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Research Article

Invertebrates assemblage captured by a pink shrimp's fishery on Amazon continental shelf

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ABSTRACT. Shrimp trawl fisheries constitute a major threat to continental shelves' biodiversity, given their profound impact on benthic communities. We investigated the composition of an invertebrate assemblage impacted by this type of fishery and possible correlations of the abundance and richness with specific environmental parameters. The activities of the industrial shrimp fleet on the north coast of Brazil were monitored over two years. We analyzed 20,303 specimens belonging to seven phyla (Porifera, Cnidaria, Mollusca, Sipuncula, Annelida, Arthropoda, Echinodermata) and 154 species. There was a predominance of generalist and rare species, given that most species (86) were sporadic. Taxonomic composition patterns were complex, dynamic, and were correlated mainly with the temperature and depth of the Amazon continental shelf, the largest in extension and low depth of the South Atlantic. The crustaceans were dominant in both abundance and taxonomic richness. The influence of environmental factors on the abundance of the main species is discussed. The invertebrates are a neglected component in studies of fisheries impact and important components of the ecological structure of the Amazon coast. They are an essential group for developing a holistic fisheries management approach, which will support the sustainability of the region's fisheries and preserve local aquatic communities.

Keywords: *Farfantepenaeus subtilis*; shrimp trawl; bycatch; taxonomic composition; benthos; environmental factors

INTRODUCTION

The animals rejected by the shrimp trawling fisheries, the bycatch of these operations, constitute one of the most chronic ecological problems of continental shelves. In tropical regions, the reduced selectivity of the nets combined with these regions' high biological diversity results in capturing a much larger proportion of bycatch than the target species itself (Zeller & Pauly 2005). Impacts from trawl fisheries may be modified significantly by the patterns of abundance, taxonomic richness, species dominance, and species dominance trophic structure (Fulton et al. 2005). The most preoccupying consequence of this scenario is the loss of biological and functional diversity, given the weakening of ecosystem structure and reducing its services (Buhl-Mortensen et al. 2016).

The bycatch's invertebrate component is frequently overlooked, not only by scientists but also by fishery managers and conservationists, due to a lack of emblematic species or an inadequate understanding of these organisms vulnerability (Guerra et al. 2011). The invertebrate diversity has been decreasing steadily since the 1960s (Philippart 1998) around the world, when trawling operations began, highlighting the negative effects of this activity, and its broad impacts, including a large part of the benthic community (Frid et al. 2000).

On the Amazon continental shelf, benthic invertebrates' biological activity, together with that of fish and mixotrophic animals, contributes to constructing carbonated structures that form the region's recently-discovered coral reefs (Moura et al. 2016). Fragments of invertebrates are an integral part of the rhodolite beds,

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in particular in the northwest of the shelf, and in many cases, small animals, such as annelids, ophiuroids, and mollusks, are found in the holes in these structures (Vale et al. 2018). Larger animals, such as crustaceans, echinoderms, and fish, together with wave action, also contribute to the rhodolite beds' morphology and mobility (Vale et al. 2018).

The benthic invertebrates are closely dependent on abiotic variables, which can interfere with the animals' physiological performance and reproductive success, which respond to this variation through either an increase or decrease in abundance, shifts in the distribution, or the taxonomic composition (Harley et al. 2006). Determining which patterns of the taxonomic organization reflect over-exploited environments and, in particular, those at risk of the loss of ecological function may contribute to the development of more effective species monitoring practices and conservation measures.

The massive discharge of this river forms the Amazon plume, a mass of low saline water that extends into the Atlantic Ocean off the north coast of Brazil, varying in extension and disposition over the year. The North Brazil Current and wind influence the circulation of these waters, regulating the plume's dispersal, direction, and velocity (Molleri et al. 2010). The rainy season in this region typically lasts from December to June, while the second half of the year (July to November) is considered the dry or less rainy season.

Although the knowledge of the bycatch on the north coast already exists, studies are limited to information on the occurrence of species (Cutrim et al. 2001, Aragão et al. 2015, Cintra et al. 2017), few works addressing the structure and spatial-temporal distribution of invertebrates along with the platform. Such studies lack ecological refining that allows inferring biological patterns that could be inserted in conservation and management policies. In this context, the present study investigated the structure of the invertebrates assemblage that are impacted by the shrimp fisheries of the north coast of Brazil and determining possible correlations of the abundance and richness with temperature substrates, salinity, and depth.

MATERIALS AND METHODS

Study region

The study region encompasses the Amazon continental shelf (ACS), which extends from the mouth of the Pará River north to Cape Orange, at the northern extreme of the Brazilian state of Amapá. The study area is located between 0.8-4.7ºN and 47.85-51.17ºW (Fig. 1). This area is influenced directly by the discharge of the Amazon River, which has the largest freshwater discharge of any body of water on the planet, and the principal outflow of the freshwater of the Amazon region (Masson & Delecluse 2001).

Given the scale of the study area, the fishery operation zone was divided into four sub-regions, two located in the northern portion of the zone (NA: 4.7-3.7ºN, and NB: 3.8-2.8ºN), and two in the southern portion (SC: 1.8-2.7ºN, and SD: 1.7-0.8ºN) (Fig. 1). The two northern sub-regions are influenced more intensively and constantly by the Amazon plume, while the two southern sub-regions are influenced directly by the discharge of the Amazon River and are more subject to the seasonal variation in the characteristics of the plume. The sub-regions were divided equidistantly and with equal sampling effort in terms of the extent and hours of trawling. The shrimping ground name at which each sample was obtained was also recorded, based on the information provided by the master of the vessel.

Field and laboratory procedures

The samples were collected during the operations of the industrial shrimp fleet of the north coast of Brazil, which is composed of medium-sized boats with double-rig bottom trawls of 18.0×22.4×1.2 m and a mesh of 30×21 mm and 20×20 mm in the cod end. A total of 169 trawls were monitored, over 887.54 h, between July 2015 and May 2017, bimonthly. According to the migration of adults of the target species, the operational area of the fleet shifts over the year, with the lower latitudes being focused on during the first few months of the year and operations shifting to the northwest as the year progresses, according to the migration of adults of the target species the pink shrimp *Farfantepenaeus subtilis*. This displacement obeys resource utilization's logic since the pink shrimp uses the mangroves of the Brazilian north coast to grow juveniles and adults migrate towards Guyana, following the south equatorial current the largest specimens of the species. Thus, the boats drag practically in a straight northwest direction, following the adult stock's migration.

The invertebrates found in the bycatch were collected from the net by an onboard sampler and immediately deposited on the vessel's deck, where they were placed in two 30 kg baskets. These samples remained frozen until processed in the laboratory, where they were identified to the lowest possible taxonomic level. For this study, we defined bycatch as all animals that were not destined for sale, including the target species, *F. subtilis*, when rejected due to the shrimp's small size.

The abiotic factors temperature, salinity, and depth of the water were measured through samples obtained at the moment of collection. The temperature was mea-

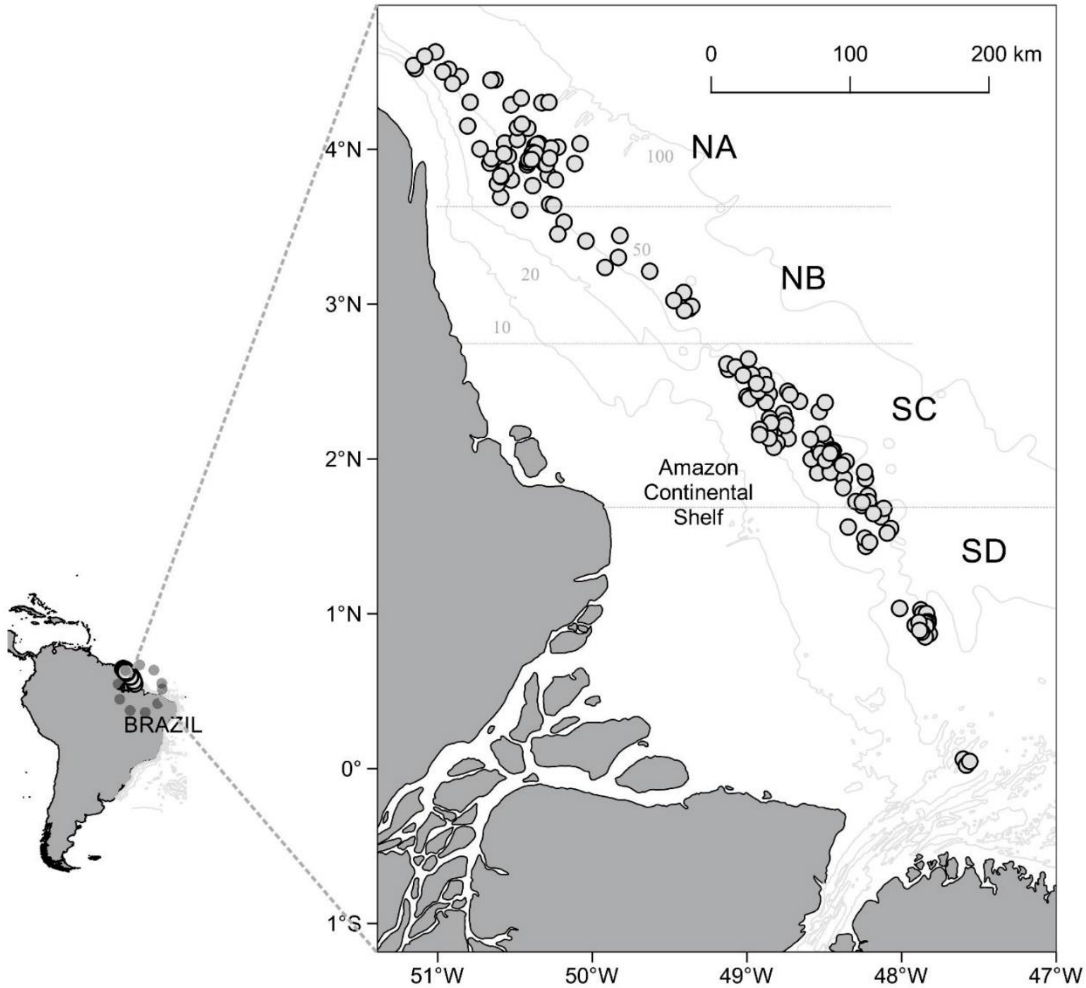

Figure 1. Points at which the invertebrate bycatch of the north coast of Brazil's industrial shrimp fleet was sampled between July 2015 and May 2017. NA: 4.7-3.7ºN, NB: 3.8-2.8ºN, SC: 1.8-2.7ºN, and SD: 1.7-0.8ºN.

sured with a mercury thermometer, salinity with an optical refractometer, and the vessel's depth sounder. The substrate was classified according to Nittrouer et al. (1986), who defined three principal categories for the study region: i) mottled mud, ii) mud intercalated with sand, and iii) partially laminated mud.

Analysis of the data

To identify the similarity of environmental factors (temperature, salinity, pH, and substrate) of the shrimping ground it was used a hierarchical Cluster analysis, based on the Ward method and Euclidian distance, was run in the Past 3.20.

Relative abundance (RA) of each species was calculated by dividing the total number of individuals of each species by the total number of individuals captured in all the trawls. We established three abundance categories: i) very abundant (Va), when the species represented more than 5% of the individuals captured in all the trawls, ii) abundant (Ab), when the species contributed 1-5% of the individuals captured, and iii) rare (Ra) when the species represented less than 1% of the individuals captured (Graça-Lopes et al. 1993).

To understand predictors of species richness, we defined a series of GLM (generalized linear model) that was adjusted to the data (McCullagh & Nelder 1989), including all the principal effects, based on:

$$\eta_{abcdehijk} = \beta_0 + \beta_{1a} + \beta_{2b} + \beta_{3c} + \beta_{4d} + \beta_{5e} + \beta_6 p_h + \beta_7 t_i + \beta_8 s_j + \beta_9 w_k, \quad (1)$$

where $\eta_{abcdefghijk} = g(EY_{abcdehijk})$ is the linear predictor of the value number of species ($EY_{abcdehijk}$) in the -th phase of the moon ($a = \{1,2,3,4\}$), in the -th region ($b = \{1,2,4,5\}$), in the -th substrate ($c = \{1,2,3,4,5\}$), in the -th bimester ($d = \{1,2,\ldots,9\}$) of the -th year ($e = \{1,2,3\}$), with depth p_h, temperature t_i, salinity s_j and sampling effort w_k. The covariables with indices of a to e were considered qualitative, while those with h to k were treated as quantitative covariables.

Given the possibility of overdispersal, a common problem with count data (Hinde & Demétrio 1998), two random components were considered for the distribution of $Y_{abcdefghijk}$ a Poisson distribution and a negative binomial distribution. In both cases, the logarithmic link function was applied, i.e. g(·) = ln(·).

The covariates were then selected in a stepwise fashion from the adjustments of Equation (1) models and tests of likelihood rates. The final Poisson and negative binomial models were submitted to an analysis of residuals and diagnostics, particularly quantile-quantile plots with simulated envelopes (Flack & Flores 1989). Following the covariates' selection for each component and identifying the best random component, multiple comparisons were applied to all possible pairs of contrasts between one-factor levels, based on the Tukey test. All these analyses were run in the R 3.5 environment (R Core Team 2017), in the 'hnp' (Moral et al. 2017), 'MASS' (Venables & Ripley 2002), and 'multcomp' (Hothorn et al. 2008) packages.

A redundancy analysis (RDA) was then applied to identify which predictors (temporal, spatial, or environmental) best explain the distribution of the occurrence of the species (response variable). The variables temperature, salinity, and depth are continuous, while the substrate, area, and month are categorical. Only the 11 species with the greatest frequency of occurrence were included in the analysis due to the enormous discrepancies in the species abundance scale. Hellinger's transformation (Legendre 2008) was applied to the abundance matrix data to reduce the importance of the most abundant taxa, given that it is indifferent to the number of zeros. A permutational ANOVA with 999 permutations was used to determine the significance of this analysis, run in the R 3.5 platform (R Core Team 2017).

RESULTS

Environmental variables

The trawls' mean depth varied significantly among months, with deeper trawls recorded during the least rainy months (June to December) and shallower trawls during the rainy season (December to May). Depths of between 35 m (February 2016) and 85 m (September 2016) were recorded during the study, with an overall mean depth of 54.22 ± 7.89 m (standard deviation).

Salinity was the only variable that presented range amplitude, from 10 to 36 (overall mean of 28.52 ± 5.71), with the highest values being recorded during the second half of 2015 and 2016. The water was more saline in 2015 than in the other years (Fig. 2).

The environmental characteristics (temperature, salinity and sediments) of the shrimping grounds in the two sub-zones (northern and southern) are distinct (Fig. 3). One exception is the "Beiradão" (4.42-4.50ºN, 50.90-51.2ºW) which, despite being located in the northern sub-zone, was more similar to the grounds located in the southern portion of the shelf (see the dark gray area in the right half of the dendrogram).

Biological variables

We analyzed 20,303 specimens representing seven phyla (Annelida, Arthropoda, Cnidaria, Echinodermata, Mollusca, Porifera, Sipuncula), 67 families, and 154 species. Rare species were predominant, given that a majority (86) was sporadic and together contributed only 1% of total abundance, whereas the other 68 species contributed 99% of the total number of individuals captured as bycatch by the shrimp fleet of the Amazon continental shelf. The species with the greatest abundance (23.0% of the total) was the crab *Achelous rufiremus* (Holthuis, 1959), followed by the shrimp species *Rimapenaeus similis* (Smith, 1885) with 18.7% of the total, and *Xiphopenaeus kroyeri* (Heller, 1862), which contributed with 10.9% of the bycatch. The subphylum Crustacea predominated in terms of both the number of individuals (17.5 or 86.4%) and species (67 or 43.5%), followed by: Mollusca, with 1524 (7.4%) individuals and 53 (35%) species (Fig. 4). In the Mollusca phyla, the greatest abundance groups were the *Ostrea* sp. with 2.0% of the total, followed by *Abra lioica* (Dall, 1881), which contributed with 0.7% of the bycatch (Table 1). In the Cnidaria phylum, the greatest abundance was the Renillidae sp. 1 (3.89%), followed by *Chiropsalmus quadrumanus* (F. Muller, 1859).

Interaction between biological and environmental variables

As the model with the negative random binomial component was better according to the residuals analysis (Fig. 5), all the statistical inferences of the GLM were based on this model. The estimates of the parameters of the final model selected by the analysis are presented in Table 2.

The lunar phase and sub-region were the most important qualitative descriptors for adjusting the model and the covariables' depth and temperature. Increasing temperature and depth are both associated with a reduction in the expected number of species. Similarly, the NB, SC, and SD sub-regions all presented a reduction in expected species richness, while richness increased between the waning crescent and new moon.

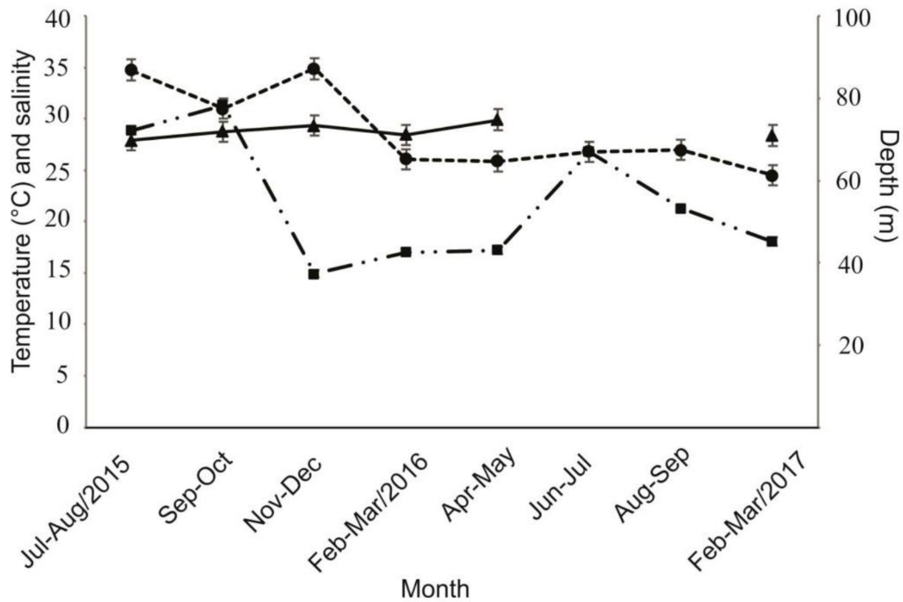

Figure 2. Mean depth (m), salinity, and temperature (ºC) recorded on the Amazon continental shelf bimonthly of the study period. The vertical bars represent the standard deviation. Continuous line: temperature. Dashed line: salinity. Dashed and dotted line: depht.

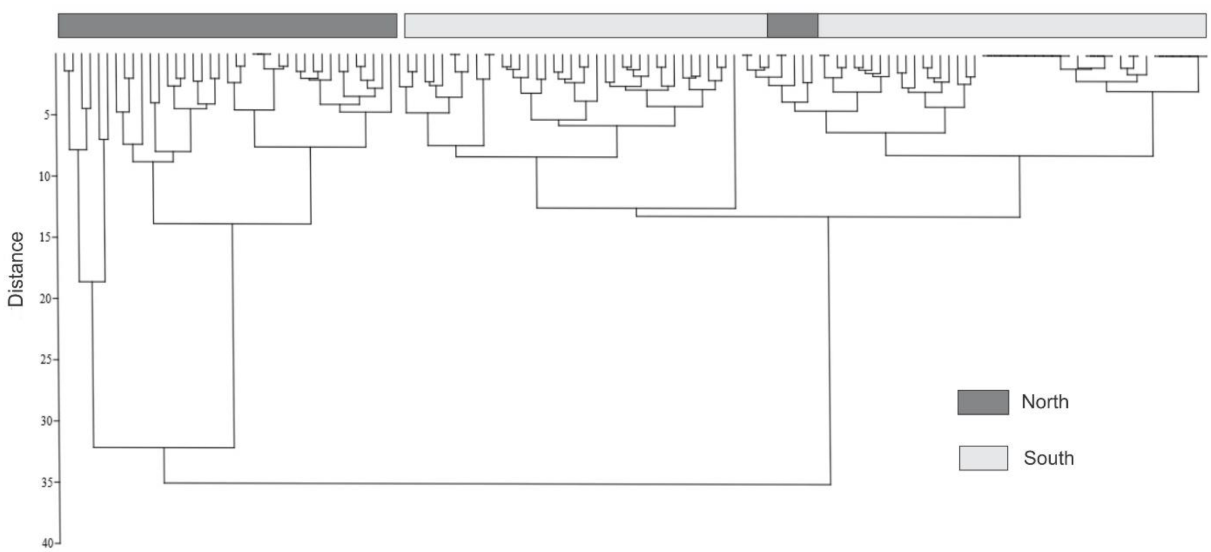

Figure 3. Dendrogram produced by the Cluster analysis of the shrimping grounds located in the northern and southern subzones of the Amazon continental shelf, based on their environmental characteristics. Cophenetic coefficient = 0.913.

Significant differences were found in the expected number of species between the new and full moons and between the new and waning moons (Table 3). Given the positive estimates of the contrasts, also, it is possible to conclude that the expected number of species is greater during the new moon.

Significant variation was also found among the different sub-regions (Table 4), which formed two groups. One group was formed by the sub-regions NA and NB, and the other by sub-regions SC and SD. The analyses indicate that greater species richness is expected in the northern sub-zone compared to the southern zone.

In the RDA, only the variables temperature and shrimping ground were correlated strongly (>0.7) with abundance, both negatively (Fig. 6). The correlation coefficients obtained by the RDA are presented in Table 5. The RDA explained approximately 25% of the data variability (adjusted R2: 24.7), with axis 1 being responsible for 55.2% of the variation, while axis 2

Table 1. Invertebrate species are captured as bycatch by the industrial shrimp fleet operating on the Amazon continental shelf. n: number of individuals, RA: relative abundance, FR: frequency of occurrence (%). Va: very abundant; Ab: abundant; Ra: rare.

Taxon	n	RA	FR
ANNELIDA			
Echiura	24	Ra	0.118
Polychaeta 1	1	Ra	0.005
Polychaeta 2	1	Ra	0.005
Aphroditidae			
Aphroditidae	50	Ra	0.246
Nereididae			
Nereididae	2	Ra	0.01
Sabellaridae			
Sabellaridae	4	Ra	0.02
CNIDARIA			
Actiniaria 1	13	Ra	0.064
Actiniaria 2	5	Ra	0.025
Actiniaria 3	1	Ra	0.005
Chiropsalmidae			
Chiropsalmus quadrumanus	48	Ra	0.236
Renillidae			
Renilla 1	791	Ab	3.896
Renilla 2	43	Ra	0.212
Renilla 3	16	Ra	0.079
Renilla 4	17	Ra	0.084
CRUSTACEA			
Diogenidae			
Clibanarius foresti	105	Ra	0.517
Dardanus fucosus	36	Ra	0.177
Dardanus venosus	7	Ra	0.034
Petrochirus diogenes	2	Ra	0.01
Dromiidae			
Dromia erythropus	1	Ra	0.005
Moreiradromia antillensis	1	Ra	0.005
Epialtidae			
Stenocionops furcatus	1	Ra	0.005
Libinia ferreirae	1	Ra	0.005
Inachidae			
Ericerodes gracilipes	1	Ra	0.005
Inachoididae			
Anasimus latus	671	Ab	3.305
Collodes inermis	32	Ra	0.158
Stenorhynchus seticornis	4	Ra	0.02
Paulita tuberculata	1	Ra	0.005
Parasquillidae			
Parasquilla meridionalis	1	Ra	0.005
Parthenopidae			
Agolambrus agonus	3	Ra	0.015
Leiolambrus nitidus	31	Ra	0.153
Leptochela (Leptochela) serratorbita	3	Ra	0.015
Platylambrus serratus	6	Ra	0.03
Penaeidae			
Litopenaeus schmitti	5	Ra	0.025
Penaeus sp.	190	Ra	0.936
Farfantepenaeus subtilis	1683	Va	8.289
Rimapenaeus similis	3789	Va	18.662

Taxon	n	RA	FR
CRUSTACEA			
Axiidea	1	Ra	0.005
Caridea 1	1	Ra	0.005
Caridea 2	1	Ra	0.005
Caridea 3	1	Ra	0.005
Caridea 4	2	Ra	0.01
Isopoda	9	Ra	0.044
Cirripedia	26	Ra	0.128
Aethridae			
Hepatus gronovii	6	Ra	0.03
Hepatus pudibundus	18	Ra	0.089
Hepatus scaber	87	Ra	0.429
Aethridae	6	Ra	0.03
Alpheidae			
Alpheus macrocheles	1	Ra	0.005
Alpheus sp.	2	Ra	0.01
Calappidae			
Calappa ocellata	75	Ra	0.369
Calappa sulcata	261	Ab	1.286
Chasmocarcinidae			
Amboplax peresi	2	Ra	0.01
Leucosiidae			
Acanthilia intermedia	2	Ra	0.01
Persephona lichtensteinii	171	Ra	0.842
Persephona mediterranea	15	Ra	0.074
Persephona punctata	454	Ab	2.236
Lysiosquillidae			
Lysiosquilla scabricauda	5	Ra	0.025
Lysmatidae			
Exhippolysmata oplophoroides	1	Ra	0.005
Menippidae			
Menippe nodifrons	1	Ra	0.005
Mithracidae			
Mithrax tortugae	4	Ra	0.02
Palaemonidae			
Nematopalaemon schmitti	5	Ra	0.025
Pandalidae			
Plesionika ensis	1	Ra	0.005
Panopeidae			
Panopeus occidentalis	1	Ra	0.005
Portunidae			
Achelous gibbesii	4	Ra	0.02
Achelous rufiremus	4675	Va	23.026
Achelous spinicarpus	348	Ab	1.714
Callinectes bocourti	2	Ra	0.01
Callinectes ornatus	1183	Va	5.827
Charybdis (Charybdis) hellerii	1	Ra	0.005
Cronius ruber	1	Ra	0.005
Sicyoniidae			
Sicyonia burkenroadi	12	Ra	0.059
Sicyonia dorsalis	270	Ab	1.33
Sicyonia stimpsoni	108	Ra	0.532

Continuation

Taxon	n	RA	FR
Xiphopenaeus kroyeri	2213	Va	10.9
Pilumnidae			
Pilumnus diomedeae	3	Ra	0.015
Porcellanidae			
Porcellana sayana	23	Ra	0.113
ECHINODERMATA			
Asteroidea 1	1	Ra	0.005
Asteroidea 2	41	Ra	0.202
Asteroidea 3	9	Ra	0.044
Asteroidea 4	3	Ra	0.015
Asteroidea 5	4	Ra	0.02
Asteroidea 6	26	Ra	0.128
Asteroidea 7	1	Ra	0.005
Asteroidea 8	12	Ra	0.059
Ophiuroidea 1	97	Ra	0.478
Ophiuroidea 2	1	Ra	0.005
Echinoidea	1	Ra	0.005
Holothuroidea	3	Ra	0.015
Gorgonocephalidae			
Gorgonocephalidae	2	Ra	0.010
SIPUNCULA			
Sipuncula	8	Ra	0.039
MOLLUSCA			
Cymatiidae			
Monoplex parthenopeus	1	Ra	0.005
Dentaliidae			
Dentalium sp.	1	Ra	0.005
Fasciolariidae			
Aurantilaria aurantiaca	1	Ra	0.005
Fusinus helenae	3	Ra	0.015
Loliginidae			
Doryteuthis (Amerigo) pealeii	127	Ra	0.626
Lucinidae			
Divalinga quadrisulcata	1	Ra	0.005
Margaritidae			
Pinctada imbricata	1	Ra	0.005
Prunum storeria	1	Ra	0.005
Muricidae			
Stramonita brasiliensis	3	Ra	0.015
Chicoreus brevifrons	12	Ra	0.059
Mytilidae			
Modiolus americanus	9	Ra	0.044
Musculus lateralis	1	Ra	0.005
Personidae			
Distorsio clathrata	5	Ra	0.025
Pinnidae			
Atrina seminuda	7	Ra	0.034
Plicatulidae			
Plicatula gibbosa	4	Ra	0.02
Pteriidae			
Pteria colymbus	16	Ra	0.079
Semelidae			
Abra lioica	150	Ra	0.739
Tellinidae			
Eurytellina trinitatis	8	Ra	0.039

Taxon	n	RA	FR
Sicyonia typica	1	Ra	0.005
Solenoceridae			
Solenocera atlantidis	7	Ra	0.034
Solenocera geijskesi	265	Ab	1.305
Squillidae			
Squilla lijdingi	696	Ab	3.428
MOLLUSCA			
Bursidae			
Marsupina bufo	77	Ra	0.379
Calliostomatidae			
Calliostoma sp.	1	Ra	0.005
Calyptraeidae			
Crepidula intratesta	19	Ra	0.094
Calyptraea centralis	67	Ra	0.33
Cardiidae			
Americardia media	2	Ra	0.01
Chamidae			
Arcinella brasiliana	1	Ra	0.005
Columbellidae			
Anachis catenata	1	Ra	0.005
Conidae			
Conus sp.	4	Ra	0.02
Corbulidae			
Caryocorbula swiftiana	5	Ra	0.025
Crassatellidae			
Crassinella sp.	55	Ra	0.271
Nassariidae			
Phrontis alba	17	Ra	0.084
Phrontis vibex	1	Ra	0.005
Naticidae			
Natica marochiensis	4	Ra	0.02
Stigmaulax cayennensis	1	Ra	0.005
Sinum perspectivum	2	Ra	0.01
Nuculanidae			
Saccella larranagai	22	Ra	0.108
Octopodidae			
Octopus insularis	1	Ra	0.005
Olividae			
Americoliva circinata	9	Ra	0.044
Olivella sp.	3	Ra	0.015
Ostreidae			
Ostrea sp. 1	1	Ra	0.005
Ostrea sp. 2	415	Ab	2.044
Pectinidae			
Euvola chazaliei	67	Ra	0.33
Euvola marensis	30	Ra	0.148
Turridae			
Polystira sp.	18	Ra	0.089
Veneridae			
Tivela fulminata	1	Ra	0.005
Lirophora paphia	1	Ra	0.005
Pitar albidus	42	Ra	0.207
Verticordiidae			
Haliris sp.	1	Ra	0.005
Volutidae			

Continuation

Taxon	n	RA	FR
Strigilla carnaria	2	Ra	0.010
Terebridae			
Terebra taurina	2	Ra	0.010
Tonnidae			
Tonna galea	112	Ra	0.552
Turbinellidae			
Turbinella laevigata	25	Ra	0.123
PORIFERA			
Porifera 1	3	Ra	0.015
Porifera 2	1	Ra	0.005
Aplysinidae			
Aplysina pseudolacunosa	1	Ra	0.005
Irciniidae			
Ircinia sp.	1	Ra	0.005
Microcionidae			
Clathria (Clathria) nicoleae	3	Ra	0.015

Taxon	n	RA	FR
Voluta ebraea	1	Ra	0.005
Yoldiidae			
Adrana electa	96	Ra	0.473
Adrana sp.	67	Ra	0.33

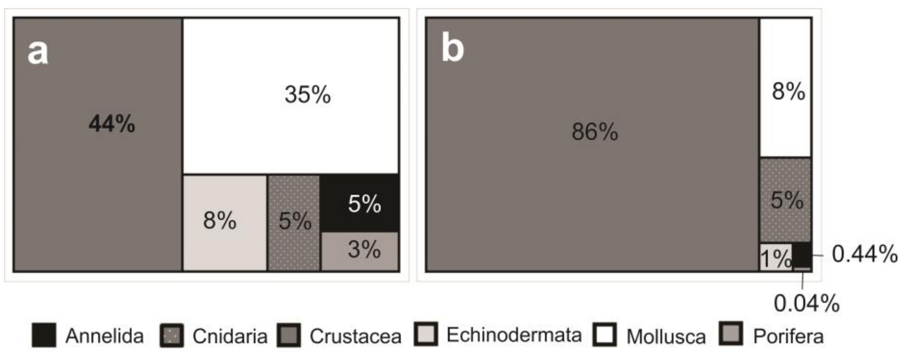

Figure 4. Relative frequency (%) of the different taxonomic groups of invertebrates captured as bycatch on the Amazon continental shelf. a) Number of species, b) number of individuals.

explained 30.7%. The first axis's negative orientation included temperature and salinity, although there was only a moderate association of *Callinectes ornatus* with temperature. By contrast, the crabs *Persephona punctata* and *Anasimus latus* were correlated positively with depth. The second axis's positive orientation was not associated with any species, whereas in the negative direction, the cnidarian *Renilla* sp. 1 and the shrimp *X. kroyeri* correlated with the type of substrate. The crab *C. ornatus* was also associated to a moderate degree with the shrimping ground. The most abundant invertebrate, *A. rufiremus*, was not correlated with any of the environmental variables. The RDA was significant at a 95% confidence level (Table 6).

DISCUSSION

The invertebrate assemblage impacted by the shrimp fisheries on the ACS had high species richness, rare species predominance, and a high proportion of sporadic captures, which translate into a highly complex taxonomic composition. This taxonomic richness is sensitive to temperature changes, which requires further attention, given the current climate change scenario, and reinforces the need for the integrated analysis of biological, physical and chemical descriptors. Fisheries that generate a large diversity of bycatch are a challenge for stock management, given the need to identify priorities to make monitoring viable, based on the different species' susceptibility (Stobutzki et al. 2001).

Bottom trawling is known to provoke the loss of both biological and functional diversity, in particular specialists and ecologically sensitive species (Hall et al. 2000, Jimenes et al. 2016). The industrial fisheries from the Brazilian north coast have been operating continuously since the 1960s, creating a high-impact scenario. Despite this, the regions' fauna is still enormously diverse, even compared with other tropical regions (Stobutzki et al. 2001, Tonks et al. 2008). This

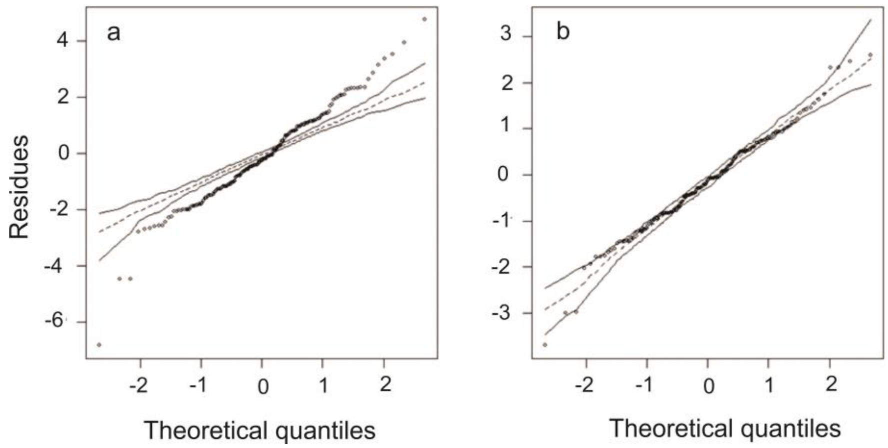

Figure 5. Normal quantile-quantile graphs with a simulated envelope of the adjusted models after covariate selection. a) Poisson random component, b) negative binomial random component.

Table 2. Estimates (and their respective standard errors) of the final model's parameters (random negative binomial component with logarithmic link function) selected for the species richness. β_{12}: effect of the waning moon phase; β_{13}: effect of the waxing moon phase; β14: effect of the new moon; β_{22}: effect of sub-region NB; β_{23}: effect of sub-region SC; β_{24}: effect of sub-region SD; β_6: effect of depth; β_7: effect of temperature; κ: parameter of overdispersal of the negative binomial distribution. Z: absolute value of Wald's statistic. *Significant values ($P < 0.5$).

Parameter	Estimate	Standard error	Z	*P*
Intercept	11.536906	1.457536	7.915	<0.0001*
β_{12}	0.087722	0.121077	0.725	0.469
β_{13}	0.103086	0.144687	0.712	0.476
β_{14}	0.468594	0.118704	3.948	<0.0001*
β_{22}	-0.176373	0.146583	1.203	0.229
β_{23}	-0.779851	0.187163	4.167	<0.0001*
β_{24}	-1.064609	0.145338	7.325	<0.0001*
β_6	-0.010157	0.003849	2.639	0.008
β_7	-0.291659	0.050843	5.736	<0.0001*
k	5.0383	-	-	-

Table 3. Contrasts (multiple comparisons) among the moon phases, based on the final model, adjusted to species richness data. Z: absolute value of Wald's statistic, *Significant values ($P < 0.5$).

Contrast	Estimate	Standard error	Z	*P*
Waning-full	0.08772	0.12108	0.725	0.8861
Waxing-full	0.10309	0.14469	0.712	0.891
New-full	0.46859	0.1187	3.948	<0.001*
Waxing-waning	0.01536	0.15646	0.098	0.9997
New-waning	0.38087	0.13004	2.929	0.0176
Waxing-new	0.36551	0.14754	2.477	0.0624

may be the result of the region's highly complex ecosystems, established through the association of the multiple features that are unique to the Amazon coast, in particular, its status as the largest freshwater drainage of the Atlantic Ocean, which creates physicochemical conditions on the continental shelf that include (i) the enormous sediment load of the Amazon River, which is deposited in distinct forms within the extension of the estuary, with the more internal and intermediate areas having significantly higher and more rapid rates of sedimentation (Nittrouer et al. 1986); (ii) differences in the intensity and frequency of the Amazon plume over the shelf, which is more constant in its northern portion and more seasonal in the south (Moura et al. 2016),

Table 4. Contrasts (multiple comparisons) among the subregions, based on the final model, adjusted to species richness data. NA: 4.7-3.7ºN, NB: 3.8-2.8ºN, SC: 1.8-2.7ºN, and SD: 1.7-0.8ºN. Z: absolute value of Wald's statistic, *Significant values (*P* < 0.5).

Contrast	Estimate	Standard error	Z	*P*
NB-NA	-0.1764	0.1466	1.203	0.61672
SC-NA	-0.7799	0.1872	4.167	<0.001*
SD-NA	-1.0646	0.1453	7.325	<0.001*
SC-NB	-0.6035	0.1906	3.166	0.00819
SD-NB	-0.8882	0.1551	5.725	<0.001*
SC-SD	-0.2848	0.1451	1.963	0.1964

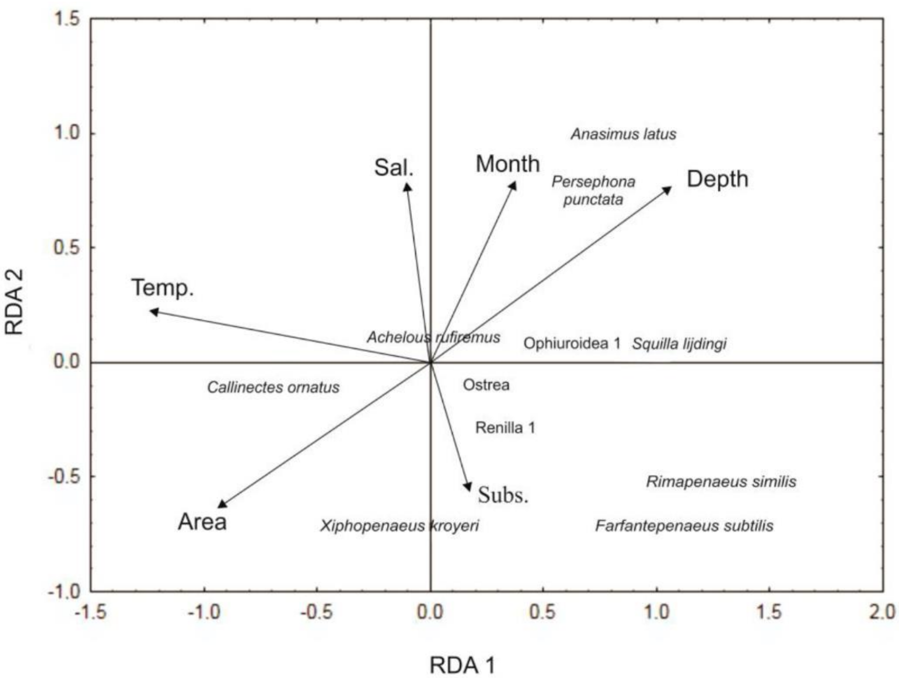

Figure 6. Ordination plot produced by the redundancy analysis (RDA) of the invertebrate bycatch of the shrimp fleet operating on the Amazon continental shelf (July 2015-May 2017). Temp: temperature, Sal: salinity, Subs: subtrate.

provoking differences in temperature, salinity and the penetration of sunlight (Molleri et al. 2010); (iii) the ample spatiotemporal variation in strength of the winds and the North Brazil Current, with the highest values being recorded at 4°N during the second half of the year (Geyer et al. 1996), with a fundamental influence on the fixation of benthos; and (iv) the mosaic of sediments, which shifts between south and north, with the southern portion being covered with mottled mud interspersed with sand, and the northern portion being characterized by both these types of sediment, as well as more consolidated and integrated beds of mud (Nittrouer et al. 1986).

Complex environments have various habitats, which can accommodate a greater diversity of life modes than homogeneous environments. The greater concentration of sponges in the southern portion of the continental shelf, and the construction of coral reefs in some specific areas, for example, reflect the environmental complexity (Moura et al. 2016). They are also reflected in the resilience of the Amazonian invertebrate assemblages, which is derived from the different types of control on their diversity, with the southern portion being regulated primarily by biological relationships such as competition and predation, and the northern portion, more by the influence of physical and chemical factors, like turbidity and the penetration of sunlight (Moura et al. 2016).

A few common species' predominances are typical of tropical regions' bycatch (Stobutzki et al. 2001). Two principal factors may account for this model: i) differences in capturability related to factors such as body size and morphology, given that the trawls do not

Table 5. Results of the canonical correlation analysis between the mean environmental variables and invertebrate densities on the Amazon continental shelf. Values in bold type were considered significant with a confidence limit of 95%.

Variable	Axis 1	Axis 2
Month	0.27	0.52
Area	**-0.76**	-0.44
Depth	0.67	0.51
Temperature	**-0.89**	0.18
Salinity	-0.03	0.52
Substrate	0.12	-0.39

sample all species with the same efficiency, and ii) distinct levels of vulnerability, which depend on the support capacity and the resilience of each species in response to the disturbances caused by fisheries (Philippart 1998).

The survival rate of a species will depend on its response to different aspects of the stress provoked by the capture process, including exposure to air, plasticity to changes in temperature, sunlight, and the capacity of the animal to recuperate from the physical damage caused by its contact with the trawl (Broadhurst & Uhlmann 2007). Characteristics such as life-history traits, body size, reproduction, and growth rates also influence these animals' vulnerability to fisheries (Tillin et al. 2006). The crustaceans were dominant in terms of both the number of individuals and species, probably because they are more tolerant to handling, storage, and transport because most species have a rigid exoskeleton, autotomy of the members, and the ability to breathe air, which all favor their survival in comparison with other invertebrates (Hill & Wassenberg 1990).

Survival rates in crustaceans may vary considerably, even among the same genus species (Hill & Wassenberg 1990, Moreira et al. 2011, Jimenes et al. 2016), in particular, because the forms that have spiny exoskeletons are more vulnerable to damage (Bergmann et al. 2001). The greater resilience of crustaceans in comparison with other invertebrates does not necessarily imply that fishing pressure does not affect their reproductive success given that, in addition to physical lesions, the behavior of some species, including mating rituals and parental care, is interrupted (Smith 1992). The present study registered the largest number of crustacean species (68) ever recorded in the region, given that Cintra et al. (2017) recorded 44 species in the region, while Cutrim et al. (2001) identified 23 species in the shrimping ground known as "Lixeira" (0º00'-1º30'N, 46º50'-48º00'W).

Table 6. The permutational ANOVA of the canonical redundancy analysis model between the environmental variables and the invertebrate assemblage of the Amazon continental shelf (July 2015 through May 2017). Number of permutations: 999. df; degrees of freedom, F: F-ratio, *Significant values ($P < 0.05$).

	df	Variation	F	*P*
Model	6	4.22	5.54	0.001*
Residual	77	9.77		

Achelous rufiremus was the most abundant and widely-distributed species, which indicates that it is well adapted to conditions in the study area, probably because it is not correlated (that is, limited by) any of the abiotic factors analyzed in the present study, which indicates that it is tolerant of the spatiotemporal variation intrinsic to the environment. Despite its reproductive success and apparent lack of threats from human activities, given its absence from national conservation databases (Pinheiro 2016), *A. rufiremus* has a restricted geographic distribution, being found only in the equatorial western Atlantic Ocean, between Guyana and the Brazilian state of Maranhão (Melo 1996), and little is known of its biology.

Five species, three of shrimp (*Rimapenaeus similis*, *Xiphopenaeus kroyeri*, and *Farfantepenaeus subtilis*) and two of portunid crabs (*A. rufiremus* and *Callinectes ornatus*), contributed more than half (66.70% of the individuals) of all the bycatch. In general, portunids are predators (Mantelatto & Christofoletti 2001, Reigada & Negreiros-Fransozo 2001, Silva et al. 2017), while shrimp are detritivores and omnivores (Willems et al. 2016), and both are highly generalist (Eddy et al. 2017). These species' predominance is consistent with the paradigm of generalists' dominance in disturbed environments (Ramsay et al. 1998). This guild is favored by its ability to adjust its behavior in response to the abrupt physical and biological shifts caused by human activities (Tillin et al. 2006). Also, the physical destruction or mortality of animals in fishery zones increases feeding resources that benefit predators, particularly some crustaceans, which are sensitive to the chemical signals released by damaged tissue (Zimmer-Faust 1993). The predominance of more generalist species within the study region may mediate the functional deficit caused by fisheries by providing environmental redundancy, which makes the benthic ecosystem more resilient and robust (Darr et al. 2014). The swimming crabs are scavengers. The removal of predators/competitors and the abundance of bycatch available to scavenge is possibly beneficial to *A. rufiremus*.

The variables sub-region, temperature, and depth had a strong influence on taxonomic richness patterns and the variation in some species' abundance. The increasing richness found to the north towards the Caribbean is a well-known pattern in crustaceans (Boschi 2000), which made up the vast majority of the present study's specimens. The strong influence of temperature indicates that, despite the minor variation and constant thermoclines that are typical of tropical regions, the characteristics of the benthic invertebrates of the ACS are consistent with the well-documented pattern of close association with temperature (Negreiros-Fransozo et al. 1999, Gillooly et al. 2001, Brown et al. 2004). The abundance of the crab *C. ornatus* was the most closely correlated with temperature, consistent with several studies in Brazil's subtropical regions (Andrade et al. 2013, Watanabe et al. 2014). The abundance of the target species, *F. subtilis*, is also inversely proportional to temperature (Martins et al. 2015). This systematic association implies that monitoring fluctuations in temperature can offer a practical means of predicting possible biological change scenarios in any study system.

As a purely spatial factor, depth cannot in itself explain patterns of biological richness, although the factors that vary with depth, such as the temperature, salinity, and turbidity of the water, and the sediment load, do control the distribution and abundance of aquatic organisms (McArthur et al. 2010). Given the highly variable sedimentation rates found within the Amazon estuary, the continental shelf is composed of coarser, heterogeneous sediments, and more fluid mud, which is stratified in the shallower parts, that is, at depths of less than 60 m (Nittrouer et al. 1986), creating areas with a considerable energetic input (Rufino et al. 2006). These conditions are favorable to the excavator life mode of many benthic invertebrates, whose morphology and life-history traits are adapted for the modification of this type of environment, including the creation of micro-habitats and foraging substrates (Pereira et al. 2014), which would account for the decrease in taxonomic richness with increasing depth. However, as the collection of samples in the present study was not based on a systematic ecological research design, it is impossible to confirm these conclusions empirically, given that the vast majority of trawls were undertaken at depths of less than 60 m.

The greater taxonomic richness recorded at the new moon may be related to greater invertebrates capturability during this lunar phase, given that polychaetes and crustaceans, for example, take advantage of the darkness to forage at the surface of the benthic layer (while otherwise mostly remaining buried in the substrate to avoid predation), when they are more easily trapped by trawl nets (Libini & Khan 2012). The lunar cycle also provides a reliable reference for the species' reproductive behavior synchronization. It confers several advantages, such as reducing predation pressure, given the limits on the number of prey a predator can capture per unit of time (Skov et al. 2005). The new moon also provokes higher tides, which optimize the larvae's dispersal potential (Morgan 1996) and the species' migration, including *F. subtilis* (Aragão et al. 2015).

Overall, then, the invertebrates of the ACS are extremely abundant and characterized by their considerable taxonomic and functional plurality. They play a fundamental role in structuring this environment and are thus essential for developing management strategies based systematically on the relationship between biodiversity and ecosystem function. The spatiotemporal variation in this fauna should be considered in the development of any monitoring program, given that a focus on a single area or taxon will not capture the full biological complexity of the study environment. The most abundant species are generalists, and their greater abundance facilitates monitoring, which favors their adoption as biological indicators. However, it will also be necessary to investigate in more detail the functional roles of the more sensitive and specialist species identified in the present study, given that they are likely to be the most vulnerable to the processes of extinction and loss of ecological function.

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