



## Distribution and abundance of post-larvae and juveniles pink shrimp *Farfantepenaeus paulensis* (Pérez Farfante, 1967) in a subtropical estuary

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1                   **Distribution and abundance of post-larvae and juveniles pink shrimp**  
2                   ***Farfantepenaeus paulensis* (Pérez Farfante, 1967) in a subtropical estuary**

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10  
11                   **Abstract.** The spatial and temporal variability in the relative abundance of the post-  
12                   larvae (PL) and juvenile (JU) stages of the pink shrimp *Farfantepenaeus paulensis* was  
13                   investigated in the estuary of Lagoa dos Patos, southern Brazil. This analysis enabled  
14                   the identification of differential distribution patterns. Pink shrimp abundance was  
15                   studied to understand what factors influence the occupation of the estuary. Monthly  
16                   samples were taken with a trawl net at 12 sites in the estuary from September 2010 to  
17                   January 2013. Comparisons were made between protected and unprotected sites. Both  
18                   PL and JU had a wide distribution in the estuary. The temperature was not a significant  
19                   variable for explaining abundance variability. The abundance of PL increased with  
20                   salinity and influenced PL entry to the estuary. The highest abundances of PL were  
21                   found in unprotected areas and protected sites at the mouth of the estuary, while  
22                   juveniles were unevenly distributed with higher abundance in protected areas.  
23                   Recruitment period of PL in the estuary was October to March, and juveniles was  
24                   November to February. We suggest that the preservation of unprotected shallow waters  
25                   and protected areas at the mouth of the estuary are key to further recruitment of the  
26                   species in the estuary.

27                   **Keywords:** Penaeidae, fishery resource, Lagoa dos Patos, recruitment.

28  
29                   INTRODUCTION

30                   Estuaries and coastal lagoons generally provide ideal conditions for the development  
31                   of several marine organisms. They are extensively used as nursery grounds by different fish  
32                   and crustacean species, and also provide a vast source for feeding and shelter against  
33                   predators. (Boesch & Turner, 1984; Rozas & Minello, 1997). In the south and southeast  
34                   regions of Brazil, the planktonic post-larvae of the pink shrimp *Farfantepenaeus paulensis*

35 (Pérez Farfante 1967) enter these habitats carried by ocean water and develop as juveniles,  
36 following a pattern observed in other species of *Farfantepenaeus*. The cycle is completed  
37 when pre-adults return to the ocean, recruit to adult stock and reproduce (Garcia & Le Reste,  
38 1981; D'Incao, 1991; Lhomme, 1992; Cházaro-Olvera *et al.*, 2009).

39 The pink shrimp represents an important link in the local food web. It is well  
40 known, for instance, that they predate intensively on benthic invertebrates while also  
41 constitute the main food source for the blue heron *Egretta caerulea* (Linnaeus 1758)  
42 (Jorgensen *et al.*, 2009; Gianuca *et al.*, 2012). Moreover, this species is largely targeted  
43 by artisanal fisheries. This is particularly evident in the Lagoa dos Patos, which is  
44 considered its largest nursery, and where it has become the main fishing resource since  
45 other fisheries started collapsing in the early, 1980s (D'Incao *et al.*, 2002). The  
46 specimens enter the estuary as post-larvae, theoretically from September and harvest  
47 occurs in the summer and autumn (December-May) (D'Incao 1991). Pink shrimp  
48 harvests vary from zero to more than 4,000 tons with environmental conditions such as  
49 intensity and direction of the wind and the freshwater discharge from the lagoon system.  
50 (Möller *et al.*, 2009; Pereira & D'Incao, 2012; Kalikoski & Vasconcellos, 2013).

51 In estuaries in the Indo-Pacific and the Gulf of Mexico, the highest abundance of  
52 post-larvae and juvenile penaeids is associated with higher salinity, increased  
53 temperature, the presence of submerged vegetation, and debris-rich substrates (Sánchez,  
54 1997; Vance *et al.*, 1998; Pérez-Castañeda & Defeo, 2001, 2004; Adnan *et al.*, 2002;  
55 Pérez-Castañeda *et al.*, 2010; Noleto-Filho *et al.*, 2017). Higher salinities allow the  
56 *Melicertus plebejus* (Hess 1865) and *Fenneropenaeus merguensis* (De Man 1888) post-  
57 larvae to reach the innermost areas of the estuaries (Young & Carpenter, 1977; Vance *et al.*,  
58 1998). *F. paulensis* and *Farfantepenaeus aztecus* (Ives 1891) showed higher  
59 survival rates at salinities above 10, and increased mortality in scenarios with large  
60 saline variability, due to greater difficulty in osmoregulation (Tsuzuki *et al.*, 2000;  
61 Saoud & Davis, 2003). Additionally, shrimps find better survival conditions at  
62 temperatures above 25°C. This increased abundance due to higher temperatures causes  
63 seasonal growth in estuaries (D'Incao, 1991; Branco & Verani, 1998; Tsuzuki *et al.*,  
64 2000; Pérez-Castañeda & Defeo, 2001).

65 However, in the Brazilian estuaries, there is little information on the preference  
66 of the post-larvae of pink shrimp. The studies mainly analyzed juvenile populations and  
67 concluded that their abundance varies with season and that they prefer salinity levels  
68 between 15 and 30 (D'Incao, 1991; Branco & Verani, 1998; Costa *et al.*, 2008;

69 Lüchmann *et al.*, 2008; Ferreira & Freire, 2009; Noletto-Filho *et al.*, 2017). D’Incao  
70 (1991) first studied the distribution of juveniles of pink shrimp in the Lagoa dos Patos  
71 estuary and highlighted the importance of protected shallow inlets for the growth, even  
72 without a quantitative analysis. Ruas *et al.*, (2014) conducted the only available study  
73 on the habitat preference of post-larvae pink shrimp in Brazil, they showed the  
74 importance of submerged seagrass meadows. The reach of post-larvae to the innermost  
75 regions of estuaries has not been studied, and the salinity influence is mainly associated  
76 with fishery production (D’Incao, 1991; Costa *et al.*, 2008; Möller *et al.*, 2009; Pereira  
77 & D’Incao, 2012).

78 An analysis of habitat preference could help develop management and  
79 conservation measures for pink shrimp as a resource. However, little information is  
80 available on the variability of post-larvae and juvenile abundances, which could help  
81 identify the pattern of distribution and occupation in estuary. This study investigated the  
82 distribution and spatial-temporal variability in the relative abundance of post-larvae and  
83 juveniles of *F. paulensis* in the Lagoa dos Patos estuary. We analyzed the effect of  
84 salinity and temperature on the abundance of these organisms.

85

## 86 MATERIALS AND METHODS

### 87 **Study Area**

88 Lagoa dos Patos is the largest choked lagoon in the world (Kjerfve, 1986). Its  
89 estuarine portion (32°00’S, 52°04’W) with 971 Km<sup>2</sup>, lies to the south of the lagoon. A  
90 channel that measures 20 km in length and 0.5 to 3 km in width, allows ocean-estuary  
91 water exchanges (Asmus, 1998). The strength and direction of winds, and freshwater  
92 discharge control the hydrodynamics of the lagoon (Möller *et al.*, 2009; Fernandes *et al.*,  
93 2005). The main environments of this estuary are the protected shallow inlets  
94 (called P), with submerged prairies of phanerogams, small variability in salinity and  
95 current velocity, and an unprotected central water body (called U) with greater depth  
96 and higher variability of salinity and flow velocity (Asmus, 1998; Fernandes *et al.*,  
97 2007; Martins *et al.*, 2007; Copertino & Seeliger, 2010; D’Incao & Dumont, 2010).

98

### 99 **Field sampling and laboratory procedures**

100 Samplings occurred monthly from September 2010 to January 2013, at eight  
101 sampling sites in the protected shallow inlets (P1 to P8) and four sites on the margins of  
102 the unprotected central area (U1 to U4) of the estuary (Table 1), during the day and at

103 depths less than 1 m in all areas. Due to previous knowledge of species occurrence in  
104 the estuary, a one-year period was considered as starting in September and ending in  
105 August.

106 The samples were collected with a trawl net according to Renfro (1963). The net  
107 had a mesh size of 5 mm knot to knot, a codend of 500  $\mu\text{m}$ , and an invariable opening  
108 of 1.8 m. Trawling extended 40 m, with two hauls at each collection site. To minimize  
109 the effect of the boat, the engine was switched off close to trawling locations. The boat  
110 was displaced by rowing, where the fishing net was then placed in the water and the  
111 cable stretched to reach the 40 meter mark. After that, the boat was anchored to prevent  
112 variability in the trawling distance, and the trawl net was drawn manually. The salinity  
113 level and temperature were checked during each trawling through a mini portable probe  
114 YSI 556 MPS model. The collected material was stored in properly labeled plastic bags,  
115 containing 4% formaldehyde in freshwater.

116 In the laboratory, the sampled material was washed under running water in a  
117 sieve of 500  $\mu\text{m}$  and shrimp were separated and identified according to D'Incao (1999).  
118 The post-larvae pink shrimp (PL) were identified according to Calazans (1993). In this  
119 study, post-larvae were considered with up to 3 mm in carapace length - CL (Haywood  
120 *et al.*, 1995), and shrimps above this size were classified as juveniles (JU). The relative  
121 abundance was determined for PL and JU by counting the number of organisms from  
122 each trawling.

123 The CL measurements of the pink shrimp PL and JU were obtained in  
124 millimeters from the orbital angle to the dorsal edge of the carapace, with a  
125 stereomicroscope equipped with an ocular micrometer and a caliper (0.1 mm).

126

## 127 **Data analysis**

128 Descriptive analysis (means) of the data collected at all points was performed.  
129 The calculated means have a confidence interval of 95%. The size structure of the  
130 shrimps was analyzed using frequency distribution by size class (CL), grouped into 1  
131 mm intervals.

132 Generalized Linear Models (GLMs) (Nelder & Wedderburn, 1972) were used to  
133 evaluate the effect of environmental, spatial and temporal predictors on PL and JU  
134 abundances for sites P1 to P5 and U1 to U4 GLMs extend the classic framework of  
135 linear models in the sense that they the response variable can be any member of the  
136 exponential probability distribution family (McCullagh & Nelder, 1989). Thus, they are

137 well fit for modeling ecological data as they are not always restricted to a Gaussian  
138 distribution (Guisan *et al.*, 2002).

139 GLMs describe the relationship between the response variable  $Y_i$  ( $i=1, \dots, n$ ) and  
140 the predictors  $x_i$  through a linear predictor  $\eta = \sum_{j=1}^k x_j \beta_j$ , where  $x_j$  is a known function  
141 for  $k$ , the predictor variable, and  $\beta_j$  is an unknown parameter to be estimated from the  
142 data. The linear predictor  $\eta$  is linked to the mean of the response  $E(Y) = \mu$  by a known  
143 link function  $g$ , which is commonly expressed as  $\eta = g(\mu)$ . In cases where the response  
144 variable consists of discrete events, such as abundance of PL and JU, a Poisson  
145 distribution would be appropriate. However, this kind of distribution requires that the  
146 mean ( $\mu$ ) is equal to the variance ( $\sigma^2$ ), which does not necessarily correspond to  
147 biological reality. In most cases, however, the variance is usually greater than the mean  
148 (also known as overdispersion), and may be caused by the spatio-temporal  
149 heterogeneity present in the data (Lindén & Mäntyniemi, 2011).

150 Overdispersion can be handled in many different ways. Describing, for instance,  
151 the extra Poisson variance as a quadratic function of the mean is one of the most  
152 commonly used approaches which, in turn, defines a Negative Binomial distribution.  
153 (McCullagh & Nelder, 1989; Lindén & Mäntyniemi, 2011). Therefore, as both response  
154 variables were overdispersed, PL and JU abundances were fitted according a negative  
155 binomial distribution by means of the *glm.nb* function from the *MASS* R-package  
156 (Venables & Ripley, 2002). The general formulation for both models can be  
157 summarized as follows:

$$158 \quad Y_i \sim NB(\mu_i, k); E(Y_i) = \mu_i \text{ and } var(Y_i) = \mu_i + \frac{\mu_i^2}{k}$$

$$\eta_i = \beta_0 + \sum_m^M \beta_m X_{m_i} + \varepsilon$$

$$\eta_i = \log(\mu_i)$$

159 where  $Y_i$  is the number of PL or JU individuals for each sampling location  $i$ ;  $\eta_i$  is the  
160 linear predictor expressed in logarithmic scale;  $\beta_0$  is the intercept;  $\beta_M$  is a vector of the  
161 repressor's coefficient which quantify the effect of some variable predictors  $X_m$  on the  
162 response; and  $\varepsilon$  represents the error term.

163 Based on available data, we used a total of six potential predictors presumably  
164 related to the variability of PL and JU abundances. The potential predictors were  
165 salinity (ppt), temperature ( $^{\circ}\text{C}$ ), sampling sites (P1 to P5 and U1 to U4), months,

166 seasons and year. Year was based on the shrimp post-larvae entrance and harvest period  
167 (from September to August: I – 2010/2011; II – 2011/2012; III – 2012/2013). An  
168 exploratory data analysis was first applied to the database to detect possible outliers and  
169 assess statistical relationships between the variables. As multicollinearity among  
170 predictor variables may increase the probability of Type I errors, pairplots and  
171 Pearson's correlation coefficient  $\rho$  were used to check specifically for multicollinearity  
172 between environmental predictors. Provided that no high collinearity ( $\rho < 0.7$ ) was  
173 detected among these predictors, they could be simultaneously included in the tested  
174 models.

175 In the null model, predictor variables were evaluated using the forward stepwise  
176 selection procedure, which introduces all predictors one at a time progressively. Some  
177 models were tested considering only the interaction between particular predictors, as  
178 well as the quadratic term for the environmental predictors. At each model stage, the  
179 Akaike's Information Criterion (AIC) (Akaike 1973) and the maximum likelihood  
180 pseudo  $R^2$  (coefficient of determination) provided by the pscI R-package (Zeileis *et al.*,  
181 2008) were computed as indicative of "goodness-of-fit".

182 Given that the AIC accounts simultaneously for the number of parameters used  
183 in the model as well as the residual deviance; the smaller the value, the better the model  
184 (Burnham & Anderson 2002). Furthermore, models with larger  $R^2$  are better, as they  
185 express the percentage of variability in the response variable that was explained by the  
186 model. Thus, AIC and  $R^2$  are inversely related to the compromise between fit and  
187 parsimony. It is noteworthy that in cases when two or more nested models competed  
188 with each other (AIC values smaller than 5 units), we also used the Deviance hypothesis  
189 test to evaluate if the additional predictor improved the model fit (Venables &  
190 Dichmont, 2004).

191 When significant factors ( $P < 0.05$ ) were detected in the selected models for  
192 both response variables, Tukey's post-hoc test was performed using the glht function  
193 from the multcomp R-package (Hothorn *et al.*, 2008) in order to test differences  
194 between factor levels. Finally, the quality of these models was assessed through residual  
195 diagnostic plots. While residual's normality was evaluated by means of Quantile-  
196 Quantile plots, homogeneity was assessed through a residual vs. predicted values plot.  
197 Also, residuals independence was checked with the autocorrelation function. Moreover,  
198 since linearity is expected between the observed and predicted values, Pearson's  
199 correlation coefficient ( $\rho$ ) was calculated and used for model validation purposes.

## 200 RESULTS

201 **Environmental conditions**

202 Salinity in the protected area of the estuary was similar at all sites from P1 to P5  
203 with means ranging from  $10.43 \pm 2.03$  to  $14.51 \pm 2.33$  (Figure 1). The lowest mean  
204 occurred in the northern part of the estuary (P6 to P8), farthest from the estuary mouth  
205 that exchanges water with the ocean. Salinity in the unprotected area of the estuary  
206 decreased gradually toward the interior of the estuary, with the highest average salinity  
207 at U1 ( $17.99 \pm 2.75$ ) and the lowest at U4 ( $11.01 \pm 2.56$ ) (Figure 1). Average salinity  
208 increased from September ( $4.31 \pm 2.25$ ) to December, where average salinity was  $20.42$   
209 ( $\pm 2.07$ ). Salinity decreased slightly in January ( $13.30 \pm 1.71$ ), but increased on average  
210 afterwards to reach its highest value in March ( $21.39 \pm 1.89$ ). It followed a decreasing  
211 trend from April until the month of August ( $4.75 \pm 1.52$ ) (Figure 2).

212 Temperature at sites from U1 to U4 ranged from  $21.38 \pm 1.09$  to  $22.72 \pm 1.22$ .  
213 In the protected area, the lowest mean was  $21.54 \pm 1.04$  at P1 and the highest was  $23.53$   
214  $\pm 1.39$  at P4. The lowest temperatures were recorded from June to September, with  
215 mean values occurring between  $13.08 \pm 0.36$  and  $16.40 \pm 0.61$ . From October ( $20.09 \pm$   
216  $0.68$ ) the temperature increased and in January ( $28.02 \pm 0.57$ ), February ( $27.13 \pm 1.03$ )  
217 and March ( $25.71 \pm 0.81$ ) the highest values were recorded (Figure 2).

218

219 **Overall captures**

220 Throughout the study period, 9153 organisms were captured at all collection  
221 sites (2530 PL and 6623 JU). The lowest average abundance of PL and JU in the  
222 unprotected area occurred at the site U1 (PL =  $2.6 \pm 1.66$ ; JU =  $0.84 \pm 0.40$ ), the site  
223 closest to the mouth of the estuary, and the highest averages were observed at U2 (PL =  
224  $11.45 \pm 6.43$ ; JU =  $5.86 \pm 2.48$ ). In the protected area of the estuary, the lowest  
225 abundances of PL and JU occurred at P4 (PL =  $0.98 \pm 0.97$ , JU =  $7.25 \pm 2.81$ ), whereas  
226 the highest abundances were observed at P5 (PL =  $4.56 \pm 5.28$ ) and P1 (JU =  $26.83 \pm$   
227  $17.76$ ). If all sites were considered, P7 had the lowest average abundance (PL =  $0.6 \pm$   
228  $0.82$ ; JU =  $1.85 \pm 1.35$ ) and P8 had the highest abundance of JU ( $32.35 \pm 35.47$ ).  
229 Additionally, highest abundance of JU and PL were registered in the protected and  
230 unprotected sites, respectively (Figure 1).

231

232

233

### 234 **Size structure**

235           Size structure analysis identified differences in the number of post-larvae and  
236 juveniles in each site. The largest juvenile measured 25.00 mm CL, however the major  
237 size classes were between 2.00 and 15.00 mm CL. Post-larvae were more common in  
238 sites U1 to U4, with a unimodal trends frequency distribution, with peak occurrence in  
239 the 2.01 – 3.00 mm class interval, followed by a sharp drop in size classes above 3.00  
240 mm (Figure 3). At sites P1 to P8, the size distribution displayed a bimodal and  
241 multimodal trend. It can be seen in the protected area that mode can be identified in the  
242 size class over 3.01 mm (Figure 3).

243

### 244 **Model selection and estimates of explanatory variables**

245           Several models have been tested with respect to different combinations of  
246 variable predictors for PL and JU relative abundances. Although some similarities were  
247 shared among the selected GLMs, they highlighted that the relative importance of each  
248 predictor was different for each response variable.

249           The most relevant models with respect to the PL abundance are summarized in  
250 Table 2. Even though models 6-10 had the best fit qualities, the Deviance hypothesis  
251 test did not detect significant differences between these models. In this sense, model 8  
252 was selected since it showed the best fit and parsimony, as well as the most reliable  
253 biological explanation. Thus, salinity, sampling sites, year and months were important  
254 to explain the variability in the PL abundances.

255           According to Table 3, all included co-variables were statistically significant ( $P$   
256  $< 0.05$ ). Salinity showed a positive relationship with PL, indicating that a higher  
257 abundance of PL increases with salinity. Among the sampling sites, only P4 and U2  
258 were statistically different with respect to the reference level (P1). Whereas lower PL  
259 abundances occurred in P4, higher abundances occurred in U2 when compared to the  
260 reference level. Moreover, according to the post-hoc analysis (Figure 4a), a more  
261 pronounced difference occurred when contrasting the sampling sites between protected  
262 and unprotected areas, than when contrasting the sampling sites within each area. The  
263 highest relative abundances were revealed at site U2, compared to P2, P3 and P4. No  
264 differences were detected when contrasting the abundances between U1, U2, U3, U4,  
265 P1 and P5 were compared (Figure 4a).

266           Regarding the year, both year II and III were significantly different with respect  
267 to the reference level (year I) (Table 3). PL abundances increased slightly over the three

268 years, where the last year showed the highest abundance values (Figure 4b).  
269 Additionally, the *post-hoc* results showed a significant difference between year II and  
270 III, revealing the highest relative abundances in year III. Post-larvae occurred in all  
271 months, and June, October, November, December, January, February and March  
272 revealed to be statistically significant when compared to the reference level (April)  
273 (Table 3). Except June, all other months listed above were positively related to PL  
274 abundance. December particularly showed the highest mean abundance values (Figure  
275 4c) when compared to the reference level. The *post-hoc* analysis did not indicate  
276 substantial differences between months with higher mean PL abundances (October,  
277 November, December January, February and March) nor between months with lower  
278 mean PL abundances (April – September) (Figure 4c). However, significant differences  
279 were detected when comparing months with lower mean PL abundances (April –  
280 September) and those with higher mean PL abundances.

281 Of the tested models for JU abundance, models 13 and 14 had the best fit  
282 quality, but the Deviance hypothesis test indicated that model 14 was significantly  
283 better than model 13 (Table 4). Model 14 included salinity, the quadratic term of  
284 salinity, sampling sites, year, months, and the interaction between month and salinity as  
285 fixed effect. Although the salinity and its quadratic term were not significant, all the  
286 other predictors were statistically significant.

287 Sampling site P4 and all sites from the unprotected area were significant with  
288 respect to the reference level (P1) (Table 5). All these sampling sites were negatively  
289 related to JU abundance, indicating that lower abundances occur in these areas. Also,  
290 the lowest JU abundances occurred specifically in unprotected areas. The *post-hoc*  
291 analysis indicated that greater differences in JU abundance occur when comparing the  
292 sampling sites from protected areas (P1-P5) to sampling sites from unprotected areas  
293 (U1-U4), rather than comparing protected areas and unprotected areas amongst  
294 themselves. The highest relative abundances were revealed at P1 and P2 when  
295 compared to unprotected sites. The lowest abundance were found at the mouth of the  
296 estuary: site U1 (Figure 4a).

297 Years II and III were significantly different to the reference level (year I), and  
298 both had a positive relationship with JU abundance (Table 5). The *post-hoc* analysis did  
299 not detect significant difference between years II and III (Figure 4b). The lowest relative  
300 abundance was found in year I. Regarding the months, only September, November,  
301 December, January and February were significantly different when compared to the

302 reference level (April). Except September, all other months listed above were positively  
303 related to JU abundance. The *post-hoc* analysis did not indicate substantial differences  
304 between months with higher mean JU abundances (November, December January and  
305 February) nor between months with lower mean JU abundances (March – October).  
306 However, significant differences were detected when comparing months with lower  
307 mean JU abundances and those with higher mean abundances (Figure 4c).

308 The interaction term between salinity and months showed an influence in JU  
309 abundances. In particular, only salinity and the months September, October, January  
310 and March were significantly different when contrasted to the reference level (S:April).  
311 The positive relationship of all these levels indicates that JU abundances are greater at  
312 higher salinities detected in these months, and specifically in September.

313 Finally, with respect to the residuals diagnostic plots, both selected models  
314 obeyed the basic assumption of normality, homoscedasticity and independence. Two  
315 types of visual graphical checks were used to evaluate models fit, namely: quantile-  
316 quantile plots and predicted vs. observed values plots. Quantiles-quantile plots showed a  
317 reasonable normal distribution for the residuals of each selected model (Figure 5a, c).  
318 Furthermore, the predicted versus observed values were positively and significantly  
319 correlated for both PL and JU abundance models (Figure 5b, d), indicating, therefore,  
320 that both models are suitable to explain the mean tendencies for each response variable.

321

## 322 DISCUSSION

### 323 **Spatial variability in abundance**

324 This study shows that the pink shrimp *Farfantepenaeus paulensis* post-larval  
325 and juveniles stages are distributed throughout the Lagoa dos Patos estuary, extending  
326 from the mouth of the estuary, where salinity is higher, to the northernmost areas. Their  
327 distribution is marked by habitat preference, which can be recognized by the spatial  
328 variability of species abundance. D'Incao (1991) highlighted their wide distribution and  
329 the importance of shallow inlets for juvenile growth. Ruas *et al.*, (2014) analyzed the  
330 abundance variability of the pink shrimp in two inlets and observed that post-larvae and  
331 juveniles prefer submerged vegetation and higher salinity.

332 In this study, the pink shrimp showed a distinct pattern between protected and  
333 unprotected sites. A unimodal distribution with large numbers of post-larvae occurred at  
334 the unprotected sites, where the early-stage juveniles were predominant at protected  
335 sites with bimodal and multimodal distribution. These patterns of habitat use are linked

336 to habitat selection behavior during the shrimp ontogeny in the estuary, which  
337 corroborates with the research of Noieto-Filho *et al.*, (2017). Studies with other species  
338 of *Farfantepenaeus* show that spatial segregation by size occurs to reduce intraspecific  
339 competition and mitigate predation risks (Pérez-Castañeda & Defeo, 2001).

340 Habitat preference is a well-known behavior for some species of penaeid. Pérez-  
341 Castañeda *et al.*, (2010) showed *Farfantepenaeus aztecus* and *Farfantepenaeus*  
342 *dourarum* (Burkenroad 1939) preference for submerged vegetation. Pérez-Castañeda &  
343 Defeo (2001, 2004) studied species of the genus *Farfantepenaeus* in a coastal lagoon in  
344 the Gulf of Mexico. They noted intraspecific spatial segregation in shrimp distribution;  
345 the greatest abundance of recruits (CL < 8.0 mm) and juveniles were associated with  
346 higher salinity and vegetated areas in the search for protection. According to Mohan *et*  
347 *al.*, (1995), a muddy substrate, rich in organic matter, is also an important factor in  
348 habitat selection for post-larvae and juveniles of *Feneropenaeus indicus* (H. Milne-  
349 Edwards 1837) and *Farfantepenaeus merguensis*.

350 Increased abundance of post-larvae with higher salinity levels may indicate why  
351 these organisms enter the estuary. Post-larvae accompany the sea water inlet into Lagoa  
352 dos Patos. This process depends on a favorable combination of freshwater discharge and  
353 wind conditions for the entry of seawater (Möller *et al.*, 2009; Pereira & D’Incao,  
354 2012).

355 Increased salinity levels may explain post-larval arrival in shallow inlets. Vance  
356 *et al.*, (1998) analyzed *F. merguensis* in two estuaries of northeastern Australia and  
357 reported that an increased rainfall in wet seasons causes a decrease in salinity, inhibiting  
358 the post-larvae to reach the innermost parts of the estuary. These authors also  
359 emphasized that abundance varied due to a combination of hydrodynamic processes and  
360 behavioral changes associated with the development of the species. Staples (1980)  
361 observed that post-larvae of *F. merguensis* moved from the substrate to the water  
362 column and migrated up the estuary by the influence of tidal flooding (of salt water).  
363 The same behavior was observed for *F. aztecus* in their migration to estuaries in the  
364 Gulf of Mexico (Cházaro-Olvera *et al.*, 2009). It can be concluded then, that if  
365 conditions are favorable, and salt water entry intense, a favorable scenario is created for  
366 the migration of post-larvae into the Lagoa dos Patos estuary. Higher salinities increase  
367 survival rates, as older pink shrimp post-larvae (late stages) are more susceptible to  
368 mortality when exposed to low salinity levels (< 10) (Tsuzuki *et al.*, 2000), also limiting  
369 their spatial distribution.

370 The unprotected sites are the first contact that post-larvae have with low and  
371 highly variable salinity (Martins *et al.*, 2007; Dumont & D'Incao, 2010). This area  
372 represents an acclimation space to salinity conditions in the estuary, because individuals  
373 enter this environment while undergoing their most important period of osmoregulatory  
374 development (Tsuzuki *et al.*, 2000).

375 The high abundance of post-larvae, at U1 to U4 and P1 and P5, indicate the  
376 importance of these sites for pink shrimp recruitment, because they may represent a  
377 nesting area for individuals of ocean origin. The search for a substrate in marginal areas  
378 of the unprotected central area (mainly represented by U2) and shallow waters in  
379 protected areas at the mouth of the estuary as soon as they enter estuaries, may represent  
380 the attempt of post-larvae to remain in this environment, thus preventing the ebb tide  
381 from carrying them back to the ocean, as demonstrated for *F. merguensis*, *F. aztecus*  
382 and *Melicertus plebejus* (Young & Carpenter, 1977; Adnan *et al.*, 2002; Cházaro-  
383 Olvera *et al.*, 2009).

384 This study also showed that juvenile spatial distribution is uneven, with the  
385 largest abundances found in P1 and P2, showing the importance of these sites when  
386 compared to the unprotected area. The lower variability of salinity, the presence of  
387 submerged phanerogam prairies and lower current velocity are characteristic  
388 environmental factors of protected shallow inlets and can provide the ecological  
389 conditions necessary for the development of juveniles: increased food supply and  
390 protection against predators (D'Incao, 1991; Mohan *et al.*, 1995; Costa *et al.*, 1997;  
391 Fernandes *et al.*, 2007; Martins *et al.*, 2007; Copertino & Seeliger, 2010; D'Incao &  
392 Dumont, 2010; Pérez-Castañeda *et al.*, 2010; Ruas *et al.*, 2014).

393 According to D'Incao & Dumont (2010) and Ruas *et al.*, (2011), stable salinity  
394 levels are an important environmental factor associated with the greatest abundances of  
395 juveniles. Therefore, lower abundances of juveniles at unprotected sites may have  
396 occurred due to more variable environmental conditions (Martins *et al.*, 2007; D'Incao  
397 & Dumont, 2010). A wide range in salinity, for example, can impact the survival of the  
398 late stages of pink shrimp post-larvae (Tsuzuki *et al.*, 2000).

399 Pink shrimp artisanal fishing occurs both legally and illegally throughout the  
400 estuary and has detrimental effects on the benthic community and estuarine ecosystem  
401 (Benedet *et al.*, 2010). Pink shrimp fishing productivity has shown a downward trend in  
402 productivity in recent years (D'Incao & Dumont, 2010). Shrimps currently living in the  
403 Lagoa dos Patos estuary do not contribute to the adult stock of shrimp, as they are

404 prevented from returning to the ocean due to intense fishing pressure (D’Incao, 1991).  
405 This study shows the spatial variability of post-larvae and juvenile pink shrimp and key  
406 areas of recruitment in the estuary. These sites deserve special consideration in fishery  
407 management, to reduce the impact of fishing and contribute to the conservation of areas  
408 of post-larvae recruitment and juvenile growth. The conservation of these areas can help  
409 juveniles return to the ocean.

410

#### 411 **Temporal variability in abundance**

412 Annual variability in abundance of post-larvae and juvenile pink shrimp,  
413 presented in this work, should be considered characteristic of the Lagoa dos Patos  
414 estuary. Their annual variability is linked to environmental conditions and the  
415 availability of post-larvae pink shrimp in the coastal zone. The least productive catches  
416 are positively related to high rainfall in the Lagoa dos Patos drainage basin. In high  
417 rainfall conditions, a strong flow of fresh water through the narrow mouth that connects  
418 the estuary to the ocean impedes saltwater from entering and compromises pink shrimp  
419 recruitment in the estuary (Möller *et al.*, 2009, Pereira & D’Incao, 2012). The  
420 overfishing of the adult stock also causes a reduction in the number of larvae available  
421 for recruitment in the estuary (D’Incao *et al.*, 2002; Teodoro *et al.*, 2015). The current  
422 fishery production of pink shrimp adult stock varies annually (Pezzuto & Benincà,  
423 2015), and possibly has a negative effect on the reproduction dynamics of the species  
424 and consequently, there is an annual variability in larvae density.

425 Post-larvae pink shrimp captured throughout the year during all months support  
426 the idea proposed by D’Incao (1991) that, based on growth studies, post-larvae enter the  
427 estuary throughout the entire year, which also occurs in estuaries in the North of Brazil.  
428 October to March (spring to summer) is characterized as the principal period of  
429 recruitment. D’Incao (1991), analyzing the velocity and direction of marine currents and  
430 larval development to the youngest post-larvae stage in Lagoa dos Patos, suggests that  
431 post-larvae that inhabit the estuary may have originated from a spawning population off  
432 the coast of Santa Catarina State, in Southern Brazil. The pink shrimp reproduces  
433 continuously but reproductive intensity varies with latitude. In Southeast Brazil the  
434 adult stock of pink shrimp presents two reproductive peaks, while the principal  
435 reproductive period in Santa Catarina begins in spring (September) and extends to  
436 summer (D’Incao, 1991; Costa *et al.*, 2008).

437 The variability in abundance of juveniles shows a defined monthly pattern,  
438 which covers the period of November to February. Although the model did not identify  
439 temperature as a significant factor, it was evident that juvenile abundance was higher  
440 during the hottest months of the year. This reinforces the findings of D’Incao (1991),  
441 which showed an increase in abundance with temperature. The same pattern was  
442 observed in the same species by Branco & Verani (1998) e Lüchmann *et al.*, (2008) in  
443 Conceição Lagoon in Santa Catarina, and by Costa *et al.*, (2008) in an estuary along the  
444 Southeast coast of Brazil. However, it is possible that other factors, not identified in the  
445 model may have influenced the observed pattern. Fishing for example, starts at the  
446 beginning of February.

447 The monthly variability of salinity proved important for juveniles. The increase  
448 in juvenile abundance with an increase in salinity during September, October, January,  
449 and March show juveniles’ preference for elevated salinities. These results corroborate  
450 previous results from Lagoa dos Patos, that seem to be linked to annual variability  
451 patterns and present greatest abundance during periods of high salinity (D’Incao, 1991;  
452 Möller *et al.*, 2009; Ruas *et al.*, 2014). According to Tsuzuki *et al.*, (2000) the highest  
453 survival rates of this species are linked to salinities above 10.

454

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459

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SITES	COORDINATES	
	SOUTH	WEST
P1	32° 4'27.22"	52° 7'23.23"
P2	32° 1'11.90"	52° 8'21.20"
P3	32° 1'31.98"	52°12'11.09"
P4	31°57'58.12"	52°13'1.61"
P5	31°56'26.78"	52° 0'45.04"
P6	31°48'56.50"	52° 0'35.30"
P7	31°51'25.47"	51°55'49.99"
P8	31°49'7.41"	51°48'56.96"
U1	32° 8'14.20"	52° 5'18.50"
U2	32° 4'0.61"	52° 5'2.25"
U3	31°59'36.79"	52° 5'49.63"
U4	31°52'48.80"	52° 4'24.60"

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MODEL	NUMBER	RD	DF	AIC	R <sup>2</sup>
1	1	428.9	606	2124.1	0
1 + T	2	430.5	605	2090.97	0.056
1 + T + S	3	431.2	604	2086.87	0.065
1 + T + S + Ss	4	432.9	596	2064.71	0.122
1 + T + S + Ss + Y	5	430.8	594	1993.37	0.225
1 + T + S + Ss + Y + M	6	420.4	583	1878.4	0.381
1 + T + S + Ss + Y + M + Se	7	422	580	1878.74	0.387
<b>1 + S + Ss + Y + M</b>	<b>8</b>	<b>420.3</b>	<b>584</b>	<b>1876.58</b>	<b>0.381</b>
1 + S + S <sup>2</sup> + Ss + Y + M	9	419.5	583	1876.13	0.383
1 + Ss + Y + M	10	419.1	585	1878.75	0.377
1 + S + Ss + Y + M + Ss*S	11	421.9	576	1886.96	0.387
1 + S + Ss + Y + M + S*Y	12	419.5	586	1879.33	0.303

PREDICTORS	ESTIMATE	STD. ERROR	P-VALUE
(Intercept)	-2.986	0.596	< 0.05*
S	0.029	0.013	< 0.05*
Ss (P2)	-0.249	0.384	NS
Ss (P3)	-0.708	0.403	NS
Ss (P4)	-1.410	0.416	< 0.05*
Ss (P5)	0.034	0.40	NS
Ss (U1)	0.065	0.378	NS
Ss (U2)	0.961	0.360	< 0.05*
Ss (U3)	0.274	0.370	NS
Ss (U4)	0.050	0.392	NS
Y (B)	1.805	0.215	< 0.05*
Y (C)	2.634	0.29	< 0.05*
M (August)	1.273	0.703	NS
M (December)	3.094	0.523	< 0.05*
M (February)	1.954	0.575	< 0.05*
M (January)	2.931	0.527	< 0.05*
M (July)	-34.95	1.11E+07	NS
M (June)	-1.856	0.946	< 0.05*
M (May)	-0.931	0.781	NS
M (March)	1.562	0.541	< 0.05*
M (November)	2.413	0.554	< 0.05*
M (October)	3.196	0.568	< 0.05*
M (September)	0.047	0.656	NS

MODEL	NUMBER	RD	DF	AIC	R <sup>2</sup>
1	1	562.82	606	3147.82	0
1 + T	2	564.06	605	3044.5	0.159
1 + T + S	3	560.08	604	3003.62	0.217
1 + T + S + Ss	4	561.04	596	2935.59	0.318
1 + T + S + Ss + Y	5	560.16	594	2917.06	0.343
1 + T + S + Ss + Y + M	6	568.64	583	2718.71	0.543
1 + T + S + Ss + Y + M + Se	7	568.95	580	2721.11	0.546
1 + S + S <sup>2</sup> + Ss + Y + M	8	567.4	583	2714.16	0.546
1 + T + T <sup>2</sup> + Ss + Y + M	9	571.7	583	2720.39	0.542
1 + S + Ss + Y + M + Ss*S	10	568.92	576	2723.75	0.55
1 + S + Ss + Y + M + Ss*Y	11	563.59	568	2720.99	0.563
1 + S + Ss + Y + M + Y*S	12	566.31	582	2719.64	0.544
1 + S + Ss + Y + M + M*S	13	545.99	573	2662.11	0.597
<b>1 + S + S<sup>2</sup> + Ss + Y + M + M*S</b>	<b>14</b>	<b>544.2</b>	<b>572</b>	<b>2655.58</b>	<b>0.603</b>

PREDICTORS	ESTIMATE	STD. ERROR	P-VALUE
(Intercept)	-0.386	0.789	NS
S	0.022	0.052	NS
S <sup>2</sup>	-0.003	0.001	< 0.05 *
Ss (P2)	0.105	0.242	NS
Ss (P3)	-0.359	0.248	NS
Ss (P4)	-0.842	0.253	< 0.05 *
Ss (P5)	-0.284	0.259	NS
Ss (U1)	-2.614	0.303	< 0.05 *
Ss (U2)	-0.739	0.251	< 0.05 *
Ss (U3)	-1.117	0.256	< 0.05 *
Ss (U4)	-0.926	0.263	< 0.05 *
Y (II)	0.928	0.159	< 0.05 *
Y (III)	0.929	0.220	< 0.05 *
M (August)	-1.273	1.232	NS
M (December)	2.658	0.828	< 0.05 *
M (February)	2.653	0.862	< 0.05 *
M (January)	2.409	0.799	< 0.05 *
M (July)	-9.287	7.324	NS
M (June)	-0.642	1.076	NS
M (May)	-0.138	0.9745	NS
M (March)	0.486	0.911	NS
M (November)	3.114	0.834	< 0.05 *
M (October)	-0.538	0.832	NS
M (September)	-3.139	1.052	< 0.05 *
S : M (August)	0.078	0.137	NS
S : M (December)	0.062	0.044	NS
S : M (February)	0.086	0.046	NS
S : M (January)	0.103	0.044	< 0.05 *
S : M (July)	0.439	0.351	NS
S : M (June)	0.019	0.059	NS
S : M (May)	0.016	0.061	NS
S : M (March)	0.146	0.047	< 0.05 *
S : M (November)	-0.087	0.052	NS
S : M (October)	0.154	0.053	< 0.05 *
S : M (September)	0.251	0.059	< 0.05 *

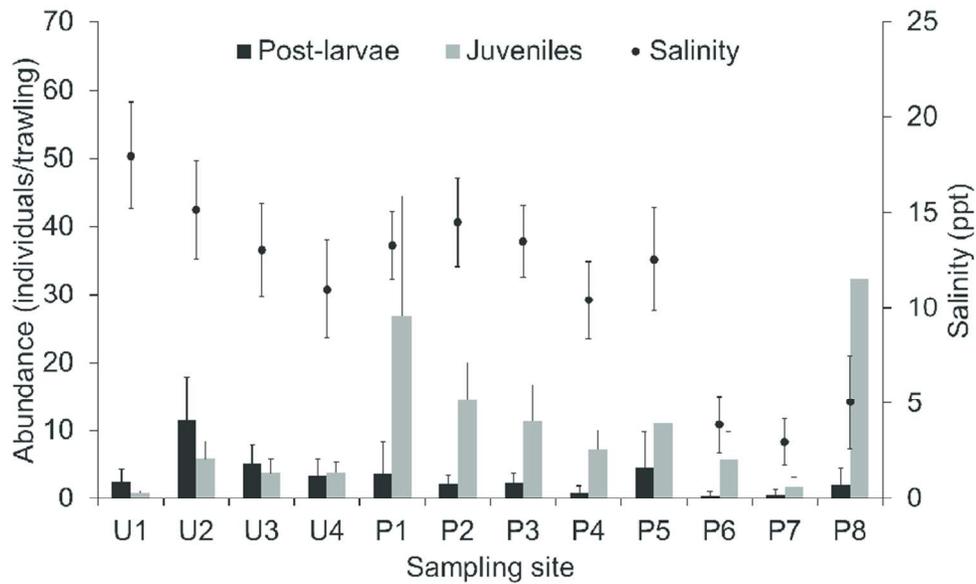


Fig. 1 Mean salinity values (black dots) and relative abundance (bars) of post-larvae and juveniles of *Farfantepenaeus paulensis* at the sampling sites of the protected (P1 to P8) and unprotected (U1 to U4) areas throughout the study period, with their respective 95% confidence intervals. Abundance is expressed by the average number of individuals caught by haul instead of trawling.

84x50mm (300 x 300 DPI)

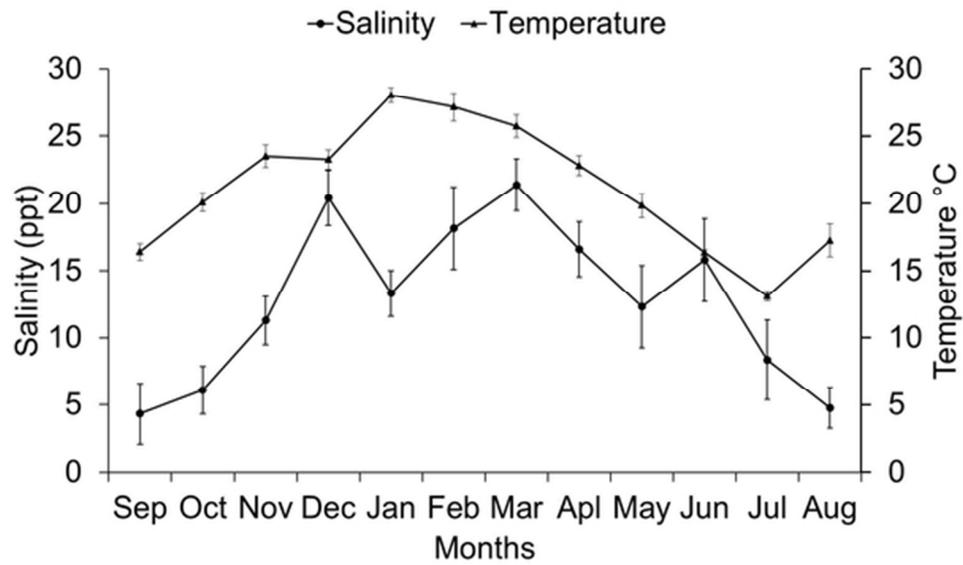


Fig. 2 Mean salinity values during the months, with their respective 95% confidence intervals.

53x31mm (300 x 300 DPI)

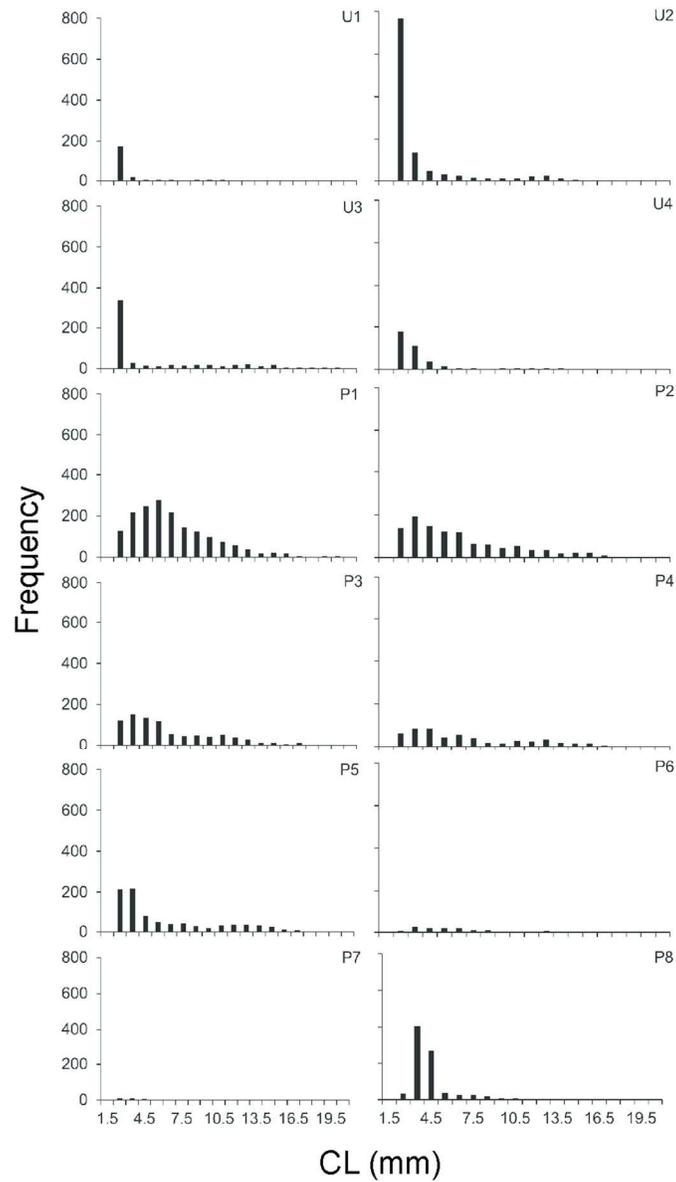


Fig. 3 Frequency distribution of carapace length (CL), grouped at intervals of 1 mm, for *Farfantepenaeus paulensis* in the protected and unprotected sites of the Patos Lagoon estuary.

83x149mm (300 x 300 DPI)

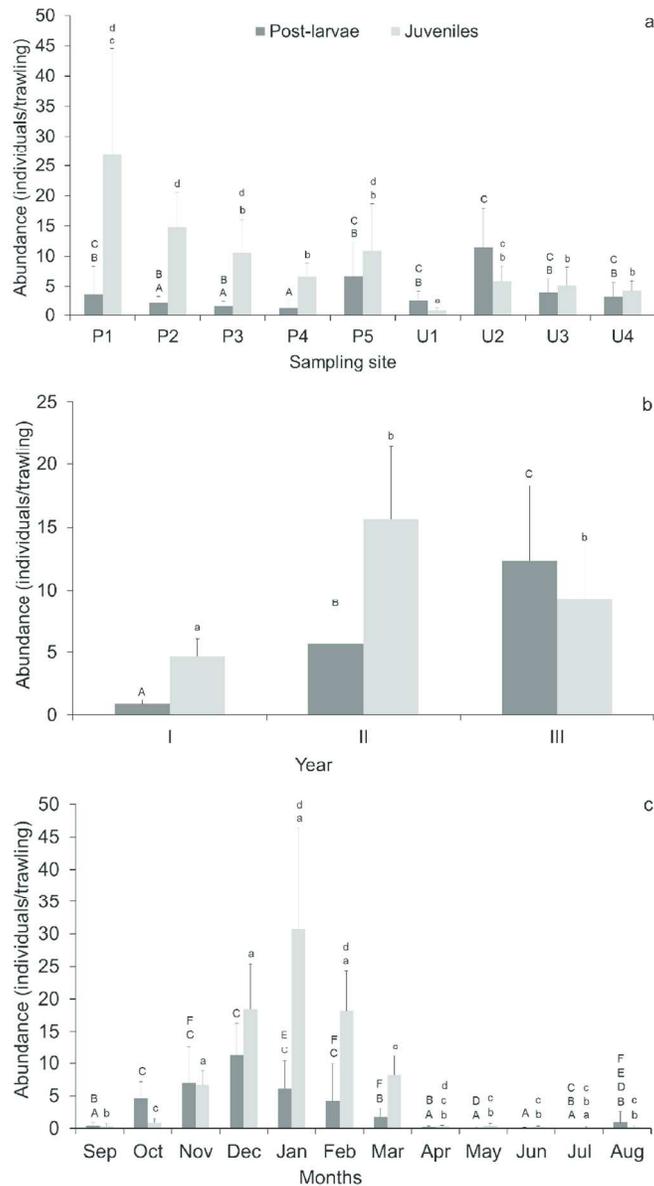


Fig. 4 Mean relative abundance of post-larvae and juveniles of *Farfantepenaeus paulensis* at the sampling sites (a), year (b) and, months (c), with their respective 95% confidence intervals. Tukey's post-hoc analysis is indicated by letters above the bars, where different letters indicate significant differences ( $p < 0.05$ ).

84x152mm (300 x 300 DPI)

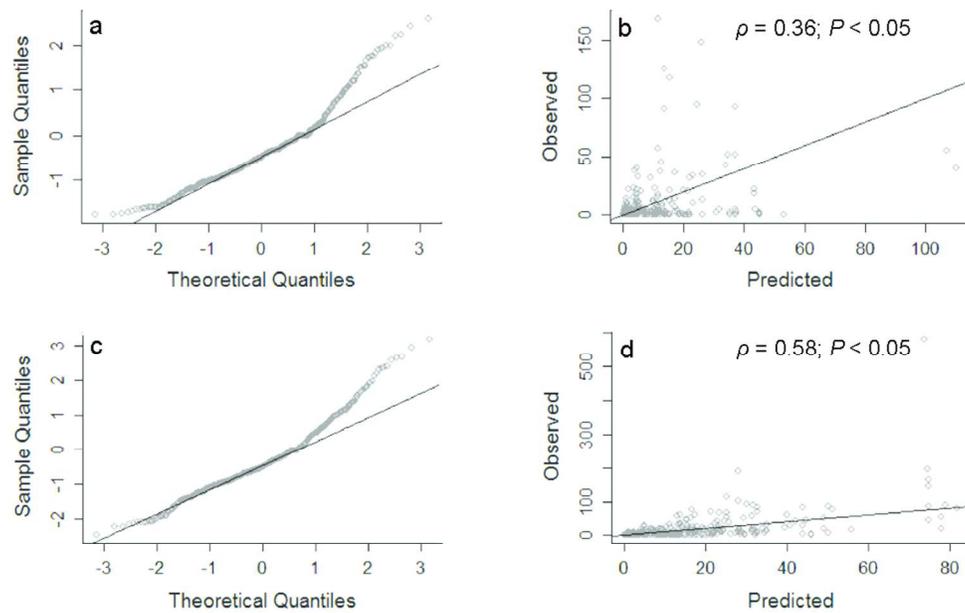


Fig. 5 Evaluation of model performance. Left panels shows the Quantiles-quantil plots provided from the post-larvae (a) and juveniles (c) models. Right panels shows the observed versus predicted values for post-larvae (b) and juveniles (d) abundances.

99x66mm (300 x 300 DPI)