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Research Article

Population genetic structure of Brazilian shrimp species (*Farfantepenaeus* sp., *F. brasiliensis*, *F. paulensis* and *Litopenaeus schmitti*: Decapoda: Penaeidae)

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Abstract

Penaeid shrimps are important resources for worldwide fisheries and aquaculture. In the Southwest Atlantic, *Farfantepenaeus brasiliensis*, *F. paulensis*, *F. subtilis*, *Farfantepenaeus* sp. and *Litopenaeus schmitti* are among the most important commercially exploited species. Despite their high commercial value, there is little information available on the different aspects of their biology or genetics and almost no data on their stock structure. We used allozymes to estimate variability levels and population genetic structure of *F. brasiliensis*, *F. paulensis*, *L. schmitti* and the recently detected species *Farfantepenaeus* sp. along as much as 4,000 km of Brazilian coastline. No population heterogeneity was detected in *F. brasiliensis* or *L. schmitti* along the studied area. In contrast, F_{ST} values found for *Farfantepenaeus* sp. and *F. paulensis* indicate that the populations of those two species are genetically structured, comprising different fishery stocks. The largest genetic differences in *F. paulensis* were found between Lagoa dos Patos (South) and the two populations from Southeast Brazil. In *Farfantepenaeus* sp., significant differences were detected between the population from Recife and those from Fortaleza and Ilhéus.

Key words: Farfantepenaeus, *Litopenaeus*, allozymes.

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Introduction

Penaeid shrimps are important resources for worldwide fisheries and aquaculture (Sunden and Davis, 1991). Population genetics have proven valuable for estimating stock boundaries and genetic variability of wild shrimp populations for fisheries (Benzie, 2000).

Along the Brazilian coast, juvenile shrimps are caught in natural nursery areas by small vessels, while the commercial fleet harvest adult populations in the open sea (Valentini *et al*., 1991). As a result of the unrestricted past growth of the industrial fleet, of the increased number of small boats fishing in natural nurseries and estuaries and of environmental degradation, there is evidence of declining stocks of shrimps along the Brazilian coast. *Farfantepenaeus brasiliensis*, *F. paulensis*, *F. subtilis* and *Litopenaeus schmitti* are among the main commercially important Brazilian species (Neto, 1991; Valentini *et al*., 1991). Populations of *F. brasiliensis* and *F. paulensis* of the South/Southeast regions showed a decrease of 87.1% in relative stock abundance between 1965-1994 (Neto and Dornelles, 1996). A decline was also observed in populations of *F. subtilis* (Neto, 1991) and *L. schmitti* (Neto and Dornelles, 1996). Despite their high commercial value and the need to understand their stock structure, so that effective management measures can be applied, there is still little information available on their population genetics (the sole exception is the analysis of *F. paulensis* in the South of Brazil; Delevedove, 1996), and even the taxonomic status of some species has just recently been clarified. Genetic analyses revealed a new (cryptic) Brazilian species of *Farfantepenaeus* (*Farfantepenaeus* sp.; formerly *Penaeus*

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subtilis[1]) ranging from Rio de Janeiro to Northeast Brazil, showing that *Penaeus subtilis* (*sensu* Pérez Farfante, 1969) was in fact a mixture of two different species (Gusmão *et al*., 2000; Maggioni *et al*., 2001).

In this paper we used allozymes to estimate the variability levels and the population genetic structure of four Brazilian species, *F. brasiliensis*, *F. paulensis*, *L. schmitti* and the new species, *Farfantepenaeus* sp., over a distance of approximately 4,000 km of coastline.

Different stocks were observed within populations of *F. paulensis* and of *Farfantepenaeus* sp., while no detectable heterogeneity could be observed for populations of *F. brasiliensis* and *L. schmitti* along the studied area.

Material and Methods

We collected 556 individuals of *F. brasiliensis*, *F. paulensis, L. schmitti* and *Farfantepenaeus* sp. from eight different sites along 4,000 km of Brazilian coastline, between October 1997 and September 1999. Sampling localities are indicated in Figure 1. Samples were stored on dry ice and transported to the laboratory where they were identified morphologically according to Pérez Farfante (1969). Muscle tissue was preserved in liquid nitrogen until required for allozyme analysis.

Horizontal 12.5% starch gel electrophoresis was carried out as previously described (Murphy *et al*., 1990; Gusmão *et al*., 2000). The 11 enzyme systems investigated are shown in Table 1. Allozyme patterns were visualised using standard enzyme stains (Manchenko, 1994). Genotype frequencies were used to estimate gene frequencies, heterozygosities, tests for Hardy-Weinberg equilibrium, and inbreeding indices, using the BIOSYS-1 programme version 1.7 (Swofford and Selander, 1981). The significance of F_{IS} (H_o: $F_{IS} = 0$) and F_{ST} (H_o: $F_{ST} = 0$) were tested according to Waples (1987).

Figure 1 - (•) Sampling sites for the populations analysed. (→) Geographical limits of the main *Farfantepenaeus paulensis* offshore fishing area and adult congregation zones (see Discussion).

Table 1 - Enzymes studied (and abbreviations), Enzyme Commission numbers (E.C.), and buffer systems analysed.

Enzyme	Abbrev.	E.C.	Buffer*
Adenylate kinase	AK	2.7.4.3	TC8
Isocitrate dehydrogenase	IDH	1.1.1.42	TC7
Lactate dehydrogenase	LDH	1.1.1.27	TEM
Malic dehydrogenase	MDH	1.1.1.37	TC8
Malic enzyme	ME	1.1.1.40	TEM
Mannose phosphate isomerase	MPI	5.3.1.8	TEM
Phosphoglucomutase	PGM	5.4.2.2	TC7
Phosphogluconic dehydrogenase	PGD	1.1.1.44	TEM
Phosphoglucose isomerase	PGI	5.3.1.9	TC7
Pro-Phe dipeptidase	PEP-A	3.4.13.18	TC8
Tripeptidase (Leu-Gly-Gly)	PEP-B	3.4.11.4	TC8

*TEM = 0.10 M Tris, 0.01 M EDTA, 0.10 M maleate, pH 7.4 (Brewer, 1970).
TC8 = 0.25 M Tris, 0.06 M citrate, pH 8.0 (Ward and Beardmore, 1977).
TC7 = 0.135 M Tris, 0.043 M citrate, pH 7.0 (Shaw and Prasad, 1970).

The mean number of migrants (N_em; Wright, 1978) between populations was estimated as $N_em \approx (1/F_{ST})-1)/4$. There have been concerns about the direct use of F_{ST} to estimate gene flow (Whitlock and McCauley, 1999). However, F_{ST} remains a robust estimate of multi-population differentiation when the number of loci analysed is not small (Neigel, 2002), so we chose to use it to facilitate comparison with data from the literature. We used a Mantel test (Sokal and Rohlf, 1995), between pairs of *Farfantepenaeus* and *Litopenaeus* populations, with 1000 replicates, to verify if geographic distances could be correlated to genetic distances.

Results and Discussion

The four species studied had distinct population structure patterns. Populations of *Farfantepenaeus brasiliensis* and *Litopenaeus schmitti* did not show any significant structuring ($F_{ST} = 0.011$ and 0.024, respectively; χ^2 test (Waples, 1987) null hypothesis: $F_{ST} = 0$; $p > 0.05$) along the studied area. In contrast, the null hypothesis of panmixia was rejected ($p < 0.005$) for populations of *Farfantepenaeus* sp. ($F_{ST} = 0.032$; $N_em = 5.31$) and *F. paulensis* ($F_{ST} = 0.045$; $N_em = 7.56$; Table 2).

1 In a recent review, the subgenera *Farfantepenaeus* and *Litopenaeus*, formerly grouped under the *Penaeus* genus, were raised to generic level (Pérez Farfante and Kensley, 1997).

Table 2 - Pair-wise χ^2 values found between populations of *Farfantepenaeus paulensis* and of *Farfantepenaeus* sp.

Species	Populations	χ^2 F_{ST}	χ^2 contingency
F. paulensis	Santos/Lagoa dos Patos	10.14**	49.69***
	Rio/Lagoa dos Patos	9.26*	42.31***
	Rio/Santos	2.52^{NS}	25.71*
Farfantepenaeus sp.	Fortaleza/Recife	5.13^{NS}	27.49*
	Fortaleza/Ilhéus	2.59^{NS}	20.69^{NS}
	Recife/Ilhéus	4.96*	30.57**

^{NS} - Not significant; $p > 0.05$.
*$p < 0.05$. **$p < 0.01$. ***$p < 0.001$.

The mean value of F_{ST} observed for the Brazilian populations of *L. schmitti* ($F_{ST} = 0.024$) is within the range reported for Cuban populations of the same species, using allozymes ($F_{ST} = 0.021$-0.038) and microsatellites ($F_{ST} = 0.005$-0.060; Espinosa *et al*., 2002). High genetic homogeneity has been reported for many other penaeid species (reviewed in Benzie, 2000).

The high F_{ST} values found for *Farfantepenaeus* sp. and *F. paulensis*, even over shorter distribution ranges and using the same allozyme systems employed for *F. brasiliensis* and *L. schmitti*, indicate that the populations of those two species are genetically structured ($p < 0.005$). Pair-wise comparisons of the populations (contingency χ^2, Table 2) show that the largest population differences in *F. paulensis* were found between Lagoa dos Patos (South) and the two populations from Southeast Brazil ($p < 10^{-4}$). In *Farfantepenaeus* sp., significant differences were detected between the population from Recife and those from Fortaleza ($\chi^2 = 27.49$; $p < 0.05$) and Ilhéus ($\chi^2 = 30.57$; $p < 0.01$). Similar levels of population genetic structuring have also been observed for several species, *e.g.*, Australian populations of *Penaeus monodon* (Benzie *et al*., 1992) and of *Melicertus latisulcatus* (Mulley and Latter, 1981); populations of *M. kerathurus* from the Mediterranean (Mattoccia *et al*., 1987); Cuban populations of *F. notialis* (Espinosa *et al*., 1996; García-Machado *et al.*, 2001); and Californian populations of *L. stylirostris* (Aubert and Lightner, 1999; De La Rosa-Velez *et al*., 2000; Ramos-Paredes and Grijalva-Chon, 2003) and of *F. californiensis* (De La Rosa-Velez *et al*., 2000).

Mean heterozygosity values observed for Brazilian species (H = 0.02-0.10) were similar to those reported in other surveys (H = 0.006-0.175) (Benzie, 2000; García-Machado *et al*., 2001; Espinosa *et al*., 2002; Ramos-Paredes and Grijalva-Chon, 2003). The *Mpi* locus showed a relatively high variability among *Farfantepenaeus* species. This could be related to its tertiary structure (Solé-Cava and Thorpe, 1989) or to some hitherto unknown balanced selection regime acting on that locus. Gene frequencies at the 14 loci analysed, and mean heterozygosity values for each population are shown in Table 3.

Significant deviations from Hardy-Weinberg expectations (heterozygote deficiencies, $p < 0.05$; Fisher's exact test, corrected with Bonferroni series; Lessios, 1992) were found for the *Pgm-1* locus in two populations of *F. paulensis*. Heterozygote deficiencies are common in marine invertebrates (Hare *et al*., 1996), and could indicate

Table 3 - Gene frequencies and sample sizes (N) at 14 loci and 15 populations of Brazilian shrimp species. H_o, H_e: observed and expected heterozygosities, respectively.

Locus	*L. schmitti*					*Farfantepenaeus* sp.			*F. brasiliensis*				*F. paulensis*		
	Atins	Fortaleza	Recife	Rio	Itajaí	Fortaleza	Recife	Ilhéus	Fortaleza	Ilhéus	Rio	Itajaí	Rio	Santos	L. Patos
Ak															
(N)	(11)	(22)	(33)	(20)	(33)	(17)	(29)	(33)	(63)	(33)	(48)	(30)	(22)	(27)	(38)
A	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0	0
B	1	1	1	1	0.98	0	0	0	0	0	0	0	0	0	0
C	0	0	0	0	0	0.03	0	0	0.02	0	0	0	0	0	0
D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E	0	0	0	0	0	0.97	1	1	0.98	1	1	1	1	1	1
Idh															
(N)	(38)	(24)	(35)	(34)	(35)	(15)	(30)	(49)	(77)	(33)	(48)	(30)	(22)	(27)	(40)
A	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0
B	1	0.98	1	1	1	1	1	1	1	1	1	1	1	1	1
Ldh															
(N)	(38)	(24)	(35)	(34)	(35)	(17)	(30)	(49)	(80)	(33)	(48)	(30)	(22)	(27)	(40)
A	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0
B	1	0.98	1	1	1	1	1	0.99	1	1	1	1	1	1	1
C	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0
Mdh-1															
(N)	(38)	(25)	(35)	(34)	(35)	(17)	(30)	(49)	(80)	(33)	(48)	(30)	(22)	(27)	(40)
A	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0.01
B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C	1	1	1	1	1	0.97	1	1	0.98	0.98	1	1	1	1	0.99
D	0	0	0	0	0	0.03	0	0	0.01	0	0	0	0	0	0
E	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0

Table 3 (Cont.)

Locus	*L. schmitti*					*Farfantepenaeus* sp.			*F. brasiliensis*				*F. paulensis*		
	Atins	Fortaleza	Recife	Rio	Itajaí	Fortaleza	Recife	Ilhéus	Fortaleza	Ilhéus	Rio	Itajaí	Rio	Santos	L. Patos
Mdh-2															
(N)	(38)	(25)	(35)	(34)	(35)	(17)	(30)	(49)	(80)	(33)	(48)	(30)	(22)	(27)	(40)
A	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
B	0	0	0	0	0	0.09	0	0.01	0	0	0	0	0	0	0
C	0	0	0	0	0	0	0.02	0	0.01	0	0	0	0	0.04	0
D	0	0	0	0	0	0.91	0.98	0.99	0.99	0.98	0.99	1	1	0.96	1
E	0	0	0	0	0	0	0	0	0	0.01	0.01	0	0	0	0
F	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0
Me-1															
(N)	(38)	(25)	(35)	(34)	(35)	(17)	(30)	(49)	(80)	(33)	(48)	(30)	(22)	(27)	(40)
A	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1
B	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
Me-2															
(N)	(38)	(25)	(35)	(34)	(35)	(17)	(30)	(49)	(80)	(33)	(48)	(30)	(22)	(27)	(40)
A	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1
B	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
Mpi															
(N)	(38)	(19)	(35)	(34)	(35)	(16)	(29)	(42)	(67)	(32)	(44)	(30)	(22)	(27)	(40)
A	0	0	0	0	0	0	0.05	0	0	0	0	0.03	0	0	0.05
B	0	0	0	0	0	0.09	0.10	0.16	0.14	0.17	0.15	0.25	0.07	0.06	0.04
C	1	1	0.97	1	0.99	0.88	0.78	0.84	0.75	0.80	0.76	0.65	0.70	0.79	0.64
D	0	0	0.03	0	0.01	0	0.07	0	0.10	0.03	0.07	0.07	0.23	0.15	0.24
E	0	0	0	0	0	0.03	0	0	0.01	0	0.02	0	0	0	0.02
F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
Pep-A															
(N)	(38)	(19)	(34)	(34)	(35)	(16)	(30)	(49)	(74)	(33)	(48)	(30)	(22)	(27)	(26)
A	0	0	0	0	0	0	0	0	0.01	0	0	0	0.09	0	0.29
B	0.99	1	1	1	1	1	1	0.98	0.99	1	1	1	0.89	0.98	0.65
C	0.01	0	0	0	0	0	0	0.02	0	0	0	0	0.02	0.02	0.06
Pep-B															
(N)	(38)	(25)	(35)	(34)	(35)	(17)	(30)	(49)	(80)	(33)	(48)	(30)	(22)	(27)	(26)
A	1	1	0.99	1	1	0	0	0	0	0	0	0	0	0	0
B	0	0	0.01	0	0	0.03	0	0	0	0	0	0	0	0	0
C	0	0	0	0	0	0.97	0.98	1	0	0	0	0	1	1	1
D	0	0	0	0	0	0	0.02	0	0	0	0	0	0	0	0
E	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0
Pgd															
(N)	(38)	(25)	(35)	(34)	(35)	(17)	(30)	(48)	(80)	(33)	(48)	(30)	(22)	(27)	(40)
A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	1	1	1	1	1	0.76	0.67	0.62	0.02	0	0.01	0	0.07	0	0.01
C	0	0	0	0	0	0.24	0.33	0.38	0.98	1	0.98	1	0.93	1	0.98
D	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0.01
Pgi															
(N)	(38)	(25)	(35)	(34)	(35)	(17)	(30)	(49)	(80)	(33)	(47)	(30)	(22)	(27)	(40)
A	0.03	0.02	0	0	0	0	0.02	0.01	0.01	0	0	0	0	0	0
B	0.89	0.98	1	0.96	0.98	0.94	0.70	0.91	0.95	0.98	0.95	0.97	0.84	0.89	0.99
C	0.08	0	0	0.03	0.01	0.06	0.28	0.08	0.04	0.02	0.01	0.03	0	0.11	0.01
D	0	0	0	0.01	0.01	0	0	0	0	0	0.04	0	0.16	0	0
Pgm-1															
(N)	(38)	(25)	(35)	(33)	(35)	(17)	(30)	(49)	(79)	(33)	(48)	(29)	(22)	(27)	(39)
A	0	0	0	0.03	0.03	0	0	0	0	0	0.01	0	0.14	0.11	0.01
B	0.12	0.16	0.14	0.03	0.17	0	0.02	0	0.01	0	0.02	0	0.09	0.11	0.05
C	0.88	0.84	0.83	0.94	0.80	1	0.98	1	0.99	1	0.97	1	0.77	0.78	0.94
D	0	0	0.03	0	0	0	0	0	0	0	0	0	0	0	0
Pgm-2															
(N)	(38)	(25)	(35)	(33)	(35)	(17)	(30)	(49)	(80)	(33)	(48)	(29)	(21)	(26)	(39)
A	0.03	0	0	0	0.07	0	0	0	0.01	0	0.01	0	0.12	0.10	0.05
B	0.97	1	0.99	1	0.92	1	0.98	0.99	0.95	0.97	0.97	0.97	0.86	0.88	0.95
C	0	0	0.01	0	0.01	0	0.02	0.01	0.04	0.03	0.02	0.03	0.02	0.02	0
H_o	0.03	0.03	0.03	0.02	0.03	0.08	0.08	0.06	0.04	0.03	0.04	0.04	0.10	0.07	0.09
H_e	0.03	0.03	0.03	0.02	0.04	0.08	0.10	0.07	0.05	0.04	0.05	0.05	0.12	0.09	0.10

population mixing or a number of actual or artifactual factors (Zouros and Foltz, 1984).

In the same way as observed here, levels of worldwide genetic population structure vary widely between dif-

ferent species of shrimp, so that populations separated by thousands of kilometres can be genetically more similar than others over very short distances (Benzie, 2000). Some authors have suggested that differences between species in levels of genetic variation and genotype distribution might be related to life history types (Mulley and Latter, 1981; De La Rosa-Velez *et al*., 2000). Recently, a major survey of published data indicates that historical events, over large biogeographic scales, may explain the patterns observed better than present day dispersal (Benzie, 2000).

The genetic structure observed in wild populations of *F. notialis* (Espinosa *et al*., 1996; García-Machado *et al*., 2001), *F. californiensis* and of *L. stylirostris* (De La Rosa-Velez *et al*., 2000) as well as those described here for the Brazilian populations of *F. paulensis* and *Farfantepenaeus* sp., does not seem to reflect large biogeographical events but, rather, patterns of present day dispersal. In Cuba, for example, the genetic differences detected between populations of *F. notialis* collected in the Batabanó and the Ana María Gulfs, which are less than 15 km apart, could be due to localized recruitment or to temporal variation in allele frequencies (García-Machado *et al*., 2001). These factors could be directly or indirectly related to the presence of the Calzones Gulf (the deepest in Cuba), which might prevent the movement of larvae and adults.

Further evidence that the patterns of differentiation observed are more likely to reflect present day dispersal, rather than biogeographical patterns in the Brazilian shrimp populations, is that in spite of their different levels of population structuring, the species studied here have quite similar distribution ranges. The two species that did not present any significant population differentiation *F. brasiliensis* and *L. schmitti* occur from the South of Brazil to the Caribbean, and have wide overlapping zones with the distributions of *F. paulensis*, in the South of Brazil, and of *Farfantepenaeus* sp. in Southeast and Northeast Brazil. Thus, the incongruence found between their population structure patterns cannot be attributed to common biogeographic boundaries. Moreover, the observed levels of differentiation among populations of *F. paulensis* and of *Farfantepenaeus* sp. do not seem to indicate a direct correlation with geographic distances (Mantel test, $p > 0.05$).

Instead of biogeographic factors, the observed differences in population structure between the four species studied seem to reflect the differences in their biology. Among Brazilian shrimp species, the periods of reproduction, estuary post-larvae penetration and sub-adult emigration vary depending on the species and even among populations of the same species in different geographical regions (reviewed in Gusmão, 2001). Differences in environmental preferences in relation to water temperature, salinity, sediment type and bathymetry are also observed among species (Holthuis, 1980; Paiva, 1997). For example, *F. paulensis* is found in cold waters where spawning occurs, usually below 50 m depth, and its migration is more related to depth than to latitude (Zenger and Agnes, 1977). *F. brasiliensis* and *L. schmitti*, on the other hand, prefer warmer waters, so that the migration of *F. brasiliensis* is more related to latitude (Zenger and Agnes, 1977).

F. paulensis ranges from Cabo Frio (Rio de Janeiro State - RJ), along the continental shelves of Brazil and Uruguay, to northeast Argentina (Pérez Farfante, 1969; Holthuis, 1980). The main *F. paulensis* offshore fishing area is located between Santos (São Paulo State - SP) and Torres (Rio Grande do Sul State - RS) (Iwai, 1973), but there are two major adult congregation zones: one off Santa Catarina State (SC), and the second between Santos and São Sebastião Island (littoral North of SP; Figure 1) (Zenger and Agnes, 1977; Melquíades, 1997). Important juvenile shrimp populations can be found in the estuaries of Rio Grande do Sul, but no adult breeding grounds are found in the offshore waters of Rio Grande do Sul or Uruguay (Iwai, 1973; Zenger and Agnes, 1977). Data on coastal currents, wind direction and velocity between Florianópolis (SC) and Laguna de Castillo (Uruguay) indicate that the post larvae that populate nursery areas of Lagoa dos Patos and Uruguay may originate in the breeding grounds off Santa Catarina State (D'Incao, 1991). This hypothesis obtained further support from an allozyme study that indicated a high level of genetic homogeneity between populations from both areas (Delevedove, 1996).

The present study shows that the populations of *F. paulensis* from Rio de Janeiro and Santos (Southeast of Brazil) are significantly different from that from Lagoa dos Patos (South). Thus, it is possible that the structuring pattern observed for *F. paulensis* reflects the presence of two breeding populations (stocks) concentrated in different geographic areas along the species range. The Southeastern stock comprises the shrimps living in the Santos/Rio de Janeiro area, and the Southern stock the shrimps from Santa Catarina/Lagoa dos Patos, and perhaps Uruguay.

Unfortunately, there is little information about the biology of *Farfantepenaeus* sp. species, which makes discussing the possible causes of the observed population heterogeneity difficult. In addition, the available information to date is based on the overlap of data about the cryptic species *F. subtilis* and *Farfantepenaeus* sp. (Gusmão *et al.*, 2000). Nevertheless, despite the factors responsible for the observed structuring patterns, the fact that genetically distinct populations exist in *Farfantepenaeus* sp. and *F. paulensis* is clear, and should be taken into account for future aquaculture programs and fisheries management of both resources.

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