions due to the peculiar characteristic and strength of this hydrological system. Other factors frequently related to the movement of planktonic larvae, such as acting tides, winds, and surface currents [19,84] were not addressed in this work, but these important parameters should be investigated in future research. In this context, the larval dispersion of each family and its distribution in the water column on the ACS is detailed below.

Grapsidae

The Grapsidae zoea (*P. gracilis* and Grapsidae n. id.) is distributed similarly in the water column and surface layer, with higher expected abundance and PO in waters with salinity between 25.5 and 33.5, estimated to be more coastal. However, the larvae moved away from the coastal region, occurring only in 198 and 233 km during the highest discharge of the Amazon River (May) but moved closer to the continent, where water salinity is higher compared to the plume, during the lowest flow period.

Our results confirm the larval export proposed for *P. gracilis* [85], however PO is higher in more coastal areas, a behavior also adopted by *P. transversus* (Gibbes, 1850) [86], *P. crassipes* Randall, 1840 [5], *P. marmoratus* (J. C. Fabricius, 1787) [87], *Hemigrapsus sanguineus* (De Haan, 1835) [88], and *Geograpsus lividus* (H. Milne Edwards, 1837) [89]. Similar to *P. gracilis*, larvae of the *Pachygrapsus* and *Hemigrapsus* Dana, 1951, genera also go through all the larval developmental stages in the mid-continental shelf [90,91], but *P. crassipes* zoeae are distributed in all water column strata, surface, and bottom [67]. Whereas *Hemigrapsus* zoeae have negative geotaxis and swim towards the surface [72], spending the entire larval cycle about 15m deep [92], revealing that the vertical arrangement varies among different genera and species of grapsids in the water column.

The *P. gracilis* zoea I, II and III were the most abundant larvae of the family in the ACS, and occurred every month, confirming the continuous reproduction, similar to *P. transversus* [93,94]. However, larval peaks for the species were observed on the ACS and estuary in October and May, respectively [29,85]. *P. gracilis* zoeae seem to have a high tolerance to varying salinity since three of at least five zoea stages that make up the genus [95,96] are found over the entire ACS extension (23 to 233 km) and in different salinity strata. No megalopa of this species was found in the ACS, despite the information that they develop on the continental shelf [97] and immigration is correlated with high salinity and current speed, typical of estuary flood tides.

Seasonal reproduction has also been observed for *G. cruentata* in subtropical regions, with reproductive peaks in the least rainy season in some places [98,99], and in the rainy season in others [100,101]. In the Amazon estuary, the ZI larval peak occurs during the transition from rainy to less rainy period (May to July), with low density in the remainder of the year [29]. Based on this, other larval stages of *G. cruentata* should be

present in the ACS throughout the year, however, a single occurrence of ZI was recorded in October. In this sense, future work should clarify such gaps regarding *G. cruentata* and other grapsids.

Panopeidae

Panopeidae larvae are distributed mainly in the surface layer of the water column, both zoea and megalopa had a higher predicted abundance and PO associated with intermediate and oceanic salinities (25.5 and 33.5), as well as lower and higher density in May and October, respectively. Because *Panopeus* H. Milne Edwards, 1834 larvae occur in the full extent of the ACS (≈ 240 km), they seem to have greater tolerance to ocean waters [53] compared to *Hexapanopeus* spp. The latter also performs larval export, but dispersal extends up to 158 km from the coast, with all its zoea stages (I to IV) developing on the mid-continental shelf, similar to *Lophopanopeus bellus* [92].

The zoeal morphology of *Hexapanopeus* spp. and *Rhithropanopeus harrisii* (Gould, 1841) is similar. They present long rostral, dorsal, lateral, and abdominal spines, in addition to long antennae [53,102] and chromatophores [1], morphological characteristics generally associated with species that perform larval retention [103,104], for providing more resistance to sinking and greater fluctuation in microcurrents [105], ensuring permanence close to the parental habitat. Still, this is a questionable argument, considering that some larvae with long spines perform larval exportation [106], such as zoeae of *Panopeus* [107] and *Callinectes* [57] (smaller spines compared to *Hexapanopeus*). This export strategy has already been suggested for other panopeids such as *Dyspanopeus sayi* (Smith, 1869) [108], *Eurypanopeus depressus* (Smith, 1869) [109], *Panopeus herbstii* H. Milne Edwards, 1834 [110], *Panopeus africanus* A. Milne Edwards, 1867 [87], and confirmed for *Panopeus lacustris* [111].

Pinnotheridae

The predicted abundance and PO for Pinnotheridae larvae were slightly higher in surface waters and with intermediate and oceanic salinity (25.5, 33.5) while all zoeal stages were present in the ACS. Further, *Pinnixa* and *Austinixa* Heard and R.B. Manning, 1997 larval dispersal reached half the extension of the continental shelf (158 km).

Pinnotheridae larval export has already been suggested based on the high abundance of zoea I larvae in the superficial layer during the estuary low tides, in addition to a positive correlation between larval density and salinity [112], which is in line with our results. There are reports in the literature on the zoea I departure from the California estuary (USA), where the complete larval development of *Pinnixa faba* (Dana, 1851), *P. tubicola* Holmes, 1895, *Pinnotheres pugettensis* Holmes, 1900, and *Scleroplax granulata* Rathbun, 1894, occurs within the continental shelf, 6 km away from the coast [92], with zoeae and megalopae collected at 17 and up to 49 m depth, respectively. However, the magnitude of this continental shelf can not be compared to the vastness of the ACS. Still, in the Chesapeake Bay, all larval stages of *Pinnixa chaetoptera* Stimpson, 1860, *Pinnixa sayana* Stimpson, 1860, *Tumidoheres maculatus* (Say, 1818) and *Zaops ostreum* (Say, 1817) were always found close to the bottom, indicating larval retention [2,113]. Likewise, larval retention for *Pinnixa gracilipes* was also suggested in an Amazonian estuary due to the presence of ZI, ZII and ZIV in the lower estuary [29].

In this context, we believe that the different patterns may be related to the host habitat, since Pinnotheridae consists basically of symbiotic crabs or parasites of benthic invertebrates, which inhabit thalassinoids burrows [114], Polychaeta tubes [115], bivalves [116], echinoderms, among others. And because the symbiotic relationships can

vary from quite host-specific to very non-specific [117], there will likely be species adaptations to the different host environments, which should be further investigated in more detail.

In our study, only the *Pinnixa* sp. distribution was influenced by the Amazon River outflow since larvae occurred 83 km and 23 km from the coast during high and low discharge, respectively. The *Austinixa* sp. distribution did not vary much while *D. crinitichelis* zoeae were found only 83 and 158 km from the coast, places that overlap the coral reefs of the ACS, potential habitats of several Echinoidea, host organisms of the adult crab (mainly the Orders Clypeasteroidea and Spatangoidea) [55], thus explaining the restricted presence of *D. crinitichelis* zoeae in these overlapping sites. Many of these ACS echinoid species are still unknown, however, possibly these organisms also occur on the Northeast continental shelf (32 species) [118,119]. In our samples, no *D. crinitichelis* megalopae were found due to the obligatory parasitism of this larva, which needs the host for feeding and metamorphosis for the first crab stage and, therefore, is not found in plankton [55].

In the ACS, the larval occurrence of *D. crinitichelis* was recorded only in October, May and January, while *Pinnixa* and *Austinixa* were present throughout the year, with a density peak in January, consistent with the reproductive habits already reported in other species of *Pinnixa* [115;120] and *Austinixa* [114;121].

Portunidae

In the Amazon region, portunids, such as the genus *Callinectes*, occur in estuaries and on the continental shelf, whereas *Achelous*, *Arenaeus* Dana, 1851, *Charybdis* De Haan, 1833 and *Cronius* Stimpson, 1860, occur on the continental shelf only [39, 40]. In the ACS, we

found all larval stages of *Achelous* spp. and *Callinectes* spp., as well as Portunidae larvae distributed in the superficial layer, with greater abundance and PO from 83 km from the coast and in high salinity (33.5), where the later developmental stages are highly abundant. Also, larvae of this family are found more distant (83 to 233 km) and closer (23 to 233 km) to the coast during the high and low outflow of the Amazon River, respectively, indicating their affinity with ocean waters while confirming this group previous work on the larval stages. We know that *Achelous rufiremus* (Holthuis, 1959) is the most abundant benthic macroinvertebrate species at almost four degrees of latitude in the ACS [40, 122] but unfortunately, there is no description of the larval stages of this species, so despite containing all the larval stages in our samples, these could not be identified.

It is known that estuarine portunids perform larval export, which begins with female spawning at the mouth of the estuaries [123–125], and after hatching, as observed in *Callinectes sapidus* Rathbun, 1896, the zoea I larvae that have strong negative geotaxis [126], remain in the upper two meters of the water column to take advantage of the bay/estuary outflow currents, which, driven by the wind, head towards the continental shelf [79, 106]. These larval patches move along with the plume edge, and after a few days drifting on the continental shelf, they move from the plume edge to the open sea [80], remaining in superficial waters during the entire larval development period [79,127,128]. This arrangement in the water column also favors the action of winds and surface currents to transport the megalopa back to coastal regions [79,81].

We assume that this *C. sapidus* dispersion model by selective transport, revised by [129], is probably followed by the *Callinectes* larvae that leave the Amazon estuaries close to the plume toward the continental shelf. Whereas marine species larvae that inhabit the ACS, such as *Achelous* and *Cronius*, for example, normally develop in the

ocean salinity range [3], from hatching to settling in the benthic or free-swimming habitat of adults. Anyway, in both cases, inhabiting high salinity waters is essential for the successful larval development of these species [130,131].

Achelous and *Callinectes* zoeae have little morphological differences, consisting basically of the number of zoea stages (ZVII in *Achelous* and ZVIII in *Callinectes*), the number of antenna setae, and the size of the antenna exopodite, which remains unchanged in *Callinectes* [57] while increasing in size during *Achelous* development [58], clearly visualized from ZIV. The larvae identified here as *Achelous* spp. are believed to correspond mostly to *A. rufiremus*, since this species is the most abundant in the bycatch pink shrimp fishing, and the most widely distributed in the ACS [40,122] and in the Western Atlantic, from New Jersey (USA) to the South of Brazil [132]. However, the description of the larval morphology is not available to confirm this hypothesis.

The little morphological differentiation among the genera added to scarce complete larval descriptions does not allow the precise identification at the species level for the zoea or megalopa stages [58,133–135]. Because this family larval development is difficult to obtain in the laboratory, few complete descriptions are available in the literature, and most species have either only ZI or no stage described [136,137]. However, this problem can be solved in the future by using DNA barcoding analysis to identify larvae originating from the natural environment.

Ocypodidae

In the ACS, all Ocypodidae larval stages were present, with zoea and megalopa concentrated up to 158 km and 83 km away from the continent, respectively. The highest predicted abundance and PO were recorded in estuarine and intermediate salinity waters

(5 and 25.5), with a greater dispersal extent (up to 233 km) and reproductive peak during the Amazon River high outflow (May), as observed in the Amazon estuary [29].

This family export strategy to the adjacent continental shelf is already known [4,138–140]. These larvae are unable to survive in the low salinity of the estuarine environment for a long time, as experimentally verified for *Austruca annulipes* (H. Milne Edwards, 1837) [141], *Leptuca leptodactyla* (Rathbun, in Rankin, 1898) [142], *Minuca minax* (Le Conte, 1855) [143], *M. rapax* [144], *Minuca vocator* (Herbst, 1804) [145] and *U. cordatus* [146]. Except for *L. cumulanta*, which retains all larval stages in the estuary [29], so that ZI and ZII larvae may have been accidentally dragged by currents to the continental shelf, thus justifying the single occurrence 23 km from the coast. However, although larval export was confirmed for most species, it is not possible to say specifically how far each one advances into the continental shelf due to the great morphological similarity between them [49–51,147], which makes larval differentiation extraordinarily difficult and imprecise.

The Ocypodidae larval density was higher in deep compared to superficial waters. Similar to observations for *Minuca pugnax* (Smith, 1870) larvae [11] and other ocypodids, where ZI and the later zoea stages occur close to the surface and deeper in the water column, respectively, suggesting an ontogenetic alteration in the vertical position [113], allowing these larvae to take advantage of the gravitational circulation for eventual transport of the megalopa back to the estuary [16], and to settle juveniles and adults in the same habitats [148,149].

The *U. cordatus* species is a particular case because, although our sample covered two reproductive cycles of this crab, which breeds seasonally in the Amazon, specifically in the rainy season full or new moon [146,150], a reduced number of larvae, only three ZI specimens were found at the estuary mouth (23 km) in January. This low abundance

probably results from the species high synchronization associated with the action of currents, since *U. cordatus* always spawns at ebb tide in the night, in new or full moons [151], and its synchronization is so strong that one day later upon release, ZI larvae are no longer found in the estuary [150]. Thus, once on the continental shelf, the larval transport may have been enhanced since, in January, the land winds blow the Amazon plume against the continental margin, which follows quickly with the North Brazil Current towards the French Guiana [33,77], justifying not being captured by our nets.

Although this crab spawning resource is similar to other Ocypodidae, this species has an inconspicuous cycle. Therefore, unlike *U. cordatus*, the possibility of finding Gelasiminae larvae is always greater since its several spawnings throughout the year guarantee a constant larval supply to the continental shelf.

***Armases rubripes* (Sesarmidae)**

This semi-terrestrial crab has continuous reproduction with a peak of ovigerous females in the summer (December, January, and February) [152]. Unlike adults living in oligohaline estuaries, *A. rubripes* larvae are not as tolerant to low salinity so that full development is only possible in more saline waters, suggesting migration to the continental shelf [153,154]. In Amazonian estuaries, only ZI is found throughout the year, and approximately 10 times more abundant in January [155]. Our results confirm larval export, with all larval stages dispersed up to 123 km from the coast, and reproductive peak in January, the high rainfall period in the Amazon region. The rainfall intensity seems to be the parameter regulating *A. rubripes* reproduction in the equatorial region [155], as observed for *Aratus pisonii* (H. Milne Edwards, 1837) [156,157] and *Armases angustipes* (Dana, 1852) [158]. The spawning in the rainy season can be advantageous to

these populations due to increased concentration of nutrients, higher tides - increasing the chance of transport over long distances - and increased seawater productivity, which favors the larval development in plankton [156,159].

In the ACS, the abundance and PO predicted for *A. rubripes* zoea and megalopa are higher in deeper water, mainly in estuarine salinity (5), with lower occurrence in intermediate salinity (25.5). These salinity values are consistent with those used in the species cultivation for the larval description (about 19) [59] but differ from the high survival range of zoea (30) for specimens grown in Uruguay [154]. Such disagreement seems to indicate that the saline tolerance varies among larval populations from different locations, adapting to the low salinity resulting from the great discharge of freshwater from the estuaries while the plume seasonality and river flow do not affect their distribution in the plankton in the Amazon region. Besides, the megalopa was observed concentrated up to 83 km away from the coast, seemingly opting for even lower salinity waters compared to the zoea, a pattern previously observed in megalopae of *A. pisonii* [160] and *Armases* spp. [161,162], and also followed by other crab species that re-migrate from the continental shelf to estuaries and rivers.

***Calappa* (Calappidae)**

The larval zoea of *Calappa* sp. occurred on the platform throughout the year, indicating continuous reproduction. The high predicted abundance and PO in deeper layers of the water column indicate that zoeae were practically absent from the surface layer. This genus inhabits coral, sand and mud bottoms, and is exclusive to the continental shelf [39]. The larvae were concentrated mainly in the coral reef regions (83 to 158 km from the coast), while adults [40] were distributed over the entire reef system area, estimated

between 9,500 and 56,000 km² [163,164]. Thus, these environments, fundamental to the development of *Calappa*, are greatly affected by humans since 1960 due to predatory bottom trawling fishing to capture the pink shrimp, which destroys the reefs and captures the genus as bycatch [40,122], and the future possibility of oil and gas exploration in the area [164].

Although adults inhabit only the continental shelf, and the genus larval distribution is not affected by the seasonality of the river flow, we find that *Calappa* zoea seems to have some affinity with plume water, perhaps by the injection of land-derived sediments, nutrients, and organic matter dissolved in the ocean environment [165]. This transition region, where the plume front meets the ocean water is an ecotone (83 to 158 km), intricately linked to the river discharge flow, being one of the ACS areas with the greatest amplitude of primary productivity when the concentration of nutrients and irradiance conditions are optimal, especially in the maximum flow period [43,78], to support larval marine species, such as *Calappa*, living close to the transition zone.

In the ACS, four species of the genus are found in the adult population [40]: *Calappa nitida* Holthuis, 1958, *Calappa ocellata* Holthuis, 1958, *Calappa sulcata* Rathbun, 1898, and *Calappa gallus* (Herbst, 1803) the latter is the only species in the region with the ZI stage described [44], which limited the identification of the specimens. The other descriptions of the genus available in the literature are either incomplete or of species that do not occur in the area: *C. japonica* Ortmann, 1892 [44], *C. granulata* (Linnaeus, 1758) [166,167], *C. lophos* (Herbst, 1782), *C. philargius* (Linnaeus, 1758) [168]. In our study, we found zoeae with morphological characteristics corresponding to the ZIV, with 10 setae on the exopod of the first and second maxillipeds, enlarged antenna, and antenna with an increased number of setae compared to the ZI, as well as highly developed pleopods, evidence of the approaching metamorphosis to megalopa.

Based on this, we believe that the larval development of the *Calappa* species in the ACS consists of ZI to IV and megalopa, which should be confirmed in later larval descriptions.

Leucosiidae

The expected abundance and PO for Leucosiidae zoea were high in waters with different salinities (5, 25.5, and 33.5) while not differing regarding the vertical arrangement in the water column. This response may be related to the combination of distinct characteristics of the two groups found. The *Persephona* Leach, 1817 zoeae were distributed more homogeneously along with the ACS and not only close to the coastal region (23 km) whereas Leucosiidae zoeae were present only away from the coast (from 83 km). Despite this, during the largest river flow, the occurrence of both taxa was restricted to 233 km from the coast, and their distribution was more homogeneous in October and January.

Similar to *Calappa*, this group inhabits the sandy and mud bottoms, and coral reefs on the continental shelf, it occurs almost all year round and is also caught as accompanying fauna in shrimp fisheries [40]. Of the eight Leucosiidae genera inhabiting the ACS, only the larval development of *Persephona mediterranea* (Herbst, 1794) has been completely described (ZI – ZIV and megalopa) [47] while *Persephona lichtensteinii* Leach, 1817 and *Persephona punctata* (Linnaeus, 1758) has been only the ZI described in the literature [48]. Little is known about the developmental stages of the life cycle of these crabs, so this is the first information about the larval ecology of the group in a natural environment.

Amazon specificity

The process of zoeal larvae leaving from estuaries and returning later as megalopa has been extensively studied and reviewed worldwide [9,10,79,129]. The larval supply of Brachyura is continuous, with few exceptions as *U. cordatus*, because the ACS is located in a tropical Amazon region, where summer lasts throughout the year, unlike temperate environments with well-defined seasons, where the spring and summer are the periods of highest larval density [169–171].

Despite this, collecting Brachyura larvae in the plankton of this area is still challenging since, besides the large ocean volume in which the larvae can potentially disperse, they are also distributed in larval patches that remain intact from spawning to the megalopa stage [172,173] and, therefore, plankton nets might not capture these fragments due to the sheer size of the largest estuary in the world. Given this, knowing the larval distribution of families in the different strata of the water column is relevant for future sampling, where oblique hauling has proven to be effective in capturing Ocypodidae larvae, *Armases* and *Calappa*, while surface hauling is ideal for sampling Panopeidae, Pinnotheridae and Portunidae in the ACS.

The Amazon fluvial discharge affects the dispersion of estuarine families while the Amazon plume influences the species of the continental shelf, being responsible for the continuous distribution of nutrients on the ACS [76] and increasing the primary ocean production in the area. Moreover, the area connecting the ACS and the coast consists of mangroves of the Amazon River mouth, considered a Ramsar site, is extremely important for numerous aquatic organisms, whether as habitat, feeding zone, or nursery [174,175]. Thus, protecting the 3.8 million hectares of extension (Amapá to Maranhão) and the 23 conservation units making up this system is a priority for the maintenance of Amazonian biodiversity and the sustainable use of its resources [176,177].

In summary, there is a Brachyura universe to be discovered in the ACS, from research in the broad benthic environment to record new occurrences, complete descriptions of the species larval stages, investigations to verify which crabs complete the life cycle in the Amazon estuaries, and which also depend on ocean waters, use of DNA barcoding associated with identification and ecology, among other studies essential to understanding and preserving the rich and complex environment that is the Amazon region.

Conclusion

Our study provides the first documentation on the larval dispersal of Brachyura from the largest estuary/sea system in the world, the Amazon Continental Shelf. Additionally, it is the first time that data on expected abundance is predicted for each group and presented as the product between the predicted abundance and the probability of occurrence. Crab larvae showed different distribution and dispersal boundaries, adapting to this particular environment. Our hypotheses were confirmed and we found that more than half of the species occurring in the PCA (62%) do not have any type of larval description. The group of estuarine species *P. gracilis*, Gelasiminae, *U. maracoani* (Latreille, 1802), *P. lacustris*, *Panopeus* sp., *Austinixa* sp., *Pinnixa* sp., *Callinectes* spp. And *A. rubripes* perform larval export to the platform, while *Calappa* sp., Leucosiidae, *Persephona* spp., *D. crinitichelis* and *Achelous* spp., inhabit the platform as adults, especially close to the rhodolith reef region and complete the larval cycle in this same environment. We confirm that the flow of the Amazon River greatly influences the dynamics of the Amazon Continental Shelf, especially the salinity, which is directly related to the larval distribution of Brachyura in this area. We emphasize that further studies on larval description and DNA barcoding could contribute to understanding the Brachyura larval ecology since to protect and value

the region biodiversity, the knowledge on species identity, spatial distribution, and correlations with environmental conditions are essential, as these existing gaps create difficulties for identifying and defining priority areas for effective species conservation in the Amazon region.

Acknowledgments

We are grateful to the Brazilian National Research Council, CNPq, for supporting this project (INCT AMBIENTES MARINHOS TROPICAIS Edital MCT / CNPq / FNDCT nº 71/2010). We would like to thank the PROPESP/FADESP (PAPQ Program) for financing the translation of the original manuscript by the native fluency English speaker Ruth Kakogiannos. We thank the students of the Amazonian Crustacean Ecology Research Group (GPECA) and other colleagues for assisting field sampling and sample processing, especially Prof. Dr. Fernando Abrunhosa for the confirmation of some larval groups. We are also grateful to the editor and reviewers for comments and suggestions which substantially improved the manuscript.

References

1. Costlow JD, Bookhout CG. Larval development of the crab, *Hexapanopeus angustifrons*. Chesapeake Sci. 1966; 7: 148. doi:10.2307/1351162
2. Sandifer PA. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968–1968. Chesapeake Sci. 1973; 14: 235–257. doi:10.2307/1350753
3. Anger K. Salinity as a key parameter in the larval biology of decapods crustaceans. Invertebr Reprod Dev. 2003; 41: 29–45. doi:10.1080/07924259.2003.9652520
4. Epifanio CE. Transport of invertebrate larvae between estuaries and the continental shelf. Am Fish Soc Symp. 1988; 3: 104–114.

5. DiBacco C, Sutton D, McConnico L. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. *Mar Ecol Prog Ser.* 2001; 217: 191–206. doi:10.3354/meps217191
6. Arana M, Sulkin SD. Behavioral basis of depth regulation in the first zoeal stage of the Pacific shore crab, *Hemigrapsus oregonensis* (Brachyura: Grapsidae). *Pac Sci.* 1993; 47: 256–262.
7. MacTavish AL, Ladah LB, Lavín MF, Filonov A, Tapia FJ, Leichter J. High frequency (hourly) variation in vertical distribution and abundance of meroplanktonic larvae in nearshore waters during strong internal tidal forcing. *Cont Shelf Res.* 2016; 117: 92–99. doi: 10.1016/j.csr.2016.02.004
8. Drake PT, Edwards CA, Morgan SG, Satterthwaite EV. Shoreward swimming boosts modeled nearshore larval supply and pelagic connectivity in a coastal upwelling region. *J Mar Syst.* 2018; 187: 96–110. doi: 10.1016/j.jmarsys.2018.07.004
9. Queiroga H, Blanton J. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Adv Mar Biol.* 2004; 47: 107–214.
10. Epifanio, C.E.; Cohen, J.H. Behavioral adaptations in larvae of brachyuran crabs: A review. *J Exp Mar Biol Ecol.* 2016; 482: 85–105. doi: 10.1016/S0065-2881(04)47002-3
11. O'Connor NJ, Epifanio CE. The effect of salinity on the dispersal and recruitment of fiddler crab larvae. *J Crustac Biol.* 1985; 5: 137–145. doi:10.2307/1548226
12. Messerknecht I, Montu M, Anger K. Larval development and salinity tolerance of brazilian *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) reared in the laboratory. *Meeresforsch.* 1991; 33: 275–296.
13. Anger K, Spivak E, Luppi T, Bas C, Ismael D. Larval salinity tolerance of the South American salt-marsh crab, *Neohelice (Chasmagnathus) granulata*: physiological constraints to estuarine retention, export and reimmigration. *Helgol Mar Res.* 2008; 62: 93–102. doi:10.1007/s10152-007-0076-5
14. Bartilotti C, Santos A, Castro M, Peliz A, Santos AMP. Decapod larval retention within distributional bands in a coastal upwelling ecosystem. *Mar Ecol Prog Ser.* 2014; 507: 233–247. doi: 10.3354/meps10817
15. Brandão MC, Garcia CAE, Freire AS. Meroplankton community structure across oceanographic fronts along the South Brazil Shelf. *J Mar Syst.* 2020; 208: 103361. doi: 10.1016/j.jmarsys.2020.103361
16. Dittel AI, Epifanio CE, Lizano O. Flux of crab larvae in a mangrove creek in the Gulf of Nicoya, Costa Rica. *Estuar Coast Shelf Sci.* 1991; 32: 129–140. doi:10.1016/0272-7714(91)90010-9
17. DeVries MC, Tankersley RA, Forward Jr RB, Kirby-Smith WW, Luettich Jr RA.

- Abundance of estuarine crab larvae is associated with tidal hydrological variables. *Mar Biol.* 1994; 118: 403–413. doi:10.1007/BF00350297
18. Neumann-Leitão S, Melo PAMC, Schwamborn R, Diaz XFG, Figueiredo LGP, Silva, AP, Campelo, RPS, Melo Júnior M, Melo, NFAC, Costa, AESF, Araújo M, Veleza DRA, Moura RL, Thompson F. Zooplankton From a reef system under the influence of the Amazon River plume. *Front Microbiol.* 2018; 9, 355. doi: 10.3389/fmicb.2018.00355
19. Morgan SG, Fisher JL, McAfee ST, Largier JL, Miller SH, Sheridan MM, Neigel JE. Transport of crustacean larvae between a low-inflow estuary and coastal waters. *Estuaries Coast.* 2014; 37: 1269–1283. doi:10.1007/s12237-014-9772-y
20. Santos A, Santos AMP, Conway DVP, Bartilotti C, Lourenço P, Queiroga H. Diel vertical migration of decapod larvae in the Portuguese coastal upwelling ecosystem: implications for offshore transport. *Mar Ecol Prog Ser.* 2008; 359: 171–183. doi:10.3354/meps07341
21. Reis RE, Kullander SO, Ferraris Jr CJ. Checklist of the freshwater fishes of South and Central America. Porto Alegre: Edipucrs, 2003.
22. Albert JS, Carvalho TP, Petry P, Holder MA, Maxime EL, Espino J, ... Reis RE. Aquatic biodiversity in the Amazon: habitat specialization and geographic isolation promote species richness. *Animals.* 2011; 1: 205–241. doi:10.3390/ani1020205
23. Azevedo-Santos VM, Garcia-Ayala JR, Fearnside PM, Esteves FA, Pelicice FM, Laurance WF, Benine RC. Amazon aquatic biodiversity imperiled by oil spills. *Biodivers. Conserv.* 2016; 25: 2831–2834. doi:10.1007/s10531-016-1192-9
24. Ruffino ML, Isaac VJ. Life cycle and biological parameters of several brazilian Amazon fish species. *The ICLARM Quartely.* 1995; 8: 40–45.
25. Barthém RB, Fabrè NN. Biologia e diversidade dos recursos pesqueiros da Amazônia. In: Ruffino ML, editor. *A pesca e os recursos pesqueiros na Amazônia Brasileira.* Manaus: ProVárzea; 2004. pp. 11–55.
26. Isaac VJ, Ferrari SF. Assessment and management of the North Brazil shelf large marine ecosystem. *Environ Dev.* 2016; 22: 97–110. doi:10.1016/j.envdev.2016.11.004/
27. Silva LS, Cavalcante-Braga DV, Lourenço CB, Schwamborn R, Martinelli-Lemos JM. Factors affecting the seasonal variability of planktonic shrimps (Dendrobranchiata) along an estuary-ocean gradient on the Amazon Continental shelf. *J Mar Biol Assoc U K.* 2021; Forthcoming.
28. Rodrigues-Inoue AC, Santos, A, Martinelli-Lemos JM. Distribution patterns of Anomura, Axiidea and Gebiidea (Crustacea, Decapoda) larvae at the Amazon shelf. Forthcoming., 2021
29. Lima FA, Oliveira TF, Martinelli-Lemos JM. Distribution of brachyuran larvae in an Amazonian estuary as evidence for retention and export. *J Crust Biol.* 2019; 39: 602–612. doi:10.1093/jcbiol/ruz051

30. Conroy BJ, Steinberg DK, Stukel MR, Goes JI, Coles VJ. Meso and microzooplankton grazing in the Amazon River plume and western tropical North Atlantic. *Limnol Oceanogr.* 2016; 61: 825–840. doi:10.1002/lno.10261
31. Nitttrouer CA, DeMaster DJ. The Amazon shelf setting: tropical, energetic, and influenced by a large river. *Cont Shelf Res.* 1996; 16: 553–573. doi:10.1016/0278-4343(95)00069-0
32. Nikiema O, Devenon JL, Baklouti M. Numerical modeling of the Amazon River plume. *Cont Shelf Res.* 2007; 27: 873–899. doi:10.1016/j.csr.2006.12.004
33. Coles VJ, Brooks MT, Hopkins J, Stukel MR, Yager PL, Hood RR. The pathways and properties of the Amazon River plume in the tropical North Atlantic Ocean. *J Geophys Res: Oceans.* 2013; 118: 6894–6913. doi:10.1002/2013JC008981
34. Dagg M, Benner R, Lohrenz S, Lawrence D. Transformation of dissolved and particulate materials on continental shelves influenced by large rivers: plume processes. *Cont Shelf Res.* 2004; 24: 833–858. doi:10.1016/j.csr.2004.02.003
35. Mikhailov VN. Water and sediment runoff at the Amazon River mouth. *Water Resour.* 2010; 37: 145–159. doi:10.1134/S009780781002003X
36. Santos MLS, Medeiros C, Muniz K, Feitosa FAN, Schwamborn R, Macedo SJ. Influence of the Amazon and Pará rivers on water composition and phytoplankton biomass on the adjacent shelf. *J Coast Res.* 2008; 24: 585–593. doi:10.2112/05-0538.1
37. Medeiros PM, Seidel M, Ward ND, Carpenter EJ, Gomes HR, Niggemann J, et al. Fate of the Amazon River dissolved organic matter in the tropical Atlantic Ocean. *Global Biogeochem Cycles.* 2015; 29: 677–690. doi:10.1002/2015GB005115
38. Smoak JM, Krest JM, Swarzenski PW. Geochemistry of the Amazon estuary. In: Wangersky P, editor. *Estuaries. Handbook of environmental chemistry.* Berlin: Springer Verlag; 2006. pp. 71–90.
39. Lima FA, Martinelli-Lemos JM. Checklist of the Brachyura of the Brazilian Amazon coastal zone and knowledge status of their larval development. *Zootaxa.* 2019; 4646: 301–321. doi: 10.11646/zootaxa.4646.2.6
40. Nóbrega PSV, Santos CRM, Cordeiro APB, Martinelli-Lemos JM. Invertebrates assemblage captured by a pink shrimp's fishery on Amazon continental shelf. *Latin Am J Aquatic Res.* 2021; 49: 227–241. DOI: 10.3856/vol49-issue2-fulltext-2600
41. Dai A, Trenberth KE. Estimates of freshwater discharge from continents: latitudinal and seasonal variations. *J Hydrometeorol.* 2002; 3: 660–687. doi:10.1175/1525-7541(2002)003<0660:EOFDfC>2.0.CO;2
42. Moller GSF, Novo EMLM, Kampel M. Space-time variability of the Amazon River plume based on satellite ocean color. *Cont Shelf Res.* 2010; 30: 342–352. doi:10.1016/j.csr.2009.11.015

43. Gouveia NA, Gherardi DFM, Wagner FH, Paes ET, Coles VJ, Aragão LEOC. The salinity structure of the Amazon River plume drives spatiotemporal variation of oceanic primary productivity. *J Geophys Res Biogeosci.* 2019; 124: 147–165. doi:10.1029/2018JG004665
44. Taishaku H, Konishi K. Zoeas of *Calappa* species with special reference to characters of the Family Calappidae (Crustacea, Brachyura). *Zool Sci.* 1995; 12: 649–654. doi:10.2108/zsj.12.649
45. Fransozo A, Cuesta JA, Negreiros-Fransozo ML. The first zoea stage of two species of Grapsidae (Decapoda, Brachyura) and a key to such larvae from the Brazilian coast. *Crustaceana.* 1998; 71: 331–343. doi:10.1163/156854098X00293
46. Bossi-Garcia AL, Rodrigues MD. Zoeal morphology of *Pachygrapsus gracilis* (Saussure, 1858) (Decapoda, Grapsidae) reared in the laboratory. *Invertebr Reprod Dev.* 1993; 24: 197–204. doi:10.1080/07924259.1993.9672352
47. Negreiros-Fransozo ML, Fransozo A, Hebling NJ. Larval development of *Persephona mediterranea* Herbst, 1794 (Brachyura, Leucosiidae) under laboratory conditions. *Crustaceana.* 1989; 57: 177–193. doi:10.1163/156854089X00509
48. Hirose GL, Gregati RA, Fransozo A, Negreiros-Fransozo ML. Morphological and morphometric comparisons of the first zoea of four species of purse crabs (Decapoda: Brachyura: Leucosiidae) from the Brazilian South Atlantic. *Zootaxa.* 2012; 3167: 17–31. doi: 10.11646/zootaxa.3167.1.2
49. Rieger PJ. Desenvolvimento larval de *Uca (Minuca) mordax* (Smith, 1870) (Crustacea, Decapoda, Ocypodidae), em laboratório. *Trab Oceanog UFPE.* 1997; 25: 225–267. doi:10.5914/tropocean.v25i1.2741
50. Rieger PJ. Desenvolvimento larval de *Uca (Minuca) burguesi* Holthuis (Crustacea, Decapoda, Ocypodidae), em laboratório. *Rev Bras Zool.* 1998; 15: 727–756. doi:10.1590/S0101-81751998000300017.
51. Rieger PJ. Desenvolvimento larval de *Uca (Minuca) vocator* (Herbst, 1804) (Crustacea, Decapoda, Ocypodidae), em laboratório. *Nauplius.* 1999; 7: 1–37.
52. Rodrigues MD, Hebling NJ. *Ucides cordatus cordatus* (Linnaeus, 1763) (Crustacea, Decapoda). Complete larval development under laboratory conditions and its systematic position. *Rev Bras Zool.* 1989; 6: 147–166. doi:10.1590/S0101-81751989000100016
53. Fransozo A, Mantelatto FL, Negreiros-Fransozo ML. Larval development of *Hexapanopeus paulensis* Rathbun, 1930 (Crustacea, Brachyura, Xanthidae) under laboratory conditions. *Zoologia.* 1991; 7: 31–45. doi:10.1590/S0101-81751990000200002
54. Lima JF. Larval development of *Austinixa bragantina* (Crustacea: Brachyura: Pinnotheridae) reared in the laboratory. *Zoologia.* 2009; 26: 143–154. doi:10.1590/S1984-46702009000100020

55. Pohle G, Telford M. The larval development of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae) in laboratory culture. Bull Mar Sci. 1981; 31: 753–773.
56. Lima JF, Abrunhosa FA, Coelho PA. The larval development of *Pinnixa gracilipes* Coelho (Decapoda, Pinnotheridae) reared in the laboratory. Rev Bras Zool. 2006; 23: 480–489. doi:10.1590/S0101-81752006000200023
57. Costlow JD, Bookhout CG. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biol Bull. 1959; 116: 373–396. doi:10.2307/1538947
58. Bookhout CG, Costlow JD. Larval development of *Portunus spinicarpus* reared in the laboratory. Bull Mar Sci. 1974; 24: 20–51.
59. Díaz H, Ewald JJ. A comparison of the larval development of *Metasesarma rubripes* (Rathbun) and *Sesarma ricordi* H. Milne Edwards (Brachyura, Grapsidae) reared under similar laboratory conditions. Crustaceana. 1968; 2: 225–248. doi:10.2307/25027398
60. Souza AS, Costa RM, Abrunhosa FA. Comparative morphology of the first zoea of twelve brachyuran species (Crustacea: Decapoda) from the Amazon region. Zoologia. 2013; 30: 273–290. doi:10.1590/S1984-46702013000300004
61. Cavalcanti EAH, Larrazábal MEL. Macrozooplâncton da Zona Econômica Exclusiva do Nordeste do Brasil (Segunda Expedição Oceanográfica - REVIZEE/NE II) com ênfase em Copepoda (Crustacea). Rev Bras Zool. 2004; 21: 467–475. doi:10.1590/S0101-81752004000300008
62. Burnham KP, Andersen DR. Model selection and multimodel inference. 2nd ed. New York: Springer; 2002.
63. McCullagh P, Nelder JA. Generalized linear models. 2nd ed. London: Chapman and Hall; 1989.
64. Devlin K. The joy of sets: fundamentals of contemporary set theory. 2nd ed. [S. l.]: Springer; 1994.
65. Johnson DH. The insignificance of statistical significance testing. J. Wildl. Manage; 1999.
66. Seidel M, Yager PL, Ward ND, Carpenter EJ, Gomes HR, Krusche AV, Richey JE, Dittmar T, Medeiros PM. Molecular-level changes of dissolved organic matter along the Amazon River-to-ocean continuum. Mar Chem. 2015; 177: 218–231. doi:10.1016/j.marchem.2015.06.019
67. Morgan SG, Fisher JL. Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. Mar Ecol Prog Ser. 2010; 404: 109–126. doi:10.3354/meps08476
68. Sulkin SD. Behavioral basis of depth regulation in the larvae of brachyuran crabs. Mar. Ecol. Prog. Ser. 1984; 15: 181–205. doi:10.3354/meps015181

69. Miller SH, Morgan SG. Phenotypic plasticity in larval swimming behavior in estuarine and coastal crab populations. *J Exp Mar Biol Ecol.* 2013; 449: 45-50. doi:10.1016/j.jembe.2013.08.013
70. Anger K, Queiroga H, Calado R. Larval development and behaviour strategies in Brachyura. In: Castro P, Davie P, Guinot D, Schram F, von Vaupel Klein C, editors. *Treatise on zoology – anatomy, taxonomy, biology.* Leiden: Brill; 2015. pp. 317–374. doi:10.1163/9789004190832_008
71. Gravinese PM. Vertical swimming behavior in larvae of the Florida stone crab, *Menippe mercenaria*. *J. Plankton Res.* 2018; 40: 643–654. doi:10.1093/plankt/fby040
72. Cohen JH, Hanson CK, Dittel AI, Miller DC, Tilburg CE. The ontogeny of larval swimming behavior in the crab *Hemigrapsus sanguineus*: Implications for larval transport. *J Exp Mar Biol Ecol.* 2015; 462: 20–28. doi:10.1016/j.jembe.2014.10.003
73. Capaldo PS. Salinity preferences in the stage I zoea of three temperate zone fiddler crabs, Genus *Uca*. *Estuaries.* 1993; 16: 784–788. doi:10.2307/1352436
74. Torres G, Giménez L, Anger K. Growth, tolerance to low salinity, and osmoregulation in decapod crustacean larvae. *Aquat Biol.* 2011; 12: 249–260. doi:10.3354/ab00341
75. Morgan SG, Anastasia JR. Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. *Proc Natl Acad Sci.* 2008; 105: 222–227. doi:10.1073/pnas.0704725105
76. Silva AC, Santos MLS, Araujo MC, Bourles B. Observações hidrológicas e resultados de modelagem no espalhamento sazonal e espacial da pluma de água Amazônica. *Acta Amaz.* 2009; 39: 361–370. doi:10.1590/S0044-59672009000200014.
77. Lentz SJ, Limeburner R. The Amazon River Plume during AMASSEDS: Spatial characteristics and salinity variability. *J Geophys Res.* 1995; 100: 2355–2375. doi:10.1029/94JC01411
78. Smith WO Jr, DeMaster DJ. Phytoplankton biomass and productivity in the Amazon River plume: correlation with seasonal river discharge. *Cont Shelf Res.* 1996; 6: 227–244. doi:10.1016/0278-4343(95)00007-N
79. Epifanio CE, Garvine RW. Larval transport on the Atlantic Continental shelf of North America: a review. *Estuar Coast Shelf Sci.* 2001; 52: 51–77. doi:10.1006/ecss.2000.0727
80. Tilburg CE, Houser LT, Steppe CN, Garvine RW, Epifanio CE. Effects of coastal transport on larval patches: models and observations. *Estuar Coast Shelf Sci.* 2006; 67: 145–160. doi:10.1016/j.ecss.2005.11.019
81. Reynolds NB, Eggleston DB, Luetlich Jr RA. Dispersal dynamics of post-larval blue crabs, *Callinectes sapidus*, within a wind-driven estuary. *Fish. Oceanogr.* 2007; 16: 257–272. doi:10.1111/j.1365-2419.2007.00420.x

82. Jackson TD, Torres G, Giménez L. Survival and development of larvae of two decapod crustaceans under limited access to prey across a thermal range. J Plankton Res. 2014; 1–12. doi:10.1093/plankt/fbu065
83. Vereshchaka AL, Anokhina LL. Composition and dynamics of the Black Sea benthopelagic plankton and its contribution to the near shore plankton communities. Plos One. 2014; 9: e99595. doi:10.1371/journal.pone.0099595
84. Forward Jr RB, Tankersley RA. Selective tidal-stream transport of marine animals. Oceanogr Mar Biol. 2001; 39: 305–353.
85. Nóbrega PSV, Quaresma MC, Lima FA, Martinelli-Lemos JM. Spatial-temporal variation of the population structure and density of the shore crab *Pachygrapsus gracilis* (Grapsidae) in an estuary on the Brazilian Amazon coast. Nauplius, 2021, 29: e2021024.
86. Bueno M, Flores AVV. Tidal-amplitude rhythms of larval release: variable departure from presumed optimal timing among populations of the mottled shore crab. J Mar Biol Assoc U K. 2010; 90: 859–865. doi:10.1017/S0025315410000044
87. Drake P, Arias AM, Rodríguez A. Seasonal and tidal abundance patterns of decapod crustacean larvae in a shallow inlet (SW Spain). J Plankton Res. 1998; 20: 585–601. doi:10.1093/plankt/20.3.585
88. Park S, Epifanio CE, Grey EK. Behavior of larval *Hemigrapsus sanguineus* (de Haan) in response to gravity and pressure. J Exp Mar Biol Ecol. 2004; 307: 197–206. doi:10.1016/j.jembe.2004.02.007
89. Flores AAV, Mazzuco ACA, Bueno M. A field study to describe diel, tidal and semilunar rhythms of larval release in an assemblage of tropical rocky shore crabs. Mar Biol. 2007; 151: 1989–2002. doi:10.1007/s00227-007-0639-7
90. Morgan SG, Fisher JL, Mace AJ. Larval recruitment in a region of strong, persistent upwelling and recruitment limitation. Mar Ecol Prog Ser. 2009; 394: 79–99. doi:10.3354/meps08216
91. Miller SH, Morgan SG. Interspecific differences in depth preference: regulation of larval transport in an upwelling system. Mar Ecol Prog Ser. 2013; 476: 301–306. doi:10.3354/meps10150
92. Morgan SG, Miller SH, Robart MJ, Largier JL. Nearshore larval retention and cross-shelf migration of benthic crustaceans at an Upwelling Center. Front Mar Sci. 2018; 5. doi:10.3389/fmars.2018.00161
93. Flores AAV, Negreiros-Fransozo ML. On the population biology of the mottled shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) in a subtropical area. Bull Mar Sci. 1999; 65: 59–73.
94. Araújo MSLC, Azevedo DS, Silva JVCL, Pereira CLF, Castiglioni DS. Population biology of two sympatric crabs: *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura,

- Grapsidae) and *Eriphia gonagra* (Fabricius, 1781) (Brachyura, Eriphidae) in reefs of Boa Viagem beach, Recife, Brazil. Pan-Am J Aquat Sci. 2016; 11: 197–210.
95. Schlotterbeck RE. The larval development of the lined shore crab, *Pachygrapsus crassipes* Randall, 1840 (Decapoda Brachyura, Grapsidae) reared in the laboratory. Crustaceana. 1976; 30: 184–200. doi:10.1163/156854076X00567
96. Cuesta JA, Rodríguez A. Zoeal stages of the intertidal crab *Pachygrapsus marmoratus* (Fabricius, 1787) (Brachyura, Grapsidae) reared in the laboratory. Hydrobiologia. 2000; 436: 119–130. doi:10.1023/A:1026576614590
97. Cházaro-Olvera S, Rocha-Ramírez A, Arellano-Rodarte P. Transport of *Pachygrapsus gracilis* megalopae from a lagoon system inlet in the Southwestern Gulf of Mexico. Crustaceana. 2007; 80: 955–968. doi:10.1163/156854007781681337
98. Lira JJPR, Calado TCS. Reproductive aspects and adaptive relative growth of the tropical crab *Goniopsis cruentata*. Anim Biol. 2013; 63: 407–424. doi:10.1163/15707563-00002422
99. Lira JJPR, Calado TCS, Araújo MSLC. Breeding period in the mangrove crab *Goniopsis cruentata* (Decapoda: Grapsidae) in Northeast Brazil. Rev Biol Trop. 2013; 61: 29–38. doi:10.15517/rbt.v61i1.10878
100. Cobo VJ, Fransozo A. External factors determining breeding season in the red mangrove crab *Goniopsis cruentata* (Latreille) (Crustacea, Brachyura, Grapsidae) on the São Paulo State northern coast, Brazil. Rev Bras Zool. 2003; 20: 213–217. doi:10.1590/S0101-81752003000200007
101. Campos CC, Garcia TM, Fortaleza MTV. Larval density of *Ucides cordatus* (Linnaeus, 1763) and *Goniopsis cruentata* (Linnaeus, 1803) in a semiarid estuary, Ceará State. Arq C Mar. 2016; 49: 77–83.
102. Vieira RRR, Rieger PJ. Larval development of *Hexapanopeus caribbaeus* (Stimpson, 1817) (Crustacea, Decapoda, Xanthoidea, Panopeidae) reared under laboratory conditions. J Plankton Res. 2004; 26: 1175–1182. doi:10.1093/plankt/fbh107
103. Cronin TW. Estuarine retention of larvae of the crab *Rhithropanopeus harrisi*. Estuar Coast Shelf Sci. 1982; 15: 207–220. doi:10.1016/0272-7714(82)90028-2
104. Christy JH. Timing of hatching and release of larvae by brachyuran crabs: patterns, adaptive significance and control. Integr Comp Biol. 2011; 51: 62–72. doi:10.1093/icb/ucr013
105. Smith AE, Jensen GC. The role of carapace spines in the swimming behavior of porcelain crab zoeae (Crustacea: Decapoda: Porcellanidae). J Exp Mar Biol Ecol. 2015; 471: 175–179. doi:10.1016/j.jembe.2015.06.007
106. Caracappa JC, Munroe DM. Variability in swimming behaviour among broods of the blue crab (*Callinectes sapidus*) zoeae. J Exp Mar Biol Ecol. 2019; 518: 151176. doi:10.1016/j.jembe.2019.151176

107. Souza AS, Costa RM, Abrunhosa FA. The complete larval development of *Panopeus lacustris* Desbonne 1867 (Brachyura: Panopeidae), from the Amazon region, reared in the laboratory. *Acta Zool.* 2012; 94: 308–323. doi:10.1111/j.1463-6395.2011.00557.x
108. DeVries MC, Forward RB. Rhythms in larval release of the sublittoral crab *Neopanope sayi* and the supralittoral crab *Sesarma cinereum* (Decapoda: Brachyura). *Mar Biol.* 1989; 248: 241–248. doi:10.1017/S0025315400071794
109. Tolley SG, Brosious BB, Peebles EB. Recruitment of the crabs *Eurypanopeus depressus*, *Rhithropanopeus harrisi*, and *Petrolisthes armatus* to oyster reefs: the influence of freshwater inflow. *Estuar Coast.* 2013; 36: 820–833. doi:10.1007/s12237-013-9590-7
110. Christy JH, Stancyk SE. Timing of larval production and flux of invertebrate larvae in a well-mixed estuary. *Estuar Comp.* 1982; 489–503. doi:10.1016/B978-0-12-404070-0.50035-1
111. Lima FA, Butturi-Gomes D, Martinelli-Lemos JM. Larval bloom of *Panopeus lacustris* (Decapoda: Panopeidae) on the Amazon Continental shelf. *Reg Stud Mar Sci* 2021; Forthcoming.
112. Breckenridge JK, Bollens SM. Vertical distribution and migration of decapod larvae in relation to light and tides in Willapa Bay, Washington. *Estuar Coast.* 2011; 34: 1255–1261. doi:10.1007/s12237-011-9405-7
113. Sandifer PA. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay Virginia USA. *Estuar Coast Mar Sci.* 1975; 3: 269–279. doi:10.1016/0302-3524(75)90028-6
114. Peiró DF, Mantelatto FL. Population dynamics of the pea crab *Austinixa aidae* (Brachyura, Pinnotheridae): a symbiotic of the ghost shrimp *Callichirus major* (Thalassinidea, Callinassidae) from the southwestern Atlantic. *Iheringia*, 2011; 101: 5–14. doi:10.1590/S0073-47212011000100001
115. McDermott JJ. Biology of the brachyuran crab *Pinnixa chaetoptera* Stimpson (Decapoda: Pinnotheridae) symbiotic with tubicolous polychaetes along the Atlantic coast of the United States, with additional notes on other polychaete associations. *Proc Biol Soc Wash.* 2005; 118:742–764. doi:10.2988/0006-324X(2005)118[742:BOTBCP]2.0.CO;2
116. Huesh PW. Intertidal distribution, symbiotic association and reproduction of *Pinnotheres bidentatus* (Brachyura: Pinnotheridae) from Taiwan. *J Nat Hist.* 2001; 35: 1681–1692. doi:10.1080/002229301317092397
117. Schmitt WL, McCain JC, Davidson ES. Decapoda I Brachyura I Fam. Pinnotheridae. In: Gruner HE, Holthuis LB, editors. *Crustaceorum Catalogus*. Den Haag; 1973. pp. 32–37.

- 1148
- 1149 118. Gondim AI, Dias TLP, Christoffersen ML. Annotated checklist of echinoderms from
- 1150 Maranhão and Piauí States, Northeastern Brazil. Check List. 2013; 9: 510–518.
- 1151
- 1152 119. Gondim AI, Moura RB, Christoffersen ML, Dias TLP. Taxonomic guide and
- 1153 historical review of echinoids (Echinodermata: Echinoidea) from northeastern Brazil.
- 1154 Zootaxa. 2018; 4529: 1–72. doi:10.11646/zootaxa.4529.1.1
- 1155
- 1156 120. Alves ES, Pezzuto PR. Population dynamics of *Pinnixa patagoniensis* Rathbun,
- 1157 1918 (Brachyura: Pinnotheridae) a symbiotic crab of *Sergio mirim* (Thalassinidea:
- 1158 Callianassidae) in Cassino Beach, Southern Brazil. Mar Ecol. 1998; 19: 37–51.
- 1159 doi:10.1111/j.1439-0485.1998.tb00452.x
- 1160
- 1161 121. Dowds RE. Distribution and reproduction of four species of *Pinnixa* (Crustacea:
- 1162 Brachyura) in a North Carolina estuary. Am Zool. 1978; 18: 599. doi:10.1163/1937240X-
- 1163 00002294
- 1164
- 1165 122. Nóbrega PSV, Santos CRM, Martinelli-Lemos JM. Impacts of trawling on the
- 1166 invertebrate assemblage of Blue Amazon. Bol Inst Pesca. 2021; Forthcoming.
- 1167
- 1168 123. Epifanio CE, Valenti CC, Pembroke AE. Dispersal and recruitment of blue crab
- 1169 larvae in Delaware Bay, U.S.A. Estuar Coast Shelf Sci. 1984; 18: 1–12.
- 1170 doi:10.1016/0272-7714(84)90002-7
- 1171
- 1172 124. Carr SD, Tankersley RA, Hench JL, Forward Jr RB, Luetlich Jr RA. Movement
- 1173 patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during the spawning
- 1174 migration. Estuar Coast Shelf Sci. 2004; 60: 567–579. doi:10.1016/j.ecss.2004.02.012
- 1175
- 1176 125. Darnell MZ, Kemberling AA. Large-Scale movements and postcopulatory female
- 1177 blue crabs *Callinectes sapidus* in tidal and nontidal estuaries of North Carolina. Trans
- 1178 Am Fish Soc. 2018; 147: 716–728. doi:10.1002/tafs.10058
- 1179
- 1180 126. Sulkin SD, Van Heukelem W, Kelly P, Van Heukelem L. The behavioral basis of
- 1181 larval recruitment in the crab *Callinectes sapidus* Rathbun: a laboratory investigation of
- 1182 ontogenetic changes in geotaxis and barokinesis. Biol Bull. 1980; 159: 402–417.
- 1183 doi:10.2307/1541103
- 1184
- 1185 127. McConaughy JR, Johnson DF, Provenzano AJ, Maris RC. Seasonal distribution of
- 1186 larvae of *Callinectes sapidus* in the waters adjacent to Chesapeake Bay. J Crust Biol.
- 1187 1983; 3: 582–591. doi:10.2307/1547953
- 1188
- 1189 128. Epifanio CE. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off
- 1190 Mid-Atlantic states. Bull Mar Sci. 1995; 57: 713–725.
- 1191
- 1192 129. Forward Jr RB, Tankersley RA, Welch JM. Selective tidal-stream transport of the
- 1193 blue crab *Callinectes sapidus*: an overview. Bull Mar Sci. 2003; 72: 347–365.
- 1194
- 1195 130. Ogburn MB, Jackson JL, Forward Jr RB. Comparison of low salinity tolerance in
- 1196 *Callinectes sapidus* Rathbun and *Callinectes similis* Williams postlarvae upon entry into
- 1197 an estuary. J Exp Mar Biol Ecol. 2007; 352: 343–350. doi:10.1016/j.jembe.2007.08.008

131. Ravi R, Manisseri MK. Survival rate and development period of the larvae of *Portunus pelagicus* (Decapoda, Brachyura, Portunidae) in relation to temperature and salinity. Fish Aquac J. 2012; FAJ-49. doi:10.4172/2150-3508.1000049
132. Melo GAS. Manual de identificação dos Brachyura (caranguejos e siris) do litoral brasileiro. São Paulo: Editora Plêiade; 1996.
133. Stuck KC, Truesdale FM. Larval development of the speckled swimming crab, *Arenaeus cribrarius* (Decapoda: Brachyura: Portunidae) reared in laboratory. Bull Mar Sci. 1988;42: 101–132.
134. Islam MS, Shokita S, Higa T. Larval development of the swimming crab *Charybdis natator* (Crustacea: Brachyura: Portunidae) reared in laboratory. Species Diversity. 2000; 5: 329–349. doi:10.12782/specdiv.5.329
135. Islam MS, Machiko K, Shokita S. Larval development of the swimming crab *Thalamita pelsarti* Montgomery, 1931 (Crustacea: Brachyura: Portunidae) reared in laboratory. Russ J Mar Biol. 2005; 31: 78–90. doi:10.1007/s11179-005-0048-z
136. Fransozo A, Mantelatto FL, Bertini G. The first zoeal stage of the genus *Cronius* (Brachyura, Portunidae) from the Brazilian coast, hatched in a laboratory. J Plankton Res. 2002; 24: 1237–1244. doi:10.1093/plankt/24.11.1237
137. Mantelatto FL, Reigada ALD, Gatti ACR, Cuesta JA. Morphology of the first zoeal stages of five species of the portunids genus *Callinectes* (Decapoda, Brachyura) hatched at the laboratory. An Acad Bras Ciênc. 2014; 86: 755–767. doi:10.1590/0001-3765201420130030
138. Dittel AIR, Epifanio CE. Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. Estuaries. 1982; 5: 197–202. doi:10.2307/1351835
139. Morgan SG. Adaptive significance of hatching rhythms and dispersal patterns of estuarine crab larvae: avoidance of physiological stress by larval export? J Exp Mar Biol Ecol. 1987; 113: 71–78. doi:10.1016/0022-0981(87)90083-9
140. Rodríguez A, Drake P, Arias AM. Reproductive periods and larval abundance patterns of the crabs *Panopeus africanus* and *Uca tangeri* in a shallow inlet (SW Spain). Mar Ecol Prog Ser. 1997; 149: 133–142. doi:10.3354/meps149133
141. Peer N, Miranda NAF, Perissinotto R. Suspended silt and salinity tolerances of the first zoeal stage of the fiddler crab *Uca annulipes* (Decapoda: Brachyura) and why marine connectivity is essential to the survival of the species. Afr J Mar Sci. 2016; 38: 161–169. doi:10.2989/1814232X.2016.1169217
142. Martins SB, Silva UAT, Masunari S. Larval export strategy as an indication of ontogenetic migrations towards open sea of the fiddler crab *Leptuca leptodactyla* (Rathbun, in Rankin, 1898) (Crustacea, Ocypodidae) from Guaratuba Bay, southern Brazil. Nauplius. 2020; 28: e2020028. doi:10.1590/2358-2936e2020028

- 1248 143. Brodie RJ, Styles R, Borgianini S, Godley J, Butler K. Larval mortality during export
1249 to the sea in the fiddler crab *Uca minax*. Mar Biol. 2007; 152: 1283–1291.
1250 doi:10.1007/s00227-007-0777-y
1251
- 1252 144. Simith DJB, Pires MAB, Abrunhosa FA, Maciel CR, Diele K. Is larval dispersal a
1253 necessity for decapod crabs from the Amazon mangroves? Response of *Uca rapax* zoeae
1254 to different salinities and comparison with sympatric species. J Exp Mar Biol Ecol. 2014;
1255 457: 22–30. doi: 10.1016/j.jembe.2014.03.021
1256
- 1257 145. Simith DJB, Souza AS, Maciel CR, Abrunhosa FA, Diele K. Influence of salinity
1258 on the larval development of the fiddler crab *Uca vocator* (Ocypodidae) as an indicator
1259 of ontogenetic migration towards offshore waters. Helgol Mar Res. 2011; 66: 77–85.
1260 doi:10.1007/s10152-011-0249-0
1261
- 1262 146. Diele K, Simith DJB. Salinity tolerance of northern Brazilian mangrove crab larvae,
1263 *Ucides cordatus* (Ocypodidae): necessity for larval export? Estuar Coast Shelf Sci. 2006;
1264 68: 600–608. doi:10.1016/j.ecss.2006.03.012
1265
- 1266 147. Anger K, Montú M, Bakker C, Fernandes LLM. Larval development of *Uca thayeri*
1267 Rathbun, 1900 (Decapoda: Ocypodidae) reared in the laboratory. Meeresforschung.
1268 1990; 32: 276–294.
1269
- 1270 148. Brodie RJ, Behum ME, Monroe E, Glenn N, Staton JL. Recruitment to adult habitats
1271 following marine planktonic development in the fiddler crabs, *Uca pugilator*, *U. pugnax*,
1272 and *U. minax*. Mar Biol. 2005; 147: 105–111. doi:10.1007/S00227-005-1557-1
1273
- 1274 149. O'Connor N. Settlement and recruitment of the fiddler crabs *Uca pugnax* and *U.*
1275 *pugilator* in a North Carolina, USA; salt marsh. Mar Ecol Prog Ser. 1993; 93: 227–234.
1276 doi:10.3354/meps093227
1277
- 1278 150. Diele K. Life history and population structure of the exploited mangrove crab *Ucides*
1279 *cordatus cordatus* (L.) (Decapoda: Brachyura) in the Caeté estuary, North Brazil. Doc
1280 Thesis, Center for Tropical Marine Ecology Contribution, Bremen. 2000. Available from:
1281 <https://core.ac.uk/download/pdf/74034627.pdf>
1282
- 1283 151. Hattori GY, Pinheiro MAA. Fertilidade do caranguejo de mangue *Ucides cordatus*
1284 (Linnaeus) (Crustacea, Brachyura, Ocypodidae), em Iguape (São Paulo, Brasil). Rev Bras
1285 Zool. 2003; 20: 309–313. doi:10.1590/S0101-81752003000200022
1286
- 1287 152. Lima GV, Soares MRS, Oshiro LMY. Reproductive biology of the sesarmid crab
1288 *Armases rubripes* (Decapoda, Brachyura) from an estuarine area of the Sahy River,
1289 Sepetiba Bay, Rio de Janeiro, Brazil. Iheringia. 2006; 96: 47–52. doi:10.1590/S0073-
1290 47212006000100007
1291
- 1292 153. Montú M, Anger K, Bakker C. Variability in the larval development of *Metasesarma*
1293 *rubripes* (Decapoda, Grapsidae) reared in laboratory. Nerítica. 1990; 5: 113–128.
1294
- 1295 154. Luppi TA, Spivak ED, Bas CC. The effects of temperature and salinity on larval
1296 development of *Armases rubripes* Rathbun, 1897 (Brachyura, Grapsoidea, Sesarmidae),

- and the southern limit of its geographical distribution. Estuar Coast Shelf Sci. 2003; 58: 575–585. doi:10.1016/S0272-7714(03)00136-7
155. Santa Brígida YG, Lima FA, Martinelli-Lemos JM. Larvae of *Armases rubripes* (Decapoda, Brachyura) in Amazon oligohaline creeks: larval exportation? 2021. Submitted.
156. Conde JE, Diaz H. The mangrove tree crab *Aratus pisonii* in a tropical estuarine coastal lagoon. Estuar Coast Shelf Sci. 1989; 28: 639–650. doi:10.1016/0272-7714(89)90051-6
157. Leme MHA, Negreiros-Fransozo ML. Reproductive patterns of *Aratus pisonii* (Decapoda: Grapsidae) from an estuarine area of São Paulo northern coast, Brazil. Rev Biol Trop. 1998; 46: 673–678.
158. Araújo MSLC, Tenório DO, Castiglioni DS. Population biology of the crab *Armases angustipes* (Crustacea, Decapoda, Sesarmidae) at Brazilian tropical coast. Iheringia. 2014; 104: 150–161. doi:10.1590/1678-476620141042150161
159. Mantelatto FLM, Faria FCR, Garcia RB. Biological aspects of *Mithraculus forceps* (Brachyura: Mithracidae) from Anchieta Island, Ubatuba, Brazil. J Mar Biol Assoc U K. 2003; 83: 789–791. doi:10.1017/S0025315403007811h
160. Marochi MZ, Martins SB, Masunari S. The salinity during larval development affects the dispersion in adults of the tree-climbing crab *Aratus pisonii*. J Nat Hist. 2017; 51: 2271–2281. doi:10.1080/00222933.2017.1365964
161. Anger K. Salinity tolerance of the larvae and first juveniles of a semiterrestrial grapsid crab, *Armases miersii* (Rathbun). J Exp Mar Biol Ecol. 1996; 202: 205–223. doi:10.1016/0022-0981(96)00022-6
162. Anger K, Torres G, Charmantier-Daures M, Charmantier G. Adaptative diversity in congeneric coastal crabs: ontogenetic patterns of osmoregulation match life-history strategies in *Armases* spp. (Decapoda, Sesarmidae). J Exp Mar Biol Ecol. 2008; 367: 28–36. doi:10.1016/j.jembe.2008.08.009
163. Moura RL, Amado-Filho GM, Moraes FC, Brasileiro PS, Salomon PS, Mahiques MM, et al. Thompson FL. An extensive reef system at the Amazon River mouth. Sci Adv. 2016; 2: e1501252. doi:10.1126/sciadv.1501252
164. Francini-Filho RB, Asp NE, Siegle E, Hocevar J, Lowyck K, D'Avila N, et al. Thompson FL. Perspectives on the great Amazon reef: Extension, biodiversity, and threats. Front Mar Sci. 2018; 5. doi:10.3389/fmars.2018.00142
165. Hu C, Montgomery ET, Schmitt RW, Muller-Karger FE. The dispersal of the Amazon and Orinoco River water in the tropical Atlantic and Caribbean Sea: observation from space and S-PALACE floats. Deep Sea Res Part II. 2004; 51: 1155–1171. doi:10.1016/j.dsr2.2004.04.001

166. Guerao G, Abelló P, Cartes J. Morphology of the megalopa and first crab instar of the shamefaced crab *Calappa granulata* (Crustacea, Brachyura, Calappidae). *Misc Zool.* 1998; 21: 37–47.
167. Guerao G, Torres P. Morphology of the first zoea of the shamefaced crab *Calappa granulata* (Linnaeus, 1758) Crustacea, Brachyura, Calappidae), obtained in the laboratory. *Graellsia.* 1999; 55: 157–162.
168. Terada M. Zoeal forms of 14 species of crabs from the Enshunada. *Res Crust.* 1987; 16: 93–120.
169. McConaughy JR. Decapod larvae: dispersal, mortality and ecology. A working hypothesis. *Am Zool.* 1992; 32: 512–523. doi:10.1093/icb/32.3.512
170. González-Gordillo JI, Rodríguez A. Comparative seasonal and spatial distribution of decapod larvae assemblages in three coastal zones off the south-western Iberian Peninsula. *Acta Oecol.* 2003; 24: S219–S233. doi:10.1016/S1146-609X(03)00032-8
171. Christy JH. Reproductive timing and larval dispersal of intertidal crabs: the predator avoidance hypothesis. *Rev Chil Hist Nat.* 2003; 76: 177–185. doi:10.4067/S0716-078X2003000200005.
172. Natunewicz CC, Epifanio CE, Garvine RW. Transport of crab larval patches in the coastal ocean. *Mar Ecol Prog Ser* 2001; 222: 143–154. doi:10.3354/MEPS222143
173. Jones MB, Epifanio CE. Patches of crab megalopae in the mouth of Delaware Bay- An analysis of spatial scales. *J Shellfish Res.* 2005; 24: 261–267. doi:10.2983/0730-8000(2005)24[261:POCMIT]2.0.CO;2
174. Barletta M, Barletta-Bergan A, Saint-Paul U, Hubold G. Seasonal changes in density, biomass, and diversity of estuarine fishes in tidal mangrove creeks of the lower Caeté Estuary (northern Brazilian coast, east Amazon). *Mar Ecol Prog Ser.* 2003; 256: 217–228. doi:10.3354/meps256217
175. Giarrizo T, Krumme U. Heterogeneity in intertidal fish fauna assemblages along the world's longest mangrove area in northern Brazil. *J Fish Biol.* 2008; 72: 773–779. doi:10.1111/j.1095-8649.2007.01728.x
176. Mourão KRM, Filho PWMS, Alves PJO, Frédou FL. Priority areas for the conservation of the fish fauna of the Amazon Estuary in Brazil: A multicriteria approach. *Ocean Coast Manag.* 2014; 100: 116–127. doi:10.1016/j.ocecoaman.2014.08.007
177. MMA 2018. Ministério do Meio Ambiente. Available: <https://www.mma.gov.br/areas-protegidas/instrumentos-de-gestao/s%C3%ADtios-ramsar.html>

Supporting information

S1 Figure. Density of larval stages of *Calappa* sp., *Goniopsis cruentata*, and Grapsidae n. id. over the months in ACS.

S2 Figure. Density of larval stages of *Pachygrapsus gracilis*, Leucosiidae n. id., and *Persephona* spp. over the months in ACS.

S3 Figure. Density of larval stages of Gelasiminae 1, 2 and 3 over the months in ACS.

S4 Figure. Density of larval stages of Gelasiminae n. id., *Leptuca cumulanta*, and *Minuca rapax* over the months in ACS.

S5 Figure. Density of larval stages of *Uca maracoani*, *Ucides cordatus* and *Hexapanopeus* spp. over the months in ACS.

S6 Figure. Density of larval stages of *Panopeus lacustris*, *Panopeus* sp., and *Austinixa* sp. over the months in ACS.

S7 Figure. Density of larval stages of *Dissodactylus crinitichelis*, *Pinnixa* sp., and *Achelous* spp. over the months in ACS.

S8 Figure. Density of larval stages of *Callinectes* spp., Portunidae n. id., and *Armases rubripes* over the months in ACS.

Fig 1. The Amazon continental shelf, northern Brazil

Fig 2. Historical outflow variation of the Amazon River

Fig 3. Expected abundance/ probability of occurrence of Brachy

Fig 4. Expected abundance/ probability of occurrence of Brach

Oblique

Superficial

Expected abundance/ Probability of occurrence

Distance (Km)

Fig 5. Expected abundance/ probability of occurrence of Brachycephalus species