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Environmental factors associated with southern brown shrimp (*Penaeus subtilis*) yield at Brazilian Amazon coast

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Abstract

We evaluated the relationship between southern brown shrimp *Penaeus subtilis* (Pérez Farfante, 1967) yield and environmental parameters on the Amazon continental shelf. We analysed monthly fishing effort data (number of days spent at sea) and yield (kg of tails) collected between 1978 and 2009. A causal relationship had been expected between Amazon River discharge during the main period of shrimp occurrence in estuarine waters (considering post larval settlement and juvenile recruitment in second semester of each year) and adult abundance (represented by fishery yield in the first semester of the following year). We detected significant correlations between monthly river discharge and yield with a negative lag of four months, and between river discharge during the dry season (June to November) and yield in the following year. In general, low and high discharges during a given year were associated with high and low fishery yields, respectively, during the following year.

Descriptors: Amazon river discharge, Sea surface temperature, Predictive models, Penaeid shrimp.

INTRODUCTION

Small and industrial scale fishing operations targeting penaeid shrimps occur on the Amazon continental shelf, between the mouths of the Parnaíba (02°53'S) and Oiapoque (04°23'N) rivers (Figure 1), concentrated on depths between 60 and 80 m. Small-scale coastal operations are largely unmonitored, hindering reliable landings statistics; the real number of operating fishing units is unknown. Industrial fishery, on the other hand, represents most of the regional and national fishing effort and is well documented.

The industrial fleet boats usually have 22 meters of length and 365 to 425 horsepower main engines. During the second half of the 1980s, the industrial fleet reached more than 250 units in operation, decreasing to 115 units by 2006. Production is dominated by the southern brown shrimp *Penaeus subtilis* (Pérez Farfante, 1967) for export. Annual landings during the 2000s were approximately 3,500 tons of tail, generating yearly incomes of USD 30 million (Aragão et al., 2013).

Penaeid shrimps are short-lived animals with complex life cycles. Late juveniles and adults live in

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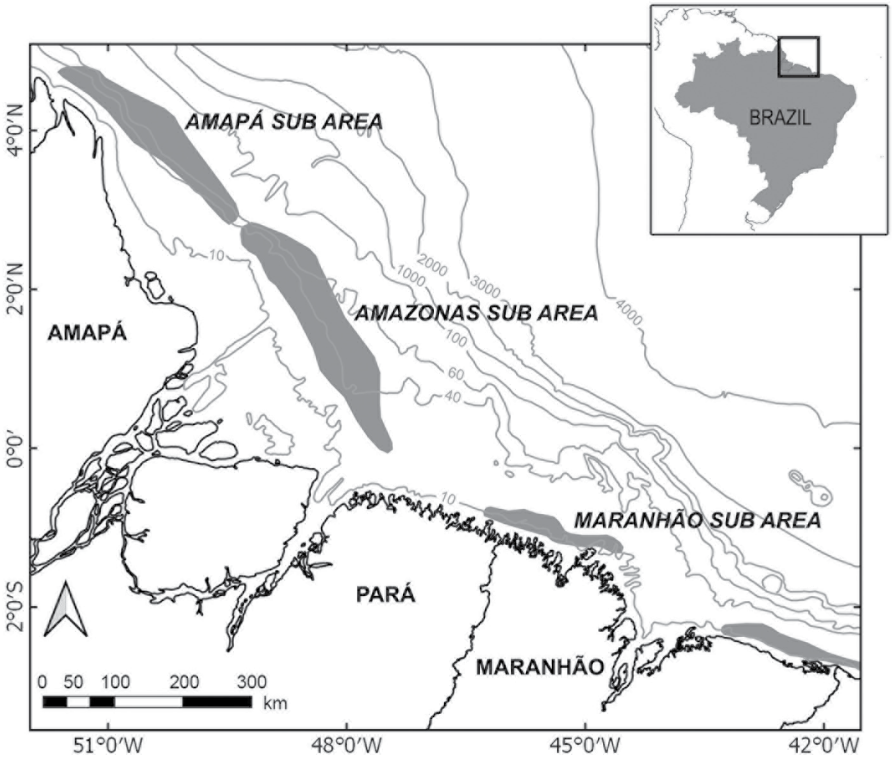

Figure 1. Main shrimp fishing grounds of *P. subtilis* on the Amazon continental shelf.

the open sea, where breeding occurs. After passing through several larval stages, metamorphosis into post-larvae triggers a migration to coastal and estuarine areas where early juveniles develop before returning to the ocean (Pérez Farfante, 1969; Larson et al., 1989; Gillet, 2008). Environmental factors lead to strong variations in annual recruitment and stock size during this coastal phase, when post-larvae and juveniles are exposed to fluctuating environmental conditions. Since young penaeid shrimps are especially sensitive to changes in water salinity, they are vulnerable to variations caused by river discharge, which may impact entire cohorts in estuarine nursery areas (Garcia and Le Reste, 1981; Rogers et al., 1993; Béné and Moguedet, 1998; Diop et al., 2007).

Investigations into the relationships between environmental factors and abundances of penaeid shrimps or other aquatic resources are generally scarce in Brazil, mainly due to the lack of data. However, industrial shrimp fishery on the Amazon continental shelf represents a unique opportunity to investigate such relationships. Industrial fishing has been monitored over a long period of time, and complementary datasets of environmental variables are available from various sources. Analysis is simplified by the fact that this represents a single stock, harvested with a uniform fleet over many years in a region where the discharge of the Amazon River, the predominant factor influencing the coastal environment, follows a clear seasonal pattern.

This paper examines the hypothesis that there is a causal relationship between variation in Amazon River discharge during the main period of ontogenetic immigration of *P. subtilis* into coastal areas and subsequent fishing yields. The most sensitive period is thought to be when post-larvae settle and continue their development through early juvenile in the second half of the year, when environmental changes are considered to influence recruitment, adult population abundance, and subsequent year yield. Variations in river discharge have a large influence on coastal water salinity (Silva et al., 2010) which, in turn, has been found to affect the behaviour and early-stage survivorship of shrimps and possibly the transport of post-larvae into nursery areas. We believe that *P. subtilis* requires relatively high levels of salinity compared to similar species such as the white shrimp *Litopenaeus schimitti*. Similar impacts on *P. aztecus* in the Gulf of Mexico have been reported by St. Amant et al. (1965).

We seek to evaluate the relationship between river discharge and yield, using available data to improve fishery management. We would thus be able to recognize and respond to variations in abundance caused by environmental factors, as recommended by Garcia (1989) and Penn and Caputi (1985). Empirical graphical analyses and multiple linear and non-linear regression models were applied to evaluate the strength of the relationships between Amazon River discharge, indices of shrimp abundance, and fishery yield. Other variables considered were surface temperature (SST) and El Niño Southern Oscillation (ENSO).

METHODS

Data source

We analysed monthly data from the southern brown shrimp *P. subtilis* industrial fishery on the Amazon continental shelf, records of Amazon River discharge, and other environmental variables (Table 1). Fishing data were comprised of records of monthly landings in kilograms of tails (deemed representative of total catch) and fishing effort in number of days at sea, to compute catch per unit effort (CPUE–kg/day at sea) as an abundance index. The former Superintendência do Desenvolvimento da Pesca (SUDEPE) compiled data from processing plants in Belém between 1978 and 1989, and Centro de Pesquisa e Gestão de Recursos Pesqueiros do Litoral Norte (CEPNOR) continued data collection thereafter.

Industry records for each fishing trip generally include the vessel name, departure date, arrival date, landing in kilograms, and the quantity of shrimp processed in industrial plants by the commercial size categories. Until 2006, industrial production of southern brown shrimp was destined almost entirely to the international market, and it is generally accepted that data gathered at industrial processing plants account for the entire fishery yield (Aragão et al., 2004). Although we do not have an estimate of shrimp discarded at sea, we assume this to be negligible due to the high demand and price, and that landings therefore represent the overall catch, hereafter referred to as “yield.”

The main environmental variable utilized in the analyses was monthly average discharge of the Amazon River in cubic meters per second, measured upstream of the study area at the Óbidos hydrological station and available from the online database of National Hydro-meteorological Net at http://hidroweb.ana.gov.br/, overseen by the Agência Nacional das Águas (ANA).

Oceanographic data, including monthly mean sea surface temperatures in the area of occurrence of *P. subtilis* and multivariate indices of *El Niño* and *La Niña* events (Multivariate ENSO index - MEI), were obtained from the *USA National Aeronautics and Space Administration* (NASA) at http://poet.jpl.nasa.gov/. Data were organized in electronic spreadsheets using the free software *OpenOffice.org* and converted to text files that were analysed using the free statistical software *R (Cran r-project.org)*.

Table 1. Fishery and environmental variables used in the analyses.

Variable	Notation	Measure unit
Yield (landings / catch)	Y	Kg
Fishing effort	FE	days at sea
Catch per unit of effort	CPUE	Kg per day at sea
Average monthly Amazon River discharge	AD	m^3/s
Average monthly Amazon River discharge June-November	ADjn	m^3/s
Average monthly rainfall	RF	mm
Sea Surface Temperature	SST	°C
Occurrences of El Niño in previous year	EN(i)	Y/N

Procedures

Analyses were carried out on monthly and annual temporal scales. As an exploratory first step, we used graphics drawn with R to visualise inter- and intra-annual patterns of variables and to evaluate correlations between the shrimp abundance index (CPUE) and Amazon River discharge, as well as between fishing yield, fishing effort, and river discharge, considering different lags.

Relationships between variables were initially evaluated through graphics of the anomalies (A_X), drawn from standardized observations for the mean and its standard deviation, given by the expression:

$$A_X = (X - \overline{X}) / std(X) \, (equation\ 1)$$

Detailed statistical analyses were then carried out to evaluate the strength of relationships between variables, considering both monthly and annual time scales. The correlation between river discharge and El Niño episodes was also taken into account in an ANCOVA framework. Years were assigned to different categories based on prior occurrence of ENSO episodes as follows: EN(1) general years; EN(2) occurrence of El Niño in the previous two years; EN(3) occurrence of El Niño in the previous three years.

This procedure was adopted on the basis that recent El Niño events result in weaker Amazon River discharge during the second semester of the year and thus favourable conditions for brown shrimp development. Good environmental conditions over successive years can result in an additional positive influence on shrimp abundance and fishing yield.

The CPUE was regressed against fishing effort and river discharge. Initially linear models were fitted using ordinary least square criteria with an analysis of residuals. Following Cowpertwait and Metcalfe (2009), generalized least square criteria were applied with a correlation term when evidence of autocorrelation was found, as is usual with time series data.

Monthly time scale

A multiple linear regression model was fitted to evaluate the strength of the relationship between monthly yields and fishing effort, with monthly data for Amazon River discharge and year as explanatory variables. The initial intention was to model this type of correlation through time series analysis (Box and Jenkins, 1970), but the lack of data for 1989, 1990, and several months during other years when closed seasons were established, precluded the correct adoption of the technique.

The linear regression model applied was:

$$\log(Y)_i = a + \beta 1 \log(FE) + \beta 2 AD_{lag} + EN_i + \varepsilon \, (equation\ 2)$$

Where Y is yield, FE is fishing effort in days at sea, AD is average monthly Amazon River discharge, EN is a factor to categorize years, and the index lag=1,2,3,…,n refers to the lag applied to a series of environmental variables. The model investigates the influence of river levels in preceding months on future monthly yields.

Besides the multiple linear regression technique, we also fitted a nonlinear model proposed by Griffin et al. (1976):

$$\log(Y) = \beta 1 (AD_{lag})^{\beta 2} (1 - \beta 3^{\log(FE)}) \, (equation\ 3)$$

The term $\beta 1 (AD_{lag})^{\beta 2}$ is the maximum yield that the function approaches for a given river discharge.

Inter-annual timescale

The same procedures used in the monthly analysis were applied on an annual time scale, fitting the relationship between annual yield and fishing effort, the Amazon River discharge, and year using the following multiple linear regression model:

$$\log(Y)_i = a + \beta 1 \log(F) + \beta 2 AD_{lag} + \beta 3 EN_i + \varepsilon \, (equation\ 4)$$

The terms are as described above, but here the aim was to analyse the influence of the average monthly river discharge index during the dry season (June–November) of each year on annual yield of the fishery of the subsequent year.

The nonlinear model of Griffin et al. (1976) was also applied to the annual data through the expression:

$$\log Y = \beta 1\,(AD_{lag})^{\beta 2}\,(1 - \beta 3^{\log(FE)})$$
$$(equation\ 5)$$

Residual analyses were carried out on the models at both scales in order to check for normality and autocorrelation. This diagnosis was accomplished through graphical analysis and the Durbin-Watson statistic (autocorrelation) and a Shapiro test (normality). When a residual series is positively autocorrelated at shorter lags, it leads to an underestimate of standard error and too narrow a confidence interval for the slope. In this situation, we followed the recommendation of Cowpertwait and Metcalfe (2009), where the model is refitted through a generalized least square criterion with an autocorrelation term.

RESULTS

Trends in yield, fishing effort and CPUE

Figure 2 shows trends in yield, fishing effort and catch per unit of fishing effort (CPUE) since 1978. A general decline in yield and fishing effort is apparent after the 1980s, reflecting the fleet reduction, while CPUE appears to fluctuate cyclically over the years. The intra-annual pattern of fishing effort and CPUE is very well defined, with peaks in the first months of the year, soon after the main period of recruitment suggested by Ehrhardt et al. (1999), followed by a decline over subsequent months, reaching the lowest values between October and November (Figure 3a). It should be noted that CPUE varies considerably over the years (Figure 3b).

Pattern of Amazon River discharge

In general, intra-annual variation in river discharge follows a clear regular cycle, with two well-defined phases (Figure 4a). Between December and January, river discharge starts to increase, peaking during May and June, the "flooding season." After June, the river discharge begins to decrease, reaching a minimum during October and November, the "dry season." The intensity of the cycle varies from year to year (Figure 4b) according to the overall hydrological cycle of the region.

Pattern of sea surface temperature (SST)

Sea surface temperature (SST) in the fishing area also follows a pattern with two phases, a general rising trend from March to June followed by a period of relatively stable high temperatures in the second semester of the year. This may be due to the decreased influence of the Amazon River. The coincidence between river discharge and lagged trends in CPUE and SST over the year (Figure 5) is remarkable.

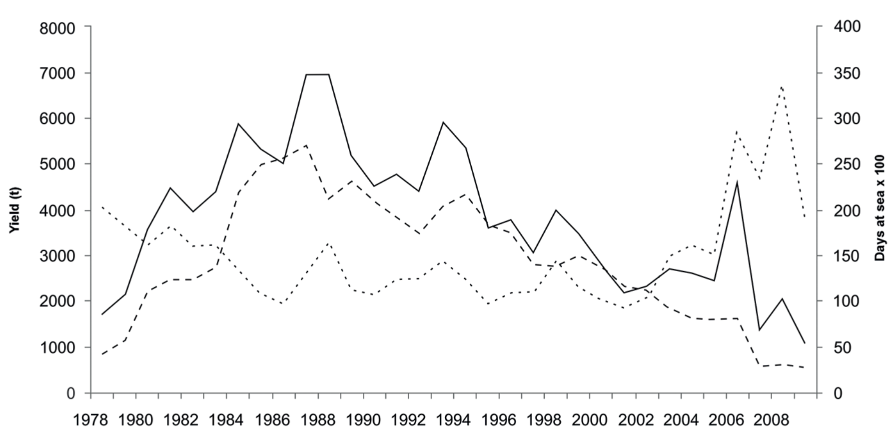

Figure 2. Tendency of the yield (tons of tail - solid line), fishing effort (number of days at sea - dashed line) and CPUE (dotted line) in the industrial fishery of *P. subtilis* on the Amazon continental shelf, Brazil.

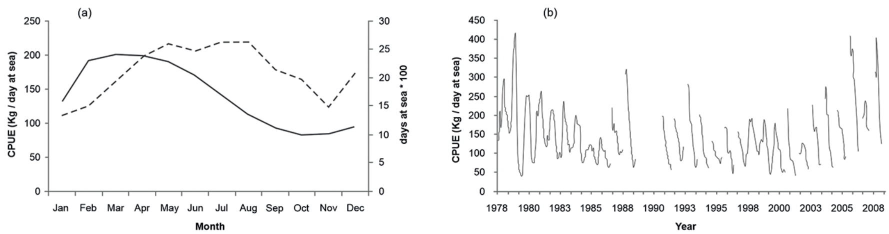

Figure 3. (a) Average monthly pattern of CPUE (solid line) and fishing effort (dashed line) and (b) annual pattern of CPUE in the industrial fishery of *P. subtilis* on the Amazon continental shelf, Brazil (1989/1990 data not available).

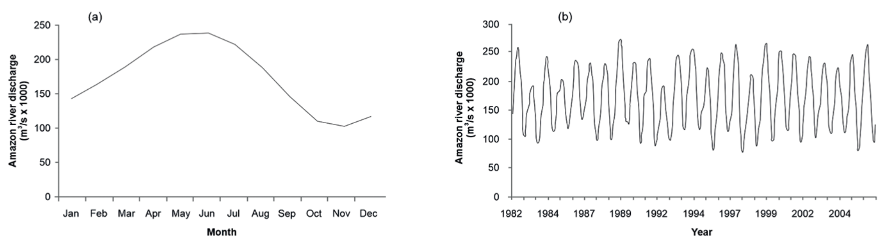

Figure 4. (a) Average intra and (b) inter annual pattern of the Amazon River discharge.

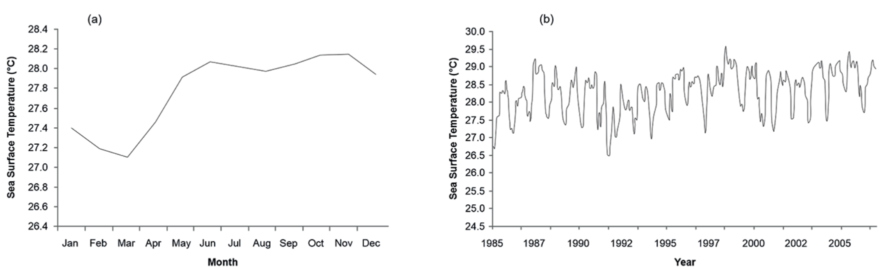

Figure 5. (a) Average intra and (b) inter annual pattern of sea surface temperature at *P. subtilis* fishing area on the Amazon continental shelf, Brazil.

Relationship between yield and environmental variables

The graphical analysis was carried out for several different lag scenarios, considering the pattern of anomalies (deviation from the means). It suggests a negative correlation between monthly CPUE and monthly Amazon River discharge, with a clearer cross-correlation when considering a negative time lag of four months (Figure 6). As shows on Figure 7, average discharge levels from June to November correlate well with average CPUE in the following year. Peaks in CPUE generally occur in years after troughs in discharge during this same period. The arrows in Figure 7 indicate El Niño years. Some coincidence can also be seen between El Niño episodes, troughs in Amazon River discharge, and peaks in the subsequent-year CPUE.

Monthly timescale

The multiple linear regression model was fitted to the relationship between yield, fishing effort, and river discharge with a negative four month lag, as indicated by the previous cross-correlation analysis. A scatter plot between each landing and its respective fishing effort indicated heterogeneity of variance, so a log transformation was applied. The model was fitted using an ordinary least

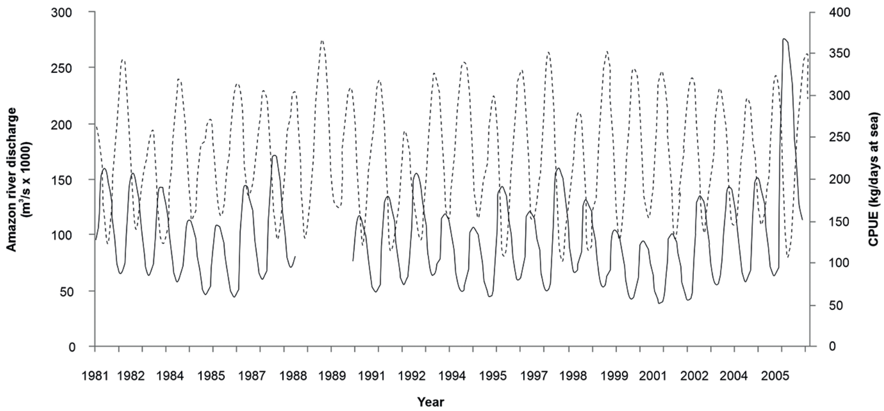

Figure 6. Pattern of Amazon River discharge lagged 5 months (solid line) and CPUE (dashed line) of the industrial fishery of *P. subtilis* on the Amazon continental shelf, Brazil.

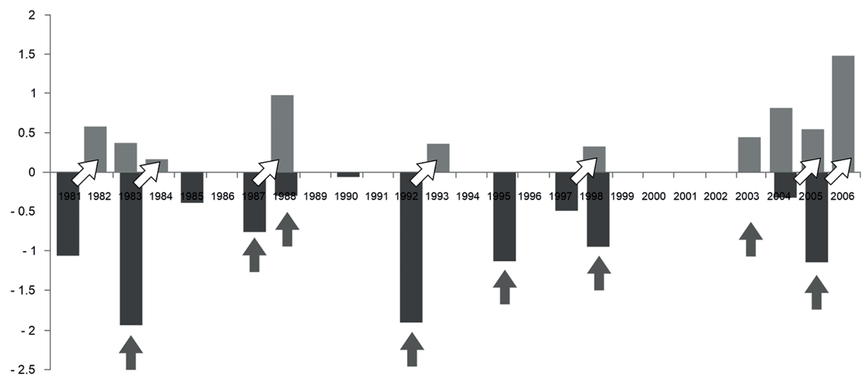

Figure 7. Sequence of troughs of Amazon River discharge (dark bars) and peaks of CPUE (gray bars) in the industrial fisheries of *P. subtilis* on the Amazon continental shelf with indication of El Niño years (dark arrows).

squares procedure, and the distribution of residuals was tested for normality using a Shapiro-Wilk test (W=9893, p-value=0.06).

The linear model explained a large proportion of the observed variation with a high level of statistical significance for both explanatory variables, resulting in a strong correlation with adjusted R^2=0.895; most of the variation in yield is explained by the joint effect of fishing effort and river discharge.

To address the significant autocorrelation observed in the residuals (D-W statistic=0.39 and autocorrelation at lag1=0.79), the model was refitted through an appropriate generalized least squares (GLS) criterion, including an autocorrelation term at negative lag 1 (Table 2). The final model is expressed by:

$$\widehat{log(Y)}_i = 4.905 + 1.127 * log(FE) -$$
$$0.0065 * AD_{lag4} + EN_i (equation\ 6)$$

$$EN_2 = 0.149\ and\ EN_3 = 0.223$$
$$(equation\ 7),$$

where Y is monthly yield (kg), FE is monthly fishing effort in days at sea, AD_{lag4} is monthly river discharge with a negative lag of 4 months, and EN_i is a factor related to the frequency of occurrence of El Niño events in previous years.

Table 2. Results of the multiple nonlinear regression analysis between monthly yield of the industrial fishery of *P. subtilis* on the Amazon continental shelf, fishing effort (FE), Amazon River discharge with a negative lag of 4 months (ADlag) and El Niño occurrence (YearType).

Generalized least squares fit by maximum likelihood				
Formula: logYield ~ logFishingEffort + AmazonRiverDischargelag + YearTypeG				
	AIC	**BIC**	**logLik**	
	-291.8485	**-267.1703**	**152.9242**	
Correlation Structure: AR(1)			**Phi = 0.8775128**	
Coefficients:	**Value**	**Std.Error**	**t-value**	**p-value**
(Intercept)	4.905069	0.20053371	24.46007	0
logFE	1.126675	0.02071207	54.39703	0
ADlag	-0.006541	0.00030186	-21.66869	0
YearTypeG2	0.149041	0.10486713	1.42123	0.1565
YearTypeG3	0.223415	0.08325739	2.68343	0.0078
Correlation	**(Intr)**	**logFE**	**AFlag**	**YrTyG2**
logFE	-0.913			
ADlag	-0.633	0.467		
YearTypeG2	0.08	-0.116	-0.079	
YearTypeG3	-0.069	-0.004	0.097	0.368
Standardized residuals:				
Min	Q1	Med	Q3	Max
-2.0639483	-0.774519	-0.1823705	0.3966785	3.1556881
Residual standard error: 0.2735623			**Df: 251 total, 246 residuals**	

In Figure 8a, yields predicted by the model are plotted against observed values. The match is generally strong, with the exception of certain extreme values, especially those observed in 2006.

The alternative nonlinear monthly regression model proposed by Griffin et al. (1976) showed a less accurate fit for monthly data than the linear model (Table 3 and Figure 8b). This was probably because the model does not consider the additional positive effect of sequential El Niño events. The equation for this model is expressed by:

$$\widehat{\log(Y)} = 29.86 * (AD_{lag4})^{-0.0768}$$

$$(1 - 0.8826^{\log(FE)})\ (equation\ 8)$$

Annual timescale

The strength of the relationship between annual yield versus fishing effort and average monthly river discharge between June and November in the prior year was also evaluated through a multiple regression model. The final model also explains a large proportion of the variance and indicates a strong correlation between variables. Although the adjusted R^2 of 0.764 (Table 4 and Figure 9a) suggests a good fit, the model does not catch the peaks of 1987-1988. At this scale, the factor corresponding to EN_2 was not significant and the expression for the model is simplified:

$$\widehat{\log(Y)}_1 = 8.54 + 0.712 * \log(FE) -$$

$$0.00462 * AD_{lag1} + EN_i\ (equation\ 9)$$

$$EN_2 = 0\ and\ EN_3 = 0.4268\ (equation\ 10),$$

where AD_{lag1} is average river discharge from June to November with a negative lag of 1 year, and EN_3 is a factor related to the frequency of El Niño events in the two previous years.

A relatively large proportion of variation in yield may also be explained by the joint effect of fishing effort and river discharge. The Durbin-Watson statistic was significant, but the residual

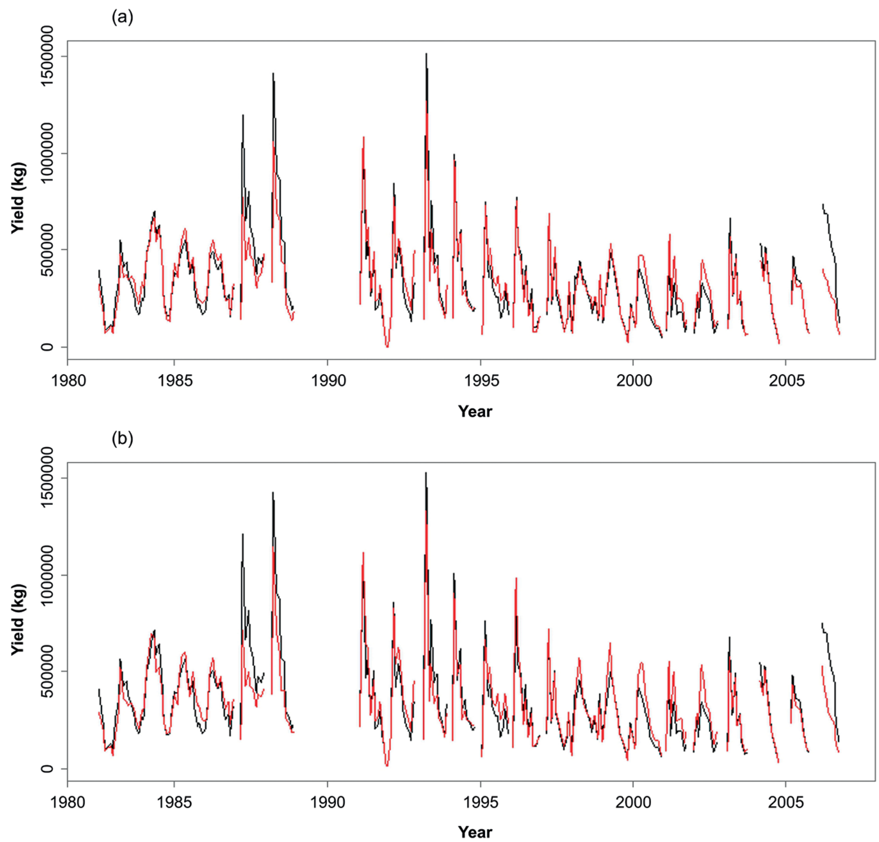

Figure 8. Observed yield (black line) of the industrial fishery of *P. subtilis* on the Amazon continental shelf versus estimated yield (red line) through (a) the multiple linear regression model (b) the multiple nonlinear regression model (Griffin model).

Table 3. Results for multiple nonlinear regression analysis (Griffin model) between monthly yield of the industrial fishing of *F. subtilis* on the Amazon continental shelf, fishing effort and Amazon River discharge.

Formula: logYield ~ Alpha * AmazonRiverDischarge^Beta1 * (1 - Beta2^logFishingEffort)					
Parameters estimate		**Std.Error**	**t value**	**Pr(>|t|)**	
Alpha	29.859692	1.230967	24.26	<2e-16	***
Beta1	-0.076825	0.004719	-16.28	<2e-16	***
Beta2	0.882625	0.00771	114.47	<2e-16	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.2839 on 248 degrees of freedom

Number of iterations to convergence: 11

Achieved convergence tolerance: 4.45e-07

(57 observations deleted due to missingness)

Table 4. Results of the multiple linear regression analysis between yearly industrial fishing yield of *P. subtilis* on the Amazon continental shelf, fishing effort (FE), Amazon River discharge (AD) with a negative lag of 1 year and El Niño occurrence (YearType).

Formula: logYield ~ logFishingEffort + AmazonRiverDischargelag + YearType					
Residuals:					
Min	**1Q**	**Median**	**3Q**	**Max**	
-0.28018	-0.11599	0.01485	0.08639	0.29763	
Coefficients estimate		**Std.Error**	**t value**	**Pr(>|t|)**	
(Intercept)	8.535214	0.987207	8.646	2.32E-08	***
logFE	0.710588	0.089549	7.935	9.38E-08	***
AD	-0.004619	0.001803	-2.563	1.81E-02	*
YearType3	0.426849	0.118686	3.596	0.0017	**
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					
Residual standard error: 0.1524 on 21 degrees of freedom					
Multiple R-squared: 0.8027, Adjusted R-squared: 0.7745					
F-statistic: 28.48 on 3 and 21 DF, p-value: 1.36e-07					

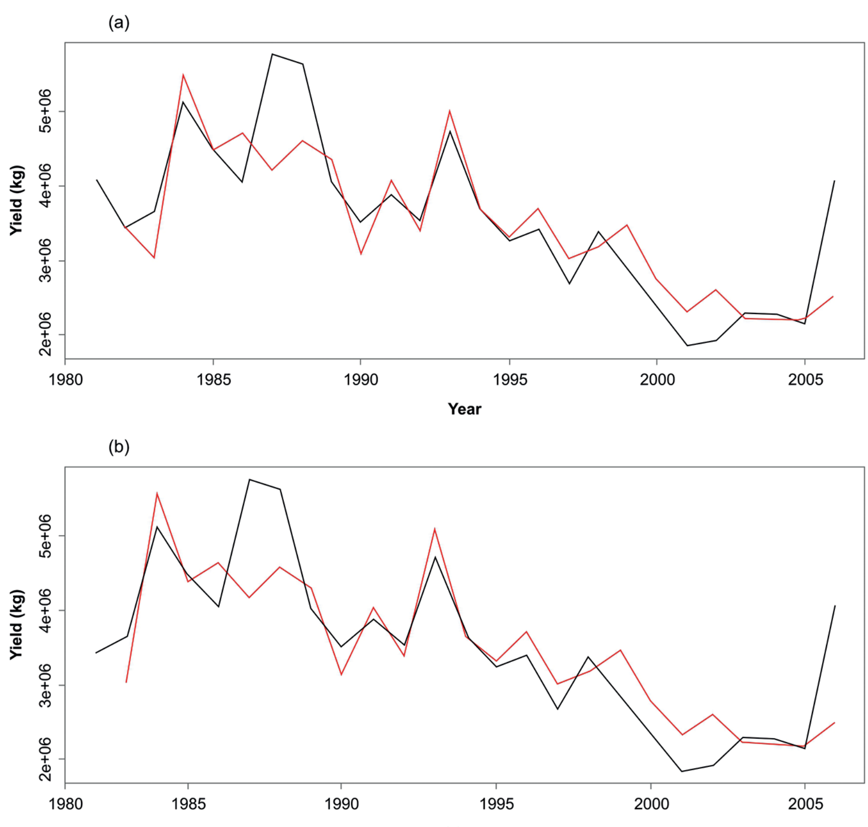

Figure 9. Observed yield (black line) for the industrial fishery of *P. subtilis* on the Amazon continental shelf versus estimated yield (red line) through (a) the multiple linear regression model and (b) the multiple non-linear regression model (Griffin model).

autocorrelation was weak (d-w=0.15 and autocorrelation at lag1=0.18) and least square fitting criteria were maintained.

The alternative nonlinear relation model proposed by Griffin et al. (1976) does not show a good fit for the annual data (Table 5 and Figure 9b). The equation describing the model is:

$$\widehat{\log(Y)} = 28.239\,(AD_{lag1})^{-0.06739}$$
$$(1 - 0.87285^{\log(FE)})\,(equation\ 11)$$

As neither model identifies the yield peak in 1987-1987, perhaps the annual scale is not appropriate to conduct the analysis.

DISCUSSION

Trends in yield and effort

CPUE declined from its initial high levels and continued to follow periodic oscillations, which may be indicative of natural fluctuations of the southern brown shrimp stock. The surprising increase in landings and in CPUE observed in 2006 and recent oscillations around a higher threshold hint at the possibility of a recovery of the stock in the last few years, a plausible hypothesis given the continuous decline in fishing effort since 2003. Favourable environmental conditions during some of these years may have also resulted in exceptionally strong recruitment, as discussed in the next section.

The monthly pattern of CPUE is consistent with the biological cycle of *P. subtilis*. Early in the year, small individuals predominate in catches. The population declines in terms of abundance over the months but increases in biomass due to the growth of individuals, such that the highest CPUEs are obtained during the second quarter of the year. The third quarter exhibits the largest individuals, but abundance, biomass, and CPUE are lower. In the last quarter of the year, the main period of recruitment begins, and mean size decreases again, reaching its smallest values in December and January, when CPUE starts to recover and the cycle restarts (Aragão et al., 2013).

Relationship between fishery performance and environmental variables

The early life stages of the southern brown shrimp *P. subtilis* on the Amazon continental shelf are little known. The presence of juveniles in estuaries has been reported, but no detailed field studies have been carried out that might shed light on the migration and settlement of post-larvae. Nevertheless, observations at estuaries, fishery data (Emerenciano, 1981; Ehrhardt et al., 1999; Silva et al., 2002a; Araújo et al., 2009), the results of previous research cruises (Jones and Dragovich, 1973; Dragovich, 1981; Aragão et al., 2013), and the life cycle of penaeid shrimps generally support our inferences on the spatial and temporal distribution of the population at different life stages.

Table 5. Results of the multiple linear regression analysis (Griffin model) between yearly industrial fishing yield of *P. subtilis* on the Amazon continental shelf, fishing effort (FE) and Amazon River discharge (AD) with a negative lag of 1 year.

Formula: logYield ~ Alpha * AmazonRiverDischarge^Beta1 * (1 - Beta2^logFishingEffort)					
Parameters estimate		Std.Error	t value	Pr(>|t|)	
Alpha	28.23944	4.10762	6.875	6.63E-07	***
Beta1	-0.06739	0.02342	-2.877	0.00875	**
Beta2	0.87285	0.02407	36.261	< 02E-16	***
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					
Residual standard error: 0.1916 on 22 degrees of freedom					
Number of iterations to convergence: 5					
Achieved convergence tolerance: 9.25E-08					

After completing larval development offshore, it is suggested that *P. subtilis* post-larvae migrate to nursery areas located mainly along the northwest coast of the state of Maranhão and the northeast coast of the state of Pará (Emerenciano, 1981; Araújo et al., 2009). The migration period and timing of subsequent settlement and development of juveniles, however, have not been precisely determined. Ehrhardt et al. (1999) reported that recruitment to the regional fishery is highly variable, occurring between the end of the last quarter of one year and the first quarter of the next. During this period, large numbers of individuals are caught in the growth area in front of the mouth of the Pará River known as "lixeira" (Silva et al., 2002b), evidencing a possible association with the abundantly vegetated habitat in the area. Aragão et al (2021) present a diagram illustrating this cycle for *P. subtilis*.

The presence of vegetation has been identified as an important factor in the development of juvenile northern brown shrimp *P. aztecus* in the Gulf of Mexico (Zimmerman et al., 1984; Minello and Zimmerman, 1991) and tiger prawns *P. esculentus* and *P. semisulcatus* in the Gulf of Carpentaria (Loneragan et al., 1994). The clear annual pattern of CPUE declining from the second quarter to the end of the year and increasing catches of larger individuals over the year in northern areas are evidence of a spatiotemporal distribution of the species and changes in local abundance (Aragão et al., 2013).

The life cycle of *P. subtilis* appears to be linked to certain abiotic habitat variables. CPUE rises and falls in line with Amazon River discharge rates. Population declines are sharper than rates of change in the river discharge, probably because fishing effort acts as an exogenous mortality factor, accelerating the reduction of shrimp numbers. Bates (1979) previously suggested that the clear-cut seasonality of the region's climate is the main factor driving the biological cycle.

The influence of the Amazon River on the waters overlying the continental shelf is more apparent during periods of elevated discharge, with low levels of salinity and increased nutrient and total particulate loads. Oceanic influence rises again as river discharge declines (Santos et al., 2008). The second quarter of the year is marked by an elevation in temperature. Wenner et al. (2005) identified a minimum coastal water threshold temperature of 27-28°C as a critical factor influencing density distributions in time and space of post-larval white shrimp *L. setiferus* within the Ossabaw Sound system, Georgia (USA). Thus, it seems like the life cycle of the *P. subtilis* of the Amazon continental shelf is in large part linked to changes in overall environmental conditions which are, in turn, driven by the Amazon River discharge.

The intensity of the Amazon discharge cycle varies from year to year according to the hydrological cycle of the entire region (Filizola et al., 2006), with discharge rates into waters of the continental shelf ranging between 100,000$m^3.s^{-1}$ and 220,000 $m^3.s^{-1}$ and an average solid discharge of 11 to 13 × 108 $tons.year^{-1}$ (Kineke et al., 1996). Meanwhile, the El Niño Southern Oscillation (ENSO) phenomenon is recognized as a dominant driver of environmental variability, especially of temperature and rainfall patterns in tropical regions around the world. El Niño and La Niña phases of the ENSO cycle appear to rule, at least in part, the cycle of floods and droughts in the Amazon region, with "average El Niño" episodes being drier and warmer than normal for the area, and "average La Niña" conditions being wetter and cooler (Poveda-Jaramilo and Mesa-Sánchez, 1997; Foley et al., 2002).

Aragão et al. (2021) proposed that the period from May to August, when a higher proportion of mature female shrimp is observed in samples obtained on commercial vessels, is the main reproduction period of *P. subtilis* in the region. This evidence, and the clear-cut two-phase pattern of environmental variables in the region, indicates a single annual reproductive season for the species. A similar pattern is apparent in the Gulf of Mexico, where reproduction of the congeneric pink shrimp (*P. duorarum*) is also limited to one main period, despite a much less regular pattern of environmental conditions (Kennedy-Jr and Barber, 1981; Ramírez-Rodrigues et al., 2003). Thus, while it is reasonable to conclude that reproduction in *P. subtilis* occurs at some level throughout the year in the region, the main period appears to be between the second and third quarter.

To be coherent with the proposed recruitment period, the bulk of post-larval migration to coastal areas should start in June–July. Juveniles might then remain in nursery areas for several months over the second half of the year, with the majority making their return to the ocean between September or October and January of the following year (Aragão et al., 2021). In other words, the post-larval migration to coastal areas begins when the river discharge starts to diminish, salinity increases, and temperatures peak. The back-to-the-sea migration should begin when the river discharge starts to increase and the salinity of coastal waters declines. Salinity is widely recognized as an environmental cue for migration (Rogers et al., 1993; Criales et al., 2006), and freshwater discharge, and its implications for the sediment load and salinity of coastal waters, has previously been implicated in the emigration of juvenile shrimp from estuaries (Staples and Vance, 1986; Vance et al., 1998).

Other potentially important abiotic factors influencing shrimp abundance include light, currents, and temperature. From the end of the third through the last quarter of the year, seawater turbidity in coastal and offshore areas is reduced due to the diminishing Amazon River discharge. A resulting increase in light penetration is likely to elevate levels of photosynthesis in marine plants and algae (Santos et al., 2008). This process should be more intense in years with lower discharge, and it is reasonable to suppose that it also favors the survival of southern brown shrimp larvae and post-larvae. Furthermore, from January to June, the North Brazilian Current moves northward along the coast of South America, but between June and December it reflects eastward at about 5°N (Müller-Karger et al., 1988; Silva et al., 2009) in a process that could also favor the displacement of larvae to coastal areas. Finally, a rise in sea surface temperature (SST) also coincides with the start of the most intense reproduction period.

We conclude that the abundances of sub-adult and adult southern brown shrimp *P. subtilis* on the Amazon continental shelf of the Brazilian coast appear to be linked mainly to rising and peak Amazon River discharge, while early life stages and juveniles are linked to phases of falling and low discharges. Although these shrimp begin their lives far out at sea, the influence of the river plume can reach hundreds of kilometers offshore (Silva et al., 2010). The main period of larval migration, their arrival in estuarine waters, settlement of post-larvae, and the development of juveniles (Aragão et al., 2021) appears to coincide with seasonal declines in Amazon River discharge.

Although the association between low Amazon River discharge and high CPUE during the following year is not always obvious or consistent, in extreme years it becomes very clear. The lack of association in some years may be linked to the impact of fishing effort and exploitation in the previous year on spawning biomass. One must also emphasize the possibility of influence of factors not considered in this analysis, on the initial stages of life of *P. subtilis*. In any event, during periods of low fishing effort, CPUE has never dipped below average in a season after a period of low river levels.

El Niño episodes influence the entire hydrological cycle on the Amazon Region. Anomalous river levels associated with El Niño appear to be indirectly responsible for fluctuations in shrimp abundance on the Amazon continental shelf. In general, we conclude that El Niño conditions result in decreased Amazon River discharge at the end of the year and increased shrimp CPUE the following year. Similar relationships between El Niño episodes, hydrological cycles, and shrimp abundance have also been reported in other parts of the world, such as in Patos Lagoon, southern Brazil (Möller et al., 2009), in Peru (Mendo and Tam, 1993), and in the Colombian Pacific (Días-Ochoa and Quiñones, 2008).

In addition to environmental factors, shrimp abundance is also affected by the pattern and intensity of fishing. The impact of a closed season, which was extended in 2003 to run from October 15 to February 15 (Garcia 1988; Gracia, 1997), requires much closer investigation. The influence of closure on abundance and size of spawning stock in a given year may be determinantal to population abundance the subsequent year; future analyses should seek a better understanding of this association.

Statistical correlation between fishery data and environmental variables

Statistical techniques including multiple regressions in time series were used to model relationships between shrimp fishery data and environmental variables, taking into account the strong environmental influence on early life stages of shrimps in coastal nursery areas. The abundance and yield of adult and subadult shrimp have previously been correlated with salinity, temperature, river discharge, precipitation, and other environmental variables (Sheridan, 1996; Haas et al., 2001; Saoud and Davis, 2003).

The multiple linear regression models and the nonlinear regression model applied in this analysis revealed a strong correlation between fishing yield and fishing effort and the discharge of Amazon River during the early estuarine stages of the southern brown shrimp life cycle. The high correlation between these variables, in both types of models and at both temporal scales, is consistent with our hypothesis and is evidence that fishery management should consider not only fishing effort but also environmental variables and some form of stock biomass index (Garcia, 1989; Penn and Caputi, 1985).

It is reasonable to conclude that fishing effort must be regulated according to expected abundance in order to protect population and future yields. The failure of the models to explain the high landings in 2006 may reflect the reduction in fishing effort in prior years and the resulting recovery of the population to a higher threshold. The autocorrelation found in the residuals of the models, according to Cryer and Chan (2008), may be evidence of a further, albeit weaker, source of variation in the relationship. Future analyses would therefore benefit from checking residuals for correlation against other environmental or fishing predictors, such as spawning stock and recruitment, in order to improve model fit.

As previously stated by Jones and Dragovich (1977), the penaeid shrimp fishery on the Amazon continental shelf operates mostly on a single year class, and so year-to-year fluctuations in abundance are to be expected given the short life cycle of the species. These fluctuations, and the resulting variation in annual yields, are partly the result of differential spawning success and survival in inshore nursery grounds, which are generally subject to more extreme variation in environmental conditions than the offshore habitats of adult shrimp.

Due to environmental variables, consistent fishing effort cannot be expected to produce consistent yields for this fishery. Predicting and utilising annual fluctuations in abundance is thus an important challenge, and identifying the mechanisms that regulate juvenile production within the estuary may be a critical step in the effective management of shrimp resources (Haas et al., 2001). Myers (1998), however, points out that when increasing emphasis on the search for environmental correlations with recruitment, managers should not neglect other important processes such as the relationship between spawning-stock levels and recruitment. According to Garcia (1996), this relationship is especially important for shrimp populations comprising a one-year class, in which a combination of low spawning biomass and high fishing effort can lead to recruitment overfishing.

CONCLUSION

Recorded catch per unit of effort (CPUE) for the southern brown shrimp fishery on the Amazon shelf has historically oscillated periodically around a relatively stable threshold until 2006, a pattern that might be regarded as natural fluctuation in abundance.

The high landings observed in 2006 and oscillations around a higher CPUE threshold in recent years may be evidence of population recovery resulting from lower fishing intensity and favourable environmental conditions.

The results presented here suggest that *P. subtilis* life cycle is closely associated with overall environmental conditions in the area, but especially salinity, which is largely driven by the Amazon River discharge.

Peaks in subadult and adult populations of *P. subtilis* in the Amazon continental shelf seems to correlate with rises and peaks of the Amazon River discharge, while the appearance of early stages and juveniles is linked to declining and low river discharge.

The main period of migration of southern brown shrimp larvae into estuaries, settlement of post-larvae, and development of juveniles (May/June to November) coincides with the start of the annual reduction in Amazon River discharge, from June/July to November (Figure 4).

Negative anomalies in Amazon River discharge are associated with positive anomalies in CPUE during the following year. In general, El Niño episodes result in reduced discharge intensity by the Amazon River at the end of the year and increased CPUE the following year.

The regression models applied in this analysis confirmed a strong correlation between fishery yield and fishing effort and Amazon River discharge during the preceding estuarine phase of larval, post-larval, and juvenile development.

In order to protect populations of *P. subtilis* and future yields of the penaeid shrimp fishery on the Amazon continental shelf, fishing intensity must be regulated according to reliable predictions of southern brown shrimp abundance. Environmental variables are an essential component of the analyses required to make these predictions.

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AUTHOR CONTRIBUTIONS

J.A.N.A.: Conceptualization; Formal Analysis; Methodology; Writing - original draft; Writing - review & editing;
I.H.A.C.: Conceptualization; Data Curation; Investigation;
K.C.A.S.: Conceptualization; Data Curation; Investigation;
D.E.G.M.: Visualization; Writing - review & editing;
M.P.J.: Methodology; Writing - review & editing.

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