

GROWTH PARAMETERS OF THE SPINY LOBSTER (*Panulirus argus*) IN THE GREAT CARIBBEAN: A REVIEW.

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ABSTRACT

The aim of this review is to compare the growth parameters of the spiny lobster (*Panulirus argus*) in three fishery regions: Caribbean Sea, Northern and Brazil. A high variability in the estimates of L_{∞} and K has been observed in the studies of 42 growth parameters in ten locations. The mean size of L_{∞} by sex was significantly different between regions ($P < 0.05$). However, there was no significantly different in parameter K between the sexes ($P = 0.2015$). The results of the nonparametric SNK test demonstrated that average L_{∞} (199.78 mm) of male were highly significant differences ($P < 0.05$) of the average L_{∞} of females in the Caribbean (172.27 mm) and Brazil (142.42 mm) region. The average L_{∞} of Northern region (male and female), female of Caribbean and male of Brazil appear to have come from the same sample. This is perhaps not viable and the reason behind such conclusion is that the multiple range test was not able to determine differences accurately when samples are small ($n=3$). In Northern and Brazil, the occurrence to detect statistical differences between growths parameters was not possible and thus, we decide to calculate the von Bertalanffy growth curve for *P. argus* at this previous regions per sex.

Key words: growth; *Panulirus argus*; ASW, Caribe.

RESUMEN

El objetivo de ésta revisión es comparar los parámetros de crecimiento de la langosta espinosa (*Panulirus argus*) en tres regiones pesqueras: Mar Caribe, región Norte y Brasil. Una elevada variabilidad en los estimados de L_{∞} y K fueron observados en el estudio de 42 parámetros de crecimiento en diez localidades. La talla media de L_{∞} por sexo fue significativamente diferente entre regiones ($P < 0.05$). Si embargo, no hubo diferencias significativas en el parámetro K entre sexos ($P = 0.2015$). Los resultados del test no paramétrico SNK demostró que el valor medio L_{∞} (199.78 mm) de los machos fue significativamente diferente ($P < 0.05$) al valor medio L_{∞} de las hembras en el Caribe (172.27 mm) y Brasil (142.42 mm). El valor medio L_{∞} de la región Norte (machos y hembras), las hembras del Caribe y los machos de Brasil parecen ser que provienen de la misma muestra. Esto quizás no sea probable y la razón de tal conclusión es que la prueba de rangos múltiples no pudo determinar diferencias con precisión cuando las muestras son pequeñas ($n=3$). En la región Norte y Brasil, la ocurrencia de detectar diferencias estadísticas entre los parámetros de crecimiento no es posible así que, nosotros decidimos calcular la curva de crecimiento de von Bertalanffy para *P. argus* en las regiones anteriores por sexo.

Palabras claves: crecimiento; *Panulirus argus*; ASW, Caribe.

The spiny lobster *Panulirus argus* (Latreille, 1804) is the most important fishery resource in the Atlantic. The knowledge of the age and growth of the lobster populations is of great importance for the study of the dynamics of these populations, as well as for the evaluation and more effective administration of the resources natural. *P. argus* growth parameters and age have been studied over the last 50 years in some locations (Cuba, Florida, Bermuda, México, Jamaica and Brazil) in the Great Caribbean.

In crustaceans, the assignment of the age in marine organisms has been carried out by following different methodologies: a) Length frequency distributions (LFDs), which allow

knowing the evolution of cohort and the average size. b) Experiences of mark and recapture (MR), with plastic or electromagnetic tags in adults and microtagging in small lobster, analyzing the size increment between tagging and recapture. c) Laboratory, growth data were obtained study the individuals in captivity.

However, in the case of the crustaceans the main difficulty resides in the impossibility of carrying out reliable estimates of the age and growth by these conventional methods. The moulting is a unique and complicated process and that involved many factors (environmental, nutritional, reproductive, behavioural and physiological) that have influence in the moult phase (Bryars and

Geddes, 2005). A recent molecular approach, well known as “lipofuscin technique”, is perhaps a better predictor of chronological age than body size in various decapods (Sheehy 1990; Sheehy et al. 1994, 1996, 1998).

Aside from reports on the economic and ecological importance of the species in the Atlantic region there have been few integrative/comparative studies concerning growth. FAO (2001) compiled the information from several workshops that have discussed biological and fisheries aspects of *P. argus* in the Great Caribbean region.

The present study has been initiated to expand, on a regional scale, the available information about the growth parameters of both sexes of *P. argus* by obtaining information on the growth of wild animals through mark and recapture (MR) and by length frequency distributions in different geographic areas within the Greater Caribbean region. This approach on estimating the growth parameters in the three principal fishery regions may be useful in forming the basis for developing both short and long-term management strategies.

METHODS

An extensive bibliographic compilation has been made in order to get a wide range of growth values for both sexes for *P. argus* in the Greater Caribbean region. For our purposes, we define the Great Caribbean region (GCR) as the region covering the continental shelf, islands and banks of the Central Western Atlantic and also northeastern Brazil. The three regions considered comprise the main fishing grounds of the species. Those fishing grounds are the Caribbean Sea (limited between Venezuela and south Cuba, and including México, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia and the Lesser and Bigger Antilles); Northern region (between North Cuba and Bermuda, including the Bahamas, Florida, Turks and Caicos); and Brazil (Fig. 1). Comparative values have been taken from local studies of the von Bertalanffy growth curve for *P. argus* using various methods and data from mark-and-recapture experiments and length-frequency analysis.

Some investigators have used total length, which is an inexact measurement, as a measure of size. To allow comparison among studies, total length (TL) measurements were converted to carapace length (CL) using the relationship developed for *P. argus* by Cruz (2002) and designed for the Caribbean

region (males: $CL = -11.7974 + 0.3925 \cdot TL$, and females: $CL = -2.3439 + 0.3374 \cdot TL$). Dos Santos *et al.* (1964) developed the relationships for the Brazilian region (males: $CL = -9.320 + 0.423 \cdot TL$ and females: $CL = -1.255 + 0.366 \cdot TL$). We converted the Caribbean data of Buesa (1965) and Cruz *et al.* (1981), Brazil data of Dos Santos *et al.* (1964) and Ivo (1996) with these equations (Table 1).

The von Bertalanffy growth curve $L_t = L_\infty [1 - \exp[-K(t - t_0)]]$ has been the function used to model the mean growth of spiny lobster (*P. argus*) in the Atlantic. Where L_∞ represent the asymptote, K represents rate of growth, t is time (age) and t_0 is the hypothetical age when size is zero, but in this case, t_0 has been taken at time of puerulus settlement (Phillips *et al.*, 1992). Cruz (2000) reported that puerulus of *P. argus* in artificial collectors have an average size of 5.63 mm (CL) with a size range between 4-6 mm (CL). Then the parameters t_0 was calculated by using the following equation:

$$t_0 = (\ln(L_\infty - L_p) / K),$$

where L_p is the average size of puerulus settlement, considering it has low variability.

The relative age (t) from length-frequencies was calculated by using the inverse von Bertalanffy growth equation:

$$t_L = t_0 - 1/K * \ln(1 - L / L_\infty)$$

All the available data have been organized within each region and a mean growth parameter was estimated for each area by sex and in combination (total). To validate the mean values per region a Phi prime test (Φ'). The relationship is: $\Phi' = \log K + 2 \cdot \log L_\infty$ (Munro and Pauly, 1983; Pauly and Munro, 1984). This test is widely used and is probably the best mean of averaging growth parameters of a particular species (Sparre and Venema, 1997).

Average growth parameters (L_∞ and $K(y^{-1})$) were calculated by sex and regions. The data on average parameters were analysed using a nonparametric ANOVA of Kruskal-Wallis test, with a p-level of 0.05. The dependent variable was average L_∞ (mm) and the variation sources were the regions and the sex (male and female). A second nonparametric ANOVA was carried out testing for differences due to K , by sex and regions. Following the ANOVAs, the nonparametric SNK (Student Newman Keuls test) has been used to evaluate differences among means.



Fig. 1. Map illustrating the three most important fishery regions in the Great Caribbean Region.

Table 1. Comparative values of the von Bertalanffy growth curve and the correspondent Phi prime (Φ') value for *Panulirus argus*, using different methods and data from mark-and-recapture experiments (MR) and length frequency distributions (LFDs), per region. N: number of male and female; K (y^{-1}): parameter K per year; L_{∞} : parameter L-infinity. SW: South Western; SE: South Eastern; NE: North Eastern. NA: not available data. \ominus – not included in the average estimation or in any other statistical treatment.

Region	Male			Female			Range CL mm	Source of Data	Authors
	K (y^{-1})	L_{∞} (mm)	Φ'	K (y^{-1})	L_{∞} (mm)	Φ'			
Cuba, SW	0.150	165.22	3.6	0.165	147.80	3.6	(NA)	LFDs (NA)	Buesa, 1965
Cuba, SW	0.220	169.00	3.8	0.310	139.00	3.8	30-160	LFDs (N=200457)	Cruz et al., 1981
Cuba, SW	0.289	250.00	4.3	0.305	209.00	4.1	20-175	MR (N=1065)	Baéz et al., 1991
Cuba, SW	0.197	175.00	3.8	0.219	151.00	3.7	25-175	LFDs (N=241468)	Baéz et al., 1999
Cuba, SW	0.270	250.35	4.2	0.391	170.95	4.1	25-125	MR (N=1088)	Phillips et al., 1992
Cuba, SW	0.313	190.00	4.1	0.235	175.00	3.9	22-197	LFDs (N=125050)	León et al., 1994
Cuba, SW	0.236	184.35	3.9	0.182	154.59	3.6	15-225	LFDs (N= 291072)	León et al., 1995
Cuba, NW	0.224	175.01	3.8	0.216	166.02	3.8	15-205	LFDs (N= 291072)	León et al., 1995
Cuba, SE	0.221	185.59	3.9	0.219	156.21	3.7	15-225	LFDs (N= 291072)	León et al., 1995
Jamaica	0.240	210.00	4.0	0.280	195.00	4.0	55-177	LFDs (N=9966)	Haughton and King, 1992
Martinique	0.250	190.00	4.0	0.234	187.60	3.9	40-136	LFDs (N=877)	Clairovin, 1980
México	0.260	198.40	4.0	0.220	164.90	3.8	56-172	LFDs (N=43821)	González-Cano, 1991
México	0.246	216.57	4.1	0.220	176.43	3.8	60-160	LFDs (N=43821)	González-Cano and Rocha, 1995
México	0.204	257.20	4.1	0.248	215.61	4.1	10-142	MR (N=1252)	Lozano-Alvarez et al., 1991
Colombia	0.260	180.00	3.9	0.230	175.00	3.8	(NA)	LFDs (NA)	Gallo et al., 2001
Cuba SW \ominus	0.219	289.66	-	0.511	144.17	-	25-125	MR (N=1088)	Phillips et al., 1992
Jamaica \ominus	0.530	193.00	-	0.480	184.00	-	46-162	LFDs (NA)	Haughton and Shaul, 1989
Virgen Is. \ominus	0.436	153.00	-	0.319	133.00	-	37-178	MR (N=102)	Olsen and Koblic, 1975
Nicaragua \ominus	0.230	168.78	-	0.399	159.51	-	(NA)	LFDs (NA)	Calero and Cadima, 1993
Average	0.239	199.78	3.97	0.245	172.27	3.85			
Stand Desv.	0.0395	30.6564		0.0565	22.0949				

Table 1. Continuation. Comparative values of the von Bertalanffy growth curve and the correspondent Phi prime (Φ') value for *Panulirus argus*, using different methods and data from mark-and-recapture experiments (MR) and length frequency distributions (LFDs), per region. N: number of male and female; K (y^{-1}): parameter K per year; L_{∞} : parameter L-infinity. SW: South Western; SE: South Eastern; NE: North Eastern. NA: not available data. \ominus – not included in the average estimation or in any other statistical treatment.

Region	Male			Female			Range CL mm	Source of Data	Authors
	K (y^{-1})	L_{∞} (mm)	Φ'	K (y^{-1})	L_{∞} (mm)	Φ'			
Northern									
Bahamas	0.256	190.00	4.0	0.222	190.00	3.9	50-76	MR (NA)	Waugh, 1981
Bermudas	0.180	204.00	3.9	0.150	192.00	3.7	(NA)	LFDs (N=1000)	Evans, 1988
Cuba, NE	0.226	185.00	3.9	0.192	153.46	3.7	15-225	LFDs (N= 291072)	León et al., 1995
Average	0.221	193.00	3.93	0.188	178.49	3.77			
Stand Desv.	0.022	5.686		0.021	12.527				
Brazil									
Brazil, NE	0.340	141.00	3.8	0.380	148.00	3.9	63-132	LFDs (N=22000)	Dos Santos et al., 1964
Brazil, NE	0.236	182.299	3.9	0.234	154.295	3.7	(NA)	LFDs (NA)	Ivo, 1996
Brazil, NE	0.260	207.20	4	0.230	124.97	3.6	50-122	LFDs (NA)	González-Cano and Rocha, 1995
Average	0.279	176.83	3.9	0.281	142.42	3.7			
Stand Desv.	0.031	19.305		0.049	8.913				

Confidence intervals (95%) for the growth parameters average were calculated by sex and regions using equations: $X \pm t_{0.05}(\alpha, v) \sqrt{s^2/n_1}$. Where X = growth parameter average, $t_{0.05}$ = critical values of the t distribution for 95% confidence interval, $\alpha = 2$, v = error degrees, s^2 = error mean square and n_1 = number of data (Zar, 1996).

RESULTS

Comparative values of the von Bertalanffy growth curve for each fishing region of the spiny lobster *P. argus* calculated by different methods, using length frequency and tagging data, have been showed in Table 1. High variability in the estimates of L_{∞} and K is evident. The number of lobsters used in each analysis by region is also very variable and the sex ratios (1:1) were not significantly different, except in the information of Olsen et al. (1975), 64 males and 38 females.

The Fig. 2 and 3 illustrate a wide range of growth estimates have been obtained in the three studies regions. The biggest variability was observed in the results of Cuba SW \ominus , Jamaica \ominus , Virgin Island \ominus and Nicaragua \ominus . A set of 42 growth values were included in the statistical treatment, where parameter K (y^{-1}) ranged from 0.15 to 0.34 for males and from 0.15 to 0.391 for females. The parameter L_{∞} of male (ranged 141 to 257 mm) is bigger than the females (ranged 125 to 215 mm) with the exceptions of the first growth parameters estimation of Bahamas (L_{∞} male = L_{∞} female) and

northeast of Brazil (L_{∞} male < L_{∞} female) in 1981 and 1964 respectively. All the Φ' values calculated presented a high value (3.6 to 4.3) and narrow amplitudes of fluctuation within each region (3.7 to 3.97), making validation of mean growth values per region possible (Table 1).

The mean size of L_{∞} by sex was significantly different between regions (Kruskal Wallis test, $H_1 = 12.96$, $df = 5$, $N = 42$, $P < 0.05$). However, there was no significantly different in parameter K between the sexes ($P = 0.2015$). The results of the SNK test demonstrated that average L_{∞} of male were highly significant differences ($P < 0.05$) of the average L_{∞} of females in the Caribbean and Brazil region. The average L_{∞} of Northern region (male and female), female of Caribbean and male of Brazil appear to have come from the same sample (Fig. 4). This is perhaps not viable and the reason behind such conclusion is that the multiple range test was not able to determine differences accurately when samples are small ($n=3$). Increasing the number of data the analysis could be more capable of locating differences among means.

In Northern and Brazil, the occurrence to detect statistical differences between growths parameters were not possible and thus, we decide to calculate the von Bertalanffy growth curve for *P. argus* at this previous regions per sex (Fig. 5). With these parameters, the total mean carapace length (CL_t mm) of lobster at age t (in years after settlement) is give by the followings equations:

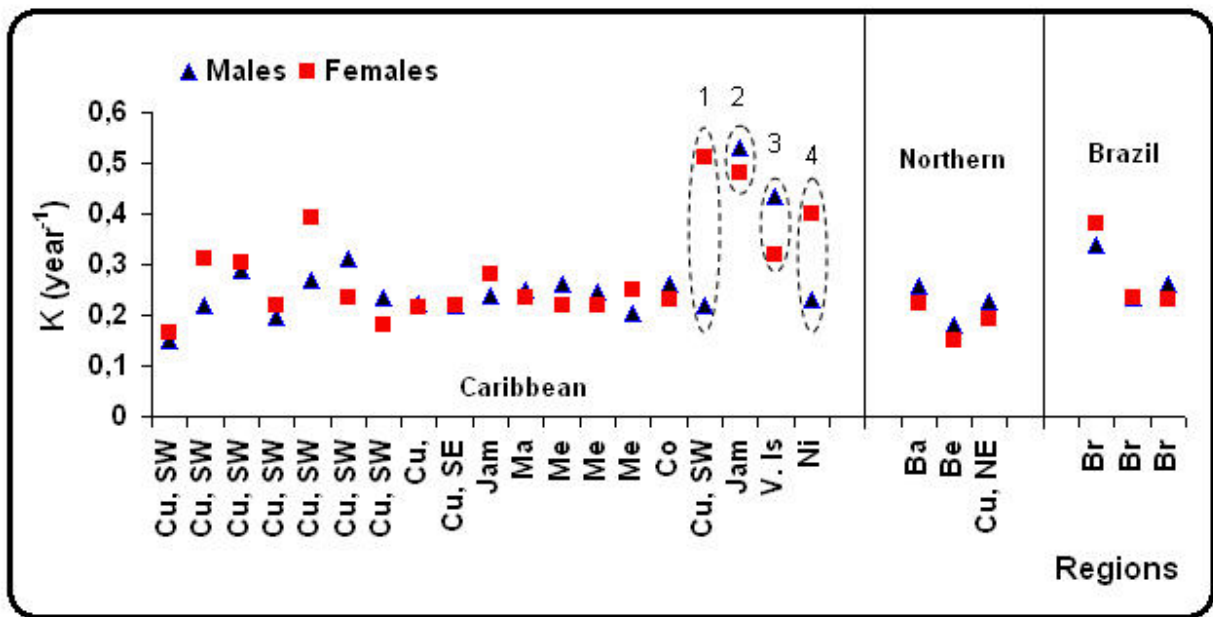


Fig. 2. Available growth estimates of K (y^{-1}) parameter for *Panulirus argus* from local studies within the Great Caribbean region, where the excluded values are marked by a discontinue circle. Regions: Cu (Cuba); Ma. (Martinique); Me. (México); Co. (Colombia); V. Is. (Virgin Islands); Jam. (Jamaica); Ni. (Nicaragua); Be. (Bermudas); Ba. (Bahamas); Br. (Brazil). SW: South Western; SE: South Eastern; NE: North Eastern. Θ (1,2,3,4) not included in the average estimation or in any other statistical treatment.

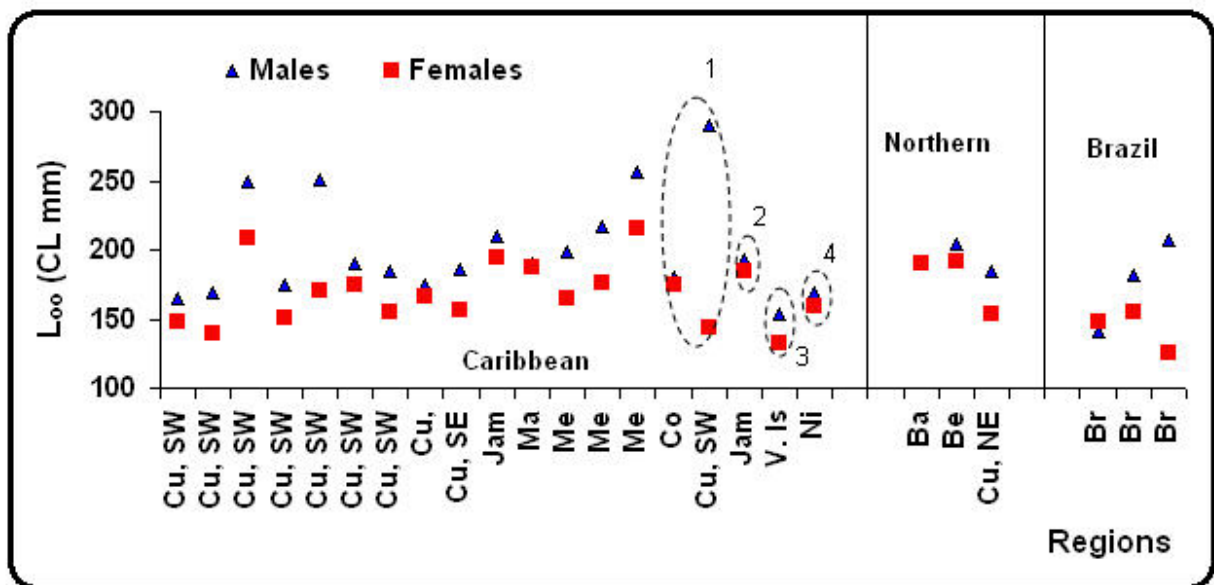


Fig. 3. Available growth estimates of L_{∞} (CL, mm) parameter for *Panulirus argus* from local studies within the Great Caribbean region, where the excluded values are marked by a discontinue circle. Regions: Cu (Cuba); Ma. (Martinique); Me. (México); Co. (Colombia); V. Is. (Virgin Islands); Jam. (Jamaica); Ni. (Nicaragua); Be. (Bermudas); Ba. (Bahamas); Br. (Brazil). SW: South Western; SE: South Eastern; NE: North Eastern. Θ (1,2,3,4) not included in the average estimation or in any other statistical treatment.

Caribbean: $CL_t = 186.03 [1 - \text{EXP}(-0.280(t + 0.115))]$

Northern: $CL_t = 185.74 [1 - \text{EXP}(-0.204(t + 0.137))]$

Brazil: $CL_t = 159.63 [1 - \text{EXP}(-0.204(t + 0.137))]$

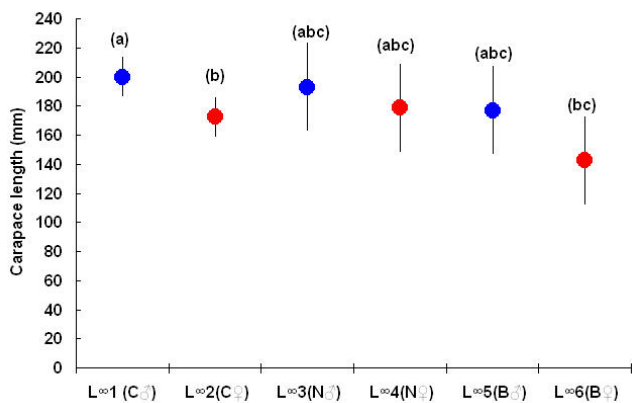


Fig. 4. Mean growth estimates of L_∞ (CL, mm) and K (y^{-1}) by sex and regions and 95% confidence limits per parameters. Different letters means significant differences ($P < 0.05$). C: Caribbean, N: Northern and B: Brazil.

DISCUSSION

During the analyses, an effort has been made to minimize potential errors. Thus, some growth parameters have been excluded for the estimation of a mean growth value per region because some estimates have been established with low accuracy (Table 1; Fig. 2 and 3). Data from Phillips *et al.* (1992), where the method used to fit the curve is that of Fabens that can not be applied to *P. argus* as it overestimates K and underestimates L_∞ (Chien and Condrey, 1987). Also excluded were data from Haughton and Shaul (1989), where the authors recognized that the values were estimated with low precision. In the case of Olsen and Koblic (1975), the Fabens method was used and the number of individuals sampled was low ($N = 102$), so the data were not included in our analysis. The study of Calero and Cadima (1993) has been excluded because of a lack of information corroborating the growth estimates.

The growth rate by sexes of *P. argus* has been studied in detail by several authors, using different methodologies. As pointed out by González-Cano and Rocha (1995), the comparison of growth estimates becomes difficult when different methods have been used for each set of data. In this case,

the nature of the length frequency distributions (LFDs), that in some situations simply cover a narrow length distribution range in addition to the sample size and the methodology used (Table 1). Thus, it would not be surprising to find that differences in growth are in reality due to the method employed and to the type of information submitted for analyses. Munro (1974) suggests that the early estimate in *P. argus* by Travis (1954) and Buesa (1965) indicate much slower growth.

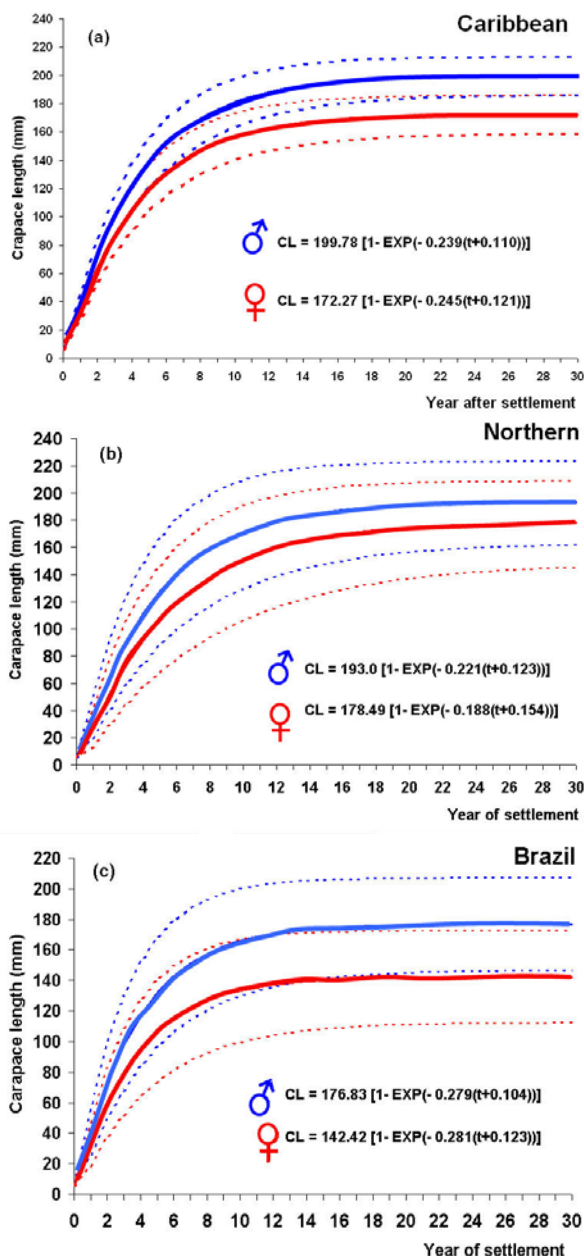


Fig. 5. Mean growth curves (with 95% confidence limits) for males and females of *Panulirus argus* in the Caribbean (a), Northern (b) and Brazil (c) region.

Many estimates of growth parameters have been calculated for *P. argus*, but growth vary markedly between localities because local variability in food abundance, population density, predatory attacks (inducing injuries) and water temperature, may affect the growth rates of the spiny lobsters (Aiken, 1980; Cruz et al., 1981; Marx and Herrnkind, 1986; Phillips *et al.*, 1992). However, the variation of L_{∞} by regions in *P. argus* is consistent with the large sized lobster (males and females) catch by the fishery.

The Phi' index between sexes or areas cover a relatively narrow range and the growth estimates are reasonably good. Males grow better than females on average and growth rates in Cuba archipelago are reasonably similar to other areas. The estimates of 4.2 and 4.3 for males might suggest that those growth parameters are a bit high for those sex or areas (Table 1). We expect low values of Phi' in areas where conditions are not good (e.g. polluted areas) and high values in very favourable environments (e.g. with good food supplies, low stock densities, etc) (Munro, pers. comm.).

Using the inverse von Bertalanffy growth equation in the Caribbean and an average recruited length of 76.8 mm CL (Cruz et al., 2001) to the lobster fishery, we calculated an age of 2.14 years after settlement and 2.8 years after spawning. The estimate in the present study is very closer to the field data of 2.3 years after spawning (Cruz et al., 2001). In the Northern region with a recruited length of 76.2 mm CL (Davis and Dodrill, 1980), their estimated was 3.21 years after spawning and is over the range of the field data, between 1.5–2 years, estimated in the Florida keys (Forcucci et al., 1994; Butler and Herrnkind 1997). When the calculated age-size data is used as a reference point, the estimates of one year after settlement between 40-50 mm CL given by Witham (1968), Eldred et al. (1972) and Ting (1973) are high in relation with the present study (35.6 mm CL).

The growth differentiation between individuals from Brazil and the regions above it revealed in the present study shows an interesting point. There are few studies comparing Brazilian populations to others. Although, the study of drive cards that remain in northeast of Brazil (Richardson, 1987), the oceanic simulation model of Patti et al. (2000) that postulate a strongly anticyclonic vortexes on the current in the same area, as well as genetic evidence that they have been suggested by Sarver *et al.* (1998) suggests strong evidence that Brazil is

a close metapopulation with a minimal connectivity.

Our results have implications for the study of growth through LFDs distributions. The time between successive samples must be designed to confidentially identify the same cohort in successive samplings periods. For this purpose, standard methodology should be applied. Fonteles-Filho (2000) and Cruz (2000) defend the importance of a minimum sampling size, of at least 200-250 individuals, covering a wide range of sizes. Phillips *et al.* (1992) suggests that the technique of microtagged in postpuerulus and early juveniles as a useful approach to obtaining better growth data on spiny lobster

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