

# Population Dynamics for Spiny Lobster *Panulirus argus* in Puerto Rico: A Progress Report

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## ABSTRACT

Estimates of growth and mortality parameters for the spiny lobster *Panulirus argus* were estimated from length frequency data collected from Puerto Rico commercial biostatistical program from 1999 through 2000 using the FISAT software package. The corresponding values of  $L_{\infty}$  for female spiny lobsters using ELEFAN I ranged from 185 to 191 mm CL, and K values were 0.23 to 0.25. For males the  $L_{\infty}$  values ranged from 195 to 197 mm CL, and K value was estimated at 0.24 for both years. The length-converted catch curve total mortality Z estimates ranged from 1.32 to 1.35 for males and from 1.25 to 1.85 for females. The Z estimated from Jones length cohort analysis ranged from 1.01 to 1.02 for males and from 1.05 to 1.11 for females. Average exploitation ratios from the two different methods were well above the optimum exploitation rate ( $E = 0.5$ ) suggesting overfishing. The Beverton relative yield per recruit model analysis for 2000 for males and females implies the Puerto Rico lobster fishery is operating very close to its Maximum Sustainable Yield (MSY) level and that no further increase in fishing effort is advisable.

KEY WORDS: Growth, mortality, *Panulirus argus*

## INTRODUCTION

The Caribbean spiny lobster (*Panulirus argus*) is a valuable exploited marine crustacean inhabiting shallow shelf waters off the Caribbean region, the southern United States and Bermuda. In Puerto Rico, spiny lobster is harvested principally by traps and diving. About 15 % of Puerto Rico catch comes from the east coast, 45 % from the south coast and 35 % from the from the West Coast. The spiny lobster has consistently ranked as the most economically important marine shellfish species landed in Puerto Rico. Based on data from the Puerto Rico Department of Natural and Environmental Resources Fisheries Laboratory, for the period 1992 through 1998, spiny lobster value per pound ranged from 4.50 to 9.00 dollars (Matos 1999).

Spiny lobster management in Puerto Rico has been conducted under territorial and federal jurisdictions with a fishery management plan (FMP) administered by the Caribbean Fishery Management Council (CFMC). Indications of overfishing were observed in the US Caribbean during the early 1980s (CMFC 1985). The established regulations are:

- i) A minimum size of 89 mm in carapace length;

- ii) A prohibition against retaining egg-bearing lobsters;
- iii) A requirement to land lobster whole, and
- iv) Gear restrictions prohibiting the use of poisons, drugs or other chemicals as well as spears, hooks explosives, or similar devices in harvesting spiny lobsters.

Due to concerns caused by the intensive exploitation of the resource, the Puerto Rico spiny lobster fishery and biological data have been periodically re-examined by the National Marine Fisheries Service (NMFS), Southeast Fisheries Science Center (Bohnsack et al. 1992, Bolden 2001). However, problems with data collection and database management procedures, have so far limited the types of analyses that were possible to provide sound stock assessment of this species.

This study attempts to evaluate the use of length frequency analysis based upon biostatistical data from the Puerto Rico commercial lobster fishery to estimate growth and mortality parameters, and to construct a reliable yield per recruit analysis.

## METHODS

Biostatistical data of *P. argus* were collected by port agents from 1999 to 2000. Carapace length (CL) was measured to the nearest 0.1 mm and sex was determined. The sample size per month ranged from 0 to 137 individuals. Biostatistical data were entered into the Trip Interview Program (TIP) developed by the National Marine Fisheries Service (NMFS), Southeast Fishery Science Center. Later, the data were converted and analyzed in Excel. To enhance modal definition for length frequency analysis, samples were pooled trimonthly for each year and assigned a single collection date.

### Estimation of Growth Parameters and Mortality

Analysis of growth parameters assumes von Bertalanffy growth:  $L_t = L_\infty (1 - e^{-kt})^{\frac{1}{\psi}}$ , where  $L_t$  is the carapace length at time  $t$ ,  $L_\infty$  is the asymptotic length an individual would reach if it lived indefinitely, and  $k$  is the rate at which  $L_\infty$  is approached. The growth parameters  $L_\infty$  and  $K$  were estimated using ELEFAN I from the FISAT software package (Gayaniolo et al. 1995). Comparisons of different estimates of growth parameters were done using the empirical equation of Pauly and Munro (1984):  $\phi = \text{Log}_{10} K + 2 \text{Log}_{10} (L_\infty)$ . Recruitment patterns for males and females were estimated using the ELEFAN II from the FISAT program.

Instantaneous total mortality ( $Z$ ) (Beverton and Holt 1957), fishing mortality ( $F$ ) and length at first capture ( $L_c$ ) were calculated using length-converted catch curve (Ricker 1975, Pauly 1984), and Jones length cohort analysis (Jones 1984). These analyses were performed by converting the data of each monthly sample to percent frequency and then weighting by square roots of the sample size. Giving all monthly samples equal weight prevents a single large monthly sample from being a major source of bias or from overly affecting the total annual sample. Since estimates of natural mortality ( $M$ ) of spiny lobster for Puerto Rico are unknown,

we are using estimates from literature for subsequent analysis ( $M = 0.34$ ) CFRAMP/FAO Spiny Lobster Stock Assessment Workshop (CFRAMP 1997). Exploitation rates were calculated with the Pauly and Soriano (1986) exploitation rate formula:  $E=F/Z$ . Yield per recruit analyses were conducted using Beverton and Holt yield/recruit relative ( $Y'/R$ ) and biomass/recruit relative ( $B'/R$ ) models (Beverton and Holt 1957).

## RESULTS

### Size Distribution

During the period of 1999 - 2000, 2,137 lobsters were measured, of which 1,037 were males and 1,100 females. The size range for males was from 62 mm to 216 mm CL whereas the size range for females was from 60 mm to 152 mm CL. The mean CL for males and females were 103.3 mm and 98.3 mm, respectively. The modes of the length frequency distribution for males and females were 89 mm and 90 mm, respectively (Figure 1). Twenty three percent and 17 % of all females and males, respectively, measured from 1999 to 2000 were below the minimum legal size (89.5mm). Figure 2 shows the recruitment patterns of *P. argus* males and females. Year round recruitment with a single peak was observed for both males and females around summer.

### Growth and Mortality Parameters

The estimated values of  $L_{\infty}$  for females ranged from 185 to 191 mm CL (Table 1), and K values ranged from 0.23 to 0.25. For males the  $L_{\infty}$  values ranged 195 to 197 mm CL, and K values were estimated at 0.24. Females had higher good fitness indices ( $R_n$ ) of ELEFAN I.

The length-converted catch curve estimates ranged from 1.32 to 1.35 for males and from 1.25 to 1.85 for females (Table 2). Length at first capture ( $L_c$ ) for males was around 88 mm and for females it ranged from 86.3 to 87.4 mm. The Z estimated from Jones length cohort analysis ranged from 1.01 to 1.02 for males and from 1.05 to 1.11 for females (Table 2). The exploitation ratios from length converted catch curve were between 0.74 - 0.75 for males and 0.73 - 0.82 for females. Whereas, exploitation rates from Jones length cohort analysis were around 0.66 for males and 0.68 to 0.71 for females. Average exploitation ratios from the two different methods were well above the optimum exploitation rate ( $E = 0.5$ ) suggesting that Puerto Rico spiny lobster is fully exploited.

The mean fishing mortalities obtained Jones length cohort analysis for fully recruited length groups were around 0.67 - 0.68 for males while 0.71 - 0.94 for females, respectively. Mortality estimates from Jones length cohort analysis were used for the yield per recruit analysis since length catch curve methods tend to overestimate mortality parameters due to variable recruitment and migration of larger specimens (Baisre and Cruz 1994).

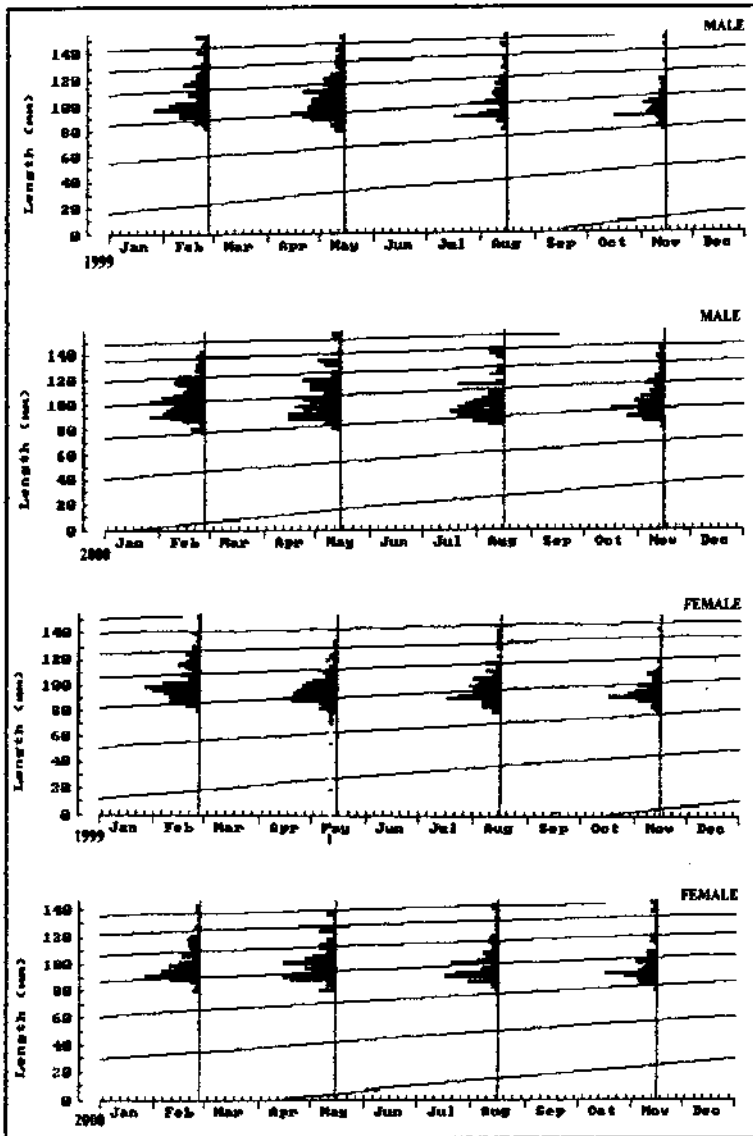


Figure 1. Length frequency distribution of the spiny lobster *Panulirus argus*, male and female, by year and von Bertalanffy growth curves produced by ELEFAN I.

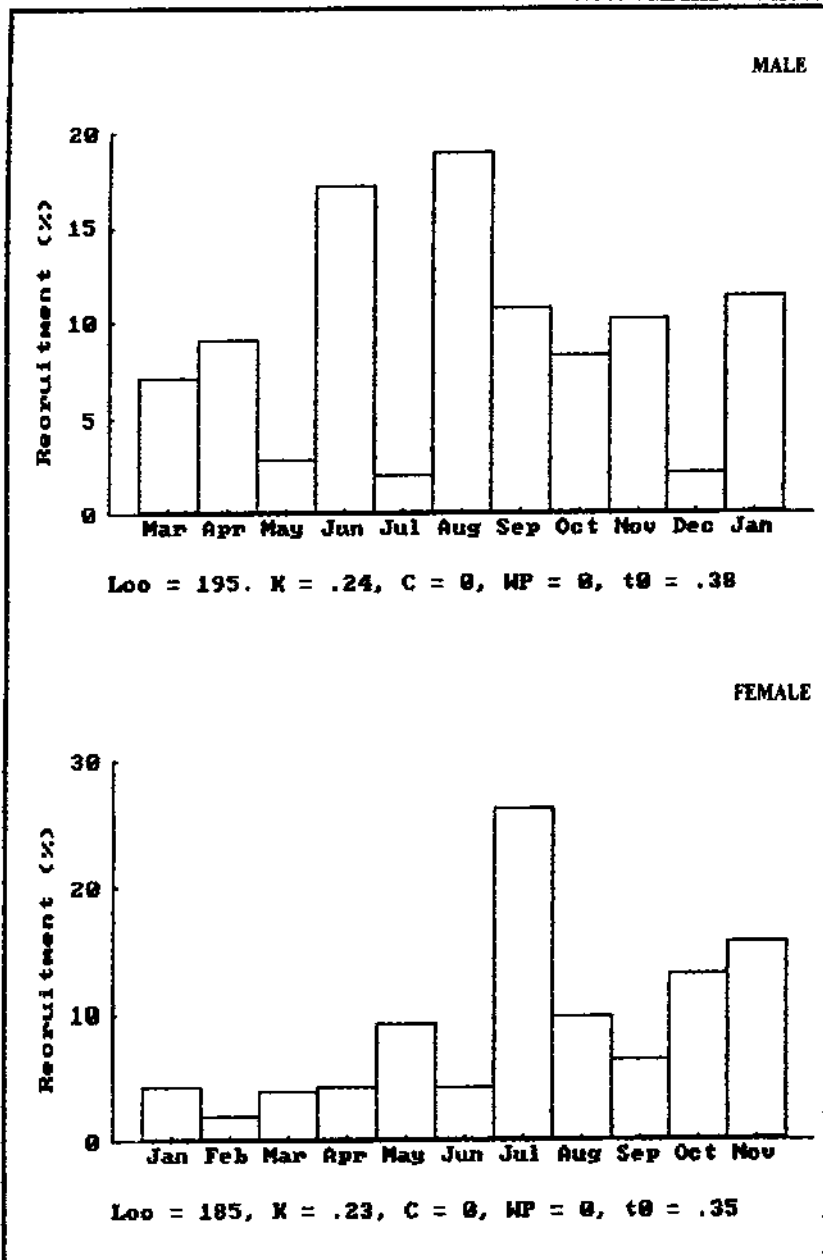


Figure 2. Recruitment patterns for *Panulirus argus*, male and female, for year 2000.

**Table 1.** Estimates of length (L<sub>∞</sub>), body growth rate (K), goodness of fit index (Rn), age at birthday (T0) and growth performance index j (phi) by sex for the spiny lobster, Puerto Rico using ELEFAN I.

Sex/Parameters		L <sub>∞</sub>	K	Rn	T0	j (phi)
Male	1999	197	0.24	0.129	0.38	3.96
	2000	195	0.24	0.138	0.38	3.96
Female	1999	191	0.25	0.142	0.29	3.96
	2000	185	0.23	0.139	0.28	3.89

**Table 2.** Estimation of fishing mortality (F), exploitation ratio (E = F/Z), and length at first capture (Lc) by sex using Length Catch Curves and Jones length cohort analysis for the spiny lobster, Puerto Rico.

Sex/Parameter		Length Catch Curve			Jones Length Cohort Analysis				
		Z	F	E	Lc	Z	F	E	Lc
Male	1999	1.32	0.98	0.74	88.02	1.02	0.68	0.66	87.96
	2000	1.35	1.01	0.75	88.35	1.01	0.67	0.66	88.05
Female	1999	1.85	1.51	0.82	87.70	1.11	0.94	0.73	87.45
	2000	1.25	0.91	0.73	86.25	1.05	0.71	0.68	86.25

### Yield Estimates

The Beverton and Holt relative yield per recruit model for males in 2000 implies that with values of  $E = 0.66$  and  $L_c = 88.05$  mm the current lobster fishery is harvesting approximately near 95.6 % of the potential yield (Figure 3). Likewise, the analysis for females show that with a value of  $E = 0.68$  and  $L_c = 86.2$  mm the fishery is harvesting 94 % of the potential yield in females (Figure 3). The results also indicate that the current levels of fishing pressure have not exceeded the maximum sustainable levels. The  $E_{MSY}$  (exploitation rate at its maximum sustainable yield) for males and females (0.69 and 0.72, respectively) have not been surpassed by the current exploitation ratios (0.66 and 0.68).

### DISCUSSION

Information on the general life history, as well as on growth rates, size frequencies, mortality rates, abundance indices and other parameters is paramount for effective fishery management of economically important species in Puerto Rico. Previous this study, no specific estimates of growth and mortality parameters existed for spiny lobsters from Puerto Rico.

On the last spiny lobster stock assessment workshop held by the Caribbean Fishery Management Council, the scientific panel attempted to build reliable yield per recruit analysis models using length frequency data from Puerto Rico commercial biostatistical data (Bohnsack et al. 1992). However, reliable estimates of growth parameters such as  $L_{\infty}$  (asymptotic length) and K (body growth coefficient) were unsuccessfully estimated for various reasons: data were limited and carapace measurements were to the nearest one tenth inch, which was too wide an interval to show distinct size frequency peaks.

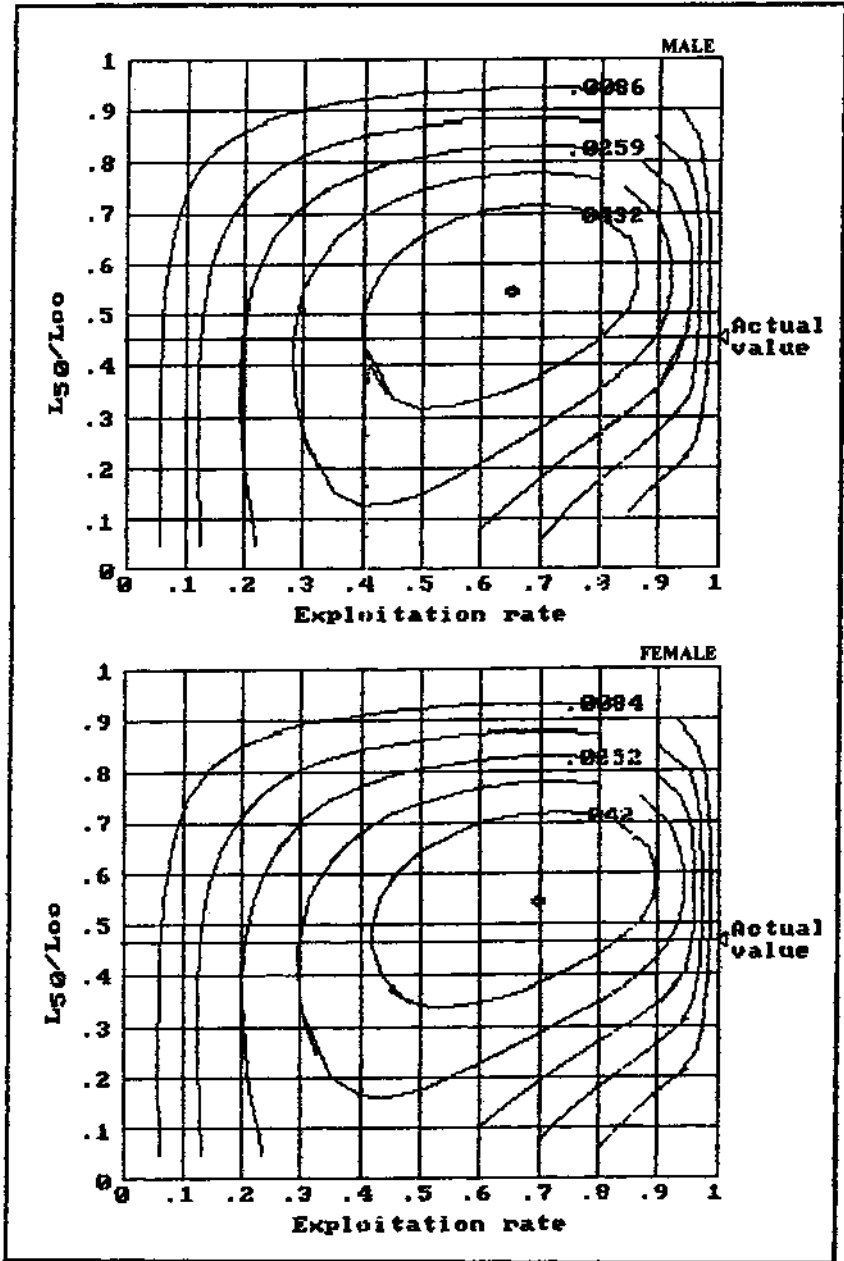


Figure 3. Yield per recruit isopleth for *Panulirus argus*, male and female, as a function of exploitation ratio (E) and size at first capture relative to asymptotic length ( $L_{50}/L_{\infty}$ ).

Growth rate is the most studied aspect of spiny lobster biology. However, accurate growth estimates are problematic due to the difficulty of separating the two main processes that affect spiny lobster growth: molting frequency and growth increment per molt. In general, the average growth rate for *Panulirus argus* of 5 - 8 mm increase in CL per month and there are four molts per year (Munro 1974; Lipcius 1985).

There are also artifacts when fitting spiny lobster growth through a von Bertalanffy growth function. The von Bertalanffy growth model simply describes the average growth of a spiny lobster cohort rather than the growth of an individual lobster which would be represented by a stepwise curve as a consequence of the moulting process (Haughton and King 1992). In addition, the model does not describe growth during larval stages. Nevertheless, it is still widely used to model spiny lobster growth although there is growing evidence that empirical growth models using moult increment and moult interval allow a better data interpretation (Baisre and Cruz 1994, Zetina and Rios 2001).

Growth curves estimated from ELEFAN I represented a rather poor fit to the peaks in the length frequency data. The goodness of fit ( $R_n$ ) ranged from a minimum of 0.129 to a maximum of 0.142. The relatively poor fit of the growth curves suggested multiple recruitment pulses probably as a result of spawning year all round.

Estimates of growth parameters from elsewhere in the Caribbean indicate that *P. argus* is long lived, slow growing and has low rates of natural mortality (Munro 1974, Clairouin 1980, Lozano et al. 1991, Phillips et al. 1992, Haughton and King 1992, Leon et al. 1995). However, there are several discrepancies when comparing growth rates by gender. Cruz and de Leon (1991), Lozano et al. (1991), Castano and Cadima (1993), and Ivo (1996) estimated higher K values for females, whereas other studies report females with lower growth rates than males (Olsen and Koblitz 1975, Waugh 1981, Gonzalez-Cano 1991, Leon et al. 1995, Gonzalez-Cano and Rocha 1995, and Mateo and Tobias 2002).

Table 3 gives estimates of growth parameters for *P. argus* from different parts of the Caribbean. Growth coefficients from *P. argus*, sexes combined, are generally low ranging from 0.16 to 0.45. Estimates of  $L_\infty$  have been reported to vary from 154 to 225 mm. The estimate of growth performance index (3.96) from *P. argus* males for year 2000 lie well within a 95 % confidence interval (3.90 - 4.02) of phi ( $\phi$ ) based on a mean of 3.96 (SE = 0.03). Similarly, the 2000 estimate of growth performance index for females using ELEFAN I (3.89) lie well within a 95 % confidence interval (3.77 - 3.91) of phi based on a mean of 3.84 (SE = 0.03).

Mortality estimates in *P. argus* are also difficult to obtain due to the lack of accurate age-based data (Baisre and Cruz 1994). Crustaceans have no permanent hard body parts, such as fish otoliths or molluscan shells, to carry a record of seasonal or annual changes in growth rates allowing actual ageing or validation of indirect ageing methods to take place. Age-based assessments of *P. argus* stocks are therefore hampered because, the calcified exoskeleton is shed at ecdysis leaving



no hard bony tissue from which annual ring markings can be distinguished. Mark and recapture methods often tend to overestimate growth and mortality parameters in panuliruds due to different sources of biases (ie higher probability of recapture of tagged individuals, loss of tags, nonreporting of recaptures, etc) (Baisre and Cruz 1994). As a result, the fitting of normal curves to polymodal length-frequency distributions appears to be the most promising means available. Size frequency distributions in animal populations are often polymodal, each mode representing an individual cohort. By separating these distributions into their component size classes, changes in position of these modes over time allow a population growth curve to be produced (Bhattacharya 1967). In *P. argus*, this method has moderate application due to the variability in individual growth; coupled with a slowing down in rates of growth in the older age classes, especially mature females (Haughton and King 1992).

Likewise, the migratory behavior of the spiny lobster can potentially give biased estimations of mortality. It is generally accepted that lobsters gradually migrate to deeper waters as they grow older. If lobsters migrate from the fishing grounds into deeper waters where they are inaccessible to fish traps and divers, such migrations would be incorporated in the total mortality value  $Z$  which therefore would be overestimated as well as the fishing mortality and exploitation ratios (Baisre and Cruz 1994).

Total mortalities ( $Z$ ) from length catch curves ranged from 1.32 to 1.35 for males and 1.25 to 1.85 for females. These mortality estimates are more in agreement with data using length based methods from other highly exploited lobster populations in the region such as those of the Bahamas:  $Z = 1.44$  (Waugh 1981); Jamaica:  $Z = 2.19$  males, 2.88 females (Haughton and King 1992); Florida:  $Z = 2.59$  (Warner et al. 1977),  $Z = 4.09$  (Lyons et al. 1981),  $Z = 1.18$  (Powers and Bannerot 1984),  $Z = 1.85$  (Powers 1985); Brazil:  $Z = 1.27$  (Fonteles-Filho 1994), Cuba:  $Z = 1.9-2$  (Baisre and Cruz 1994), and St Croix, USVI:  $Z = 1.24-1.91$  males, 0.8-1.58 females (Mateo and Tobias 2002).

However, average  $Z$  from Jones length cohort analysis for males ranged from 1.01 to 1.02 while females average instantaneous mortalities ranged from 1.05 to 1.11. These values are similar with other lobster stock assessment studies using length/age structured methods such as in Florida:  $Z = 1.09$  for females,  $Z = 1.19$  for males (Muller et al. 1997); Mexico:  $Z = 0.95$  (Zetina and Rios 1998); St. Kitts:  $Z = 1.09$  (Goodwin et al. 1986) and St Croix, USVI:  $Z = 0.83-1.13$  males, 0.72 - 0.83 females (Mateo and Tobias 2002).

Exploitation rates from males and females calculated from all methods were greater than the accepted optimum level of 0.5 (Pauly and Soriano 1986) and suggest that spiny lobster fishery in Puerto Rico is under heavy fishing pressure.

The main recruitment seasons determined by ELEFAN are in agreement with other studies by Monterrosa (1986) and Boardman (1981) in which spiny lobster recruitment in Puerto Rico occurs year around with maximum seasonal pulses around late summer-early fall.

**Table 3.** Comparison of length (L<sub>∞</sub>) and body growth rate (K) by sex using Pauly's equation  $j(\phi)$  (Pauly, 1984) for the spiny lobster from different areas in the Caribbean

Area	Sex	(L <sub>∞</sub> )	K	$j(\phi)$	Source
Brasil	M	141	0.34	3.82	Dos Santos et al., 1964
	F	148	0.38	3.92	
St John (USVI)	M	153	0.44	4.01	Olsen and Koblick, 1975
	F	133	0.32	3.72	
Martinique	M	190	0.25	3.96	Clairovin, 1980
	F	188	0.23	3.91	
Bahamas	M	190	0.26	3.97	Waugh, 1981
	F	190	0.23	3.92	
Cuba	M	169	0.22	3.80	Cruz et al., 1981
	F	139	0.31	3.77	
Bermuda	M	204	0.18	3.87	Evans, 1988
	F	192	0.15	3.74	
Cuba	M	142	0.30	3.78	Baez et al., 1991
	F	122	0.3	3.65	
Mexico	M	257	0.2	4.12	Arce et al., 1991
	F	215	0.25	4.06	
Mexico	M	198	0.24	3.97	Gonzalez-Cano, 1991
	F	185	0.22	3.77	
Cuba	M	250	0.27	4.23	Phillips et al., 1992
	F	171	0.39	4.06	
Jamaica	M	210	0.24	4.02	Houghton and King, 1992
	F	195	0.28	4.03	
Nicaragua	M	169	0.23	3.82	Castano and Cadima, 1993
	F	160	0.40	4.01	
Cuba	M	190	0.31	4.05	Leon et al., 1994
	F	174	0.24	3.86	
Cuba	M	178	0.21	3.82	Baez et al., 1994
	F	171	0.21	3.81	
Cuba	M	185	0.23	3.90	Leon et al., 1995
	F	154	0.19	3.65	
Brazil	M	207	0.26	4.04	Gonzalez-Cano and Rocha, 1995
	F	162	0.18	3.67	
Mexico	M	217	0.25	4.07	Gonzalez-Cano and Rocha, 1995
	F	146	0.22	3.67	
Brazil	M	257	0.229	4.02	Ivo, 1996
	F	233	0.236	3.92	
St. Croix (USVI)	M	192	0.25	3.96	Mateo and Tobias, 2002
	F	172	0.22	3.81	
Puerto Rico (2000)	M	195	0.24	3.96	Mateo, In press (this study)
	F	185	0.23	3.89	

Evaluation of different exploitation strategies, in particular the trade-offs between small size at first capture and large size at first capture for *P. argus* males and females was done with the Beverton yield per recruit analysis. This model incorporates estimates of growth and mortality rates to estimate potential yield for any desired combination of fishery effort and minimum size. However, the reliability of this analysis of size and yield is limited by the quality of the parameters. Some parameters are not precisely estimated. This is very important because small changes in some parameters can make large changes in the predicted size at

maximum yield. This is particularly true for the estimates of fishing and natural mortalities, which are the least reliable of all the necessary parameters. It also estimates yield from the available recruitment and does not consider the effect of variable recruitment (Baisre and Cruz 1994).

Results from the yield per recruit analysis suggest there seems to be little potential for an increase in Y/R if effort were increased with the current length at first capture. Likewise, increasing length at first capture  $L_c$  with the current level of effort will not result in a significant increase of yield per recruit. The results of the model shows that most of the potential yield might be harvested by maintaining the current fishing effort at the present level or barely reducing it. However, no account is taken of the impact of reduction of spawner biomass on recruitment.

According to the Beverton model, yield is directly proportional to yield-per-recruit over a wide range of fishing mortalities only if it can be assumed that there is no relationship over a wide range of F and E values between the size of the parental stock and its progeny. Thus, the values of F or E needed to produce a maximum yield-per-recruit will tend to generate very low yields, because  $F_{max}$  and  $E_{max}$  usually reduce the parental stock to a level at which few recruits are produced.

Although the mortality estimates may be subject to considerable errors as consequences of violations of some assumptions made during analyses, the present level of fishing mortality appears to be much greater than the optimum required level for the lobster fishery suggesting that this fishery resource is fully exploited and current management measures must be revised to sustain and probably optimize yield.

Our findings, although preliminary, are in agreement with a recent study done by Bolden 2001 in which suggested a continuing trend toward growth overfishing as first identified by Bohnsack et al. (1992) 10 years ago. When Bolden compared historical biostatistical data from USVI and Puerto Rico from 1983 to 1999, she found that PR spiny lobster populations had smaller mean carapace lengths, frequency distributions centered around a smaller length class, lower fecundity, skewed sex ratios, and a greater portion of the landings being comprised of sublegal sized females compared to USVI. Another interesting finding is that from biostatistical data individual trip information, it was found that there has been a decline in lobster catch rates in Puerto Rico across years.

Management of the spiny lobster in the US Caribbean is complicated by failure to enforce regulations, a lack of local basic information on the biology and ecology of the species, and a lack of management oriented research. Long-term research designed to understand the dynamics of different stocks is usually limited to gathering data and hardly ever reaches the stage of data processing and publication. In certain cases, regulations have no clear biological or economical bases and are not closely enforced. Fishermen cooperation along with fishery researchers and government, which is of major importance for the success of sustained management, has historically depended on political decisions and does not exist for prolonged periods.

Regulations for the Spiny lobster in the US Caribbean have not changed in 17 years (CFMC 1985). The latest NMFS stock assessment studies from Bohnsack 1992 and Bolden 2001, although they provide useful information about the current status of the spiny lobster, their information from the biostatistical data have a low number of observations and have an associated degree of uncertainty. This associated uncertainty reduces the effectiveness with which the fishery may be managed. Thus, it is major importance that fully coordinated research involving fisheries researchers, government, fishermen, and industry be initiated in the near future to obtain critical data to permit the development of sound management strategies. At this actual moment, future yield from the spiny lobster stock seems dependent on effective enforcement of the minimum legal size limit to optimize yield from the available recruitment and prevent substantial further declines in spawning stocks.

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#### LITERATURE CITED

- Arce, A. M., J.C. Seijo, and S. Salas. 1991. Estimación del crecimiento de la langosta *Panulirus argus* mediante funciones de singularidad. *Revista de Investigaciones Marinas* 12(1):184-192.
- Baez, M., E. Díaz, R. Brito, and R. Cruz. 1991. Edad y crecimiento de la langosta en la plataforma suroccidental de Cuba. *Revista de Investigaciones Marinas* 12(1-3):193-201.
- Baez, M., E. Carmenati., and R. Coyula. 1994. Edad y crecimiento de la langosta *Panulirus argus* a partir del análisis de frecuencias de tallas en la plataforma suroccidental de Cuba. *Revista de Investigaciones Marinas* 15.
- Baisre, J., R. Cruz. 1994. The Cuban Spiny lobster fishery. Pages 119-131 in: B.F. Phillips, J.S. Cobb, and J. Kittaka (eds.). *Spiny Lobster Management*. Fishing News Books, London, England.
- Bhattacharya, C.G. 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics* 23:115-135.
- Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. *Ministry of Agriculture Fisheries Investigation Series* 11.19:1-533.
- Bohnsack, J., S. Meyers, R. Appeldoorn, J. Beets, I. Sadovy, and D. Matos. 1992.

- Stock assessment of Spiny lobster *Panulirus argus* in the US Caribbean. Final Report submitted to Caribbean Fishery Management Council. 26pp.
- Boardman, C.W. 1981. Assessment and monitoring of adult and juvenile populations of spiny lobster, *Panulirus argus*, around Puerto Rico. Project rept. 2-333-R Puerto Rico Fisheries Research Laboratory, CODREMAR
- Bolden, SK 2001. Status of the US Caribbean Spiny Lobster Fishery 1980-1999. Miami Lab. Contrib. No. PRD-9900-17
- Castano, O. and E. Cadima. 1993. Biología y evaluación de la langosta espinosa *Panulirus argus*. Simposio sobre evaluación y Manejo de las pesquerías de Crustáceos en Nicaragua, Managua. Nicaragua 6-7 Diciembre 1993. Centro de Investigación de Recursos Hidrobiológicos (CIRH)/NORAD) 53pp.
- CFMC. 1985. Caribbean Fishery Management Council, Spiny Lobster Fishery Management Plan. 32pp.
- CFRAMP. [1997]. CFRAMP/FAO Spiny Lobster Stock Assessment Workshop. Belize. In press.
- Clairovin, N. 1980. Contribution a l'étude du stock de langouste *Panulirus argus* en Martinique. Science et Peche Bull. Peches Marit. 300:7-18.
- Cruz, R., Coyulla, R., Ramírez, A.T. 1981. Crecimiento y mortalidad de la langosta espinosa (*Panulirus argus*) en la plataforma suroccidental de Cuba. Rev. Cub. Inv. Pesq. 6(4):89-119.
- Cruz, R., M.E. de Leon. 1991. Dinámica reproductiva de la langosta *Panulirus argus* en el archipiélago cubano. Rev. Invest. Mar. 12(1-3):234-245.
- Dos Santos, E.D., R.S. da Costa, S.J.C. de Moura. 1964. Growth of the spiny lobster *Panulirus argus* quantitatively aspect. *Arq. Est. Biol. Mar. Univ. Ceara, Fortaleza* 4(2):41-44.
- Evans, C.R. 1988. Population dynamics of spiny lobster *Panulirus argus* and *P. guttatus* at Bermuda 1986/87. Final Report to Overseas Development Administration, UK. 98pp.
- FAO. 1993. Marine Fishery Resources of the Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba. FAO Fisheries Technical Paper. No. 326. Rome. 235pp.
- Fonteles-Filho, A.A. 1994. State of the lobster fishery in the north-east Brazil. Pages 108-188 in: B.F. Phillips, J.S. Cobb, and J. Kittaka (eds.). *Spiny Lobster Management*. Fishing News Books, London, England.
- Fox, W.W. 1970. An exponential surplus-yield model for optimizing exploited fish populations. *Transactions of the American Fisheries Society* 99(1):80-88
- Gayanilo, F.C. Jr., P. Sparre, and D. Pauly. 1995. The FAO-ICLARM stock assessment tools (FISAT) Users' s Guide FAO Computerized Information Series Fisheries, #8. Rome FAO. 126 pp.
- Gonzalez-Cano, J.M. 1991. Migration and refuge in the assessment and management of the spiny lobster *Panulirus argus* in the Mexican Caribbean. Ph.D. Thesis. Imperial College London SW7. 478 pp.
- Gonzalez-Cano, J.M. and C.A.S. Rocha. 1995. Problems on the estimation of growth parameters for the spiny lobster *Panulirus argus* in the Caribbean and

- Northeast of Brazil. *Proceedings of the World Fisheries Congress: Theme 5: Assessment, Methodologies and Management*.
- Goodwin, M.H., S.J. Heyliger, R.M. Wilkins. 1986. Progress report on development of a management plan for the St. Kitts / Nevis Spiny lobster fishery. Fisheries Division, Ministry of Agriculture, St Kitts. 19pp.
- Haughton, M. and D. King. 1992. Stock assessment of the Spiny lobster *Panulirus argus* in Jamaica. *Proceedings of the Gulf and Caribbean Fisheries Institute* 42:119-126.
- Ivo, C.T.C. 1996. Biología pesca e dinámica populacional das langostas *Panulirus argus* (Latreille) e *Panulirus laeviscauda* (Latreille) (Crustacea: Palinuridae), capturadas ao longo da plataforma continental do Brasil, entre os estados do Amapá e do Espírito Santo. Tese de Doutorado, departamento de Hidrobiologia, Universidad Federal de Sao Carlos, Sao Carlos. 277pp.
- Jones, R. 1984. Assessing the effects of changes in exploitation patterns using length composition data (with notes on VPA and cohort analysis). FAO Fish. Tech. Pap. 256:118pp.
- Leon, M.E., R. Puga and Y.R. Cruz. 1994. Estimación de los parámetros de crecimiento del *Panulirus argus* del Golfo de Batabano, Cuba. *Revista de Investigaciones Marinas* 18(10):9-12.
- Leon, M.E., R. Cruz, R. Puga. 1995. Actualización de la edad y el crecimiento de la langosta espinosa *Panulirus argus*. *Rev. Cub. Inv. Pesq.* 5:3-9.
- Lipcius, R.N. 1985. Size dependency reproduction and molting in spiny lobster and other long-lived decapods. Pages 129-148 in: H. Wenner (Ed.). *Crustacean Issues, Vol. 3: factors in Adult Growth*. Balkema, Rotterdam.
- Lozano, E., P. Briones, and B.F. Phillips. 1991. Fishing characteristics, growth and movements of spiny lobster *Panulirus argus* in Bahía de la Ascención, Mexico. *Fisheries Bulletin* 89(1):79-89.
- Lyons, W.G., D.G. Barber, S.M. Foster, F.S. Kennedy, and G.R. Milano. 1981. The Spiny Lobster *Panulirus argus*, in the middle and upper Florida keys: Population structure, seasonal dynamics and reproduction. *Florida Marine Research Publication* 38:1-38.
- Mateo I. and W. Tobias 2002. Preliminary estimations of growth, mortality and yield per recruit for the spiny lobster *Panulirus argus* in St Croix, USVI. *Proceedings of the Gulf and Caribbean Fisheries Institute* 53:58-75
- Matos D. 1999. Overview of the Spiny Lobster *Panulirus argus* Comercial Fishery in Puerto Rico during 1992-1998. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:194-203
- Monterrosa, O. 1986. Post larval recruitment of the spiny lobster, *Panulirus argus* to southwestern Puerto Rico including observations of substrate selection in aquaria. MS Thesis University of Puerto Rico, Mayaguez, Puerto Rico. 47 pp.
- Muller, R.G., J.H. Hunt, T.R. Matthews, and W.C. Sharp. 1997. Evaluation of effort reduction in the Florida Keys spiny lobster *Panulirus argus*, fishery using an age-structured population analysis. *Marine and Freshwater Research* 48:1045-1058.

- Munro, J.L. 1974. *The Biology, Ecology, Exploitation, and Management of Caribbean Reef Fishes: Crustaceans (Spiny Lobster and Crabs) 3(Part VI)*. Res. Rep. Sool. Dpr. University of the West Indies, Kingston, Jamaica. 57 pp.
- Olsen, D. and I.G. Koblic. 1975. Population dynamics ecology and behavior of spiny lobster *Panulirus argus* of St. John, Virgin Islands 2 Growth and mortality. *Natural History Museum of Los Angeles Bulletin* 20:17-21.
- Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8. Manila, Philippines. 325 pp.
- Pauly, D. and J.L. Munro. 1984. Once more on the comparison of growth of fish and invertebrates. *Fishbyte* 2(1):21.
- Pauly, D. and M.L. Soriano. 1986. Some practical extensions to Beverton and Holt relative yield per recruit model. Pages 491-496 in: J.L. Maclean, L.B. Dizon, L.V. Hosillo (eds.). *The First Asian Fisheries Forum*. Asian Fisheries Society, Manila, Philippines.
- Phillips, B.F., M.J. Palmer, R. Cruz, and J.T. Trendall. 1992. Estimating growth of the spiny lobster *Panulirus cygnus*, *Panulirus argus*, and *Panulirus ornatus*. *Australian Journal of Scientific Research* 45(5).
- Powers, J.E. 1985. An update of spiny lobster assessment data. National Marine Fisheries Service, Southeast Fisheries Center ML1-85-28. 10 pp.
- Powers, J.E. and S.P. Bannerot. 1984. Assessment of spiny lobster resources of the Gulf of Mexico and southeastern United States. National Marine Fisheries Service, Southeast Fisheries Center, Miami, FL. 25 pp.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* 191:382 pp.
- Warner, R.E., C.L. Combs, and D.R. Gregory. 1977. Biological studies of the Spiny lobster, *Panulirus argus* in South Florida. *Proceedings of the Gulf and Caribbean Fisheries Institute* 29:166-183.
- Waugh, G.T. 1981. Management of juvenile spiny lobster *Panulirus argus* based on estimated biological parameters from Grand Bahamas Island Bahamas. *Proceedings of the Gulf and Caribbean Fisheries Institute* 33:271-289.
- Zetina, M.C. and G.V. Rios. 1998. Estimación del tamaño de la población de langosta *Panulirus argus* en las costas de Yucatán, usando diferentes modelos de evaluación. *Proceedings of the Gulf and Caribbean Fisheries Institute* 50:163-175.
- Zetina, M.C. and G.V. Rios. 2001. Modelos de crecimiento de la langosta (*Panulirus argus*) y un metodo para calcular la edad. *Ciencia Pesquera* 14:57-61