Preliminary Estimations of Growth, Mortality and Yield Per Recruit for the Spiny Lobster *Panulirus argus* in St. Croix, USVI

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PRELIMINARY ESTIMATIONS OF GROWTH, MORTALITY AND YIELD PER RECRUIT FOR THE SPINY LOBSTER *PANULIRUS ARGUS* IN ST. CROIX, USVI

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ABSTRACT: Preliminary growth and mortality parameters for the spiny lobster *Panulirus argus* were estimated from length frequency data collected from the St. Croix commercial fisheries from 1995 through 1999 using the FISAT software package. The corresponding values of L_∞ for female spiny lobsters using ELEFAN I ranged from 170 to 177 mm CL, and K values were 0.20 to 0.23. For males the L_∞ values ranged from 185 to 197 mm CL, and K values ranged from 0.23 to 0.28. The length-converted catch curve and Beverton and Holt Z estimates ranged from 1.24 to 1.91 for males and 0.8 to 1.58 for females. The Z estimated from Jones length cohort analysis ranged from 0.83 to 1.15 for males and 0.65 to 0.83 for females. The exploitation ratios from length catch curve ranged from 0.73 to 0.82 for males and 0.58 to 0.76 for females. Meanwhile, exploitation rates from Jones length cohort analysis ranged from 0.59 to 0.70 for males and 0.47 to 0.64 for females. Nevertheless, average exploitation ratios from the two different methods were well above the optimum exploitation rate (E=0.5) suggesting that the St. Croix spiny lobster is overfished. The Beverton relative yield per recruit model analysis for 1999 for males implies that with values of E=0.66 and Lc =95.4 mm the current lobster fishery is harvesting approximately 98% of the potential yield. Likewise, the analysis for females shows that with a value of E=0.58 and Lc= 89.36 mm the fishery is harvesting 95% of the potential yield in females. According to these results it is very important for all fishery agencies in the US Caribbean to reevaluate the status and conditions of the spiny lobster stocks and the definitions of overfishing for this economically important resource.

Key words:Growth, mortality, *Panulirus argus*

INTRODUCTION

The spiny lobster *Panulirus argus* is the most economically important crustacean caught throughout the entire Caribbean, and it is widely distributed in the Western Atlantic from Bermuda to Brazil (FAO, 1993). In St. Croix, US Virgin Islands (USVI), the spiny lobster is fished commercially by free diving, scuba diving, and by fish traps. This species represented almost 6% of the total catch reported during 1998-1999 (Tobias, 2000). The fishery has been managed under territorial and federal jurisdictions with a fishery management plan (FMP) administered by the Caribbean Fishery Management Council (CFMC) since 1985 after indications of overfishing were observed in the US Caribbean during the early 1980's (CMFC, 1985). The established regulations are: (1) a minimum size of 89 mm in carapace length; (2) a prohibition against retaining egg-bearing lobsters; (3) a requirement to land lobster whole; and (4) gear restrictions prohibiting the use of poisons, drugs or other chemicals as well as spears, hooks explosives, or similar devices in harvesting spiny lobsters.

Growth and mortality parameters have been estimated for the spiny lobster throughout the Caribbean using different techniques, such as tagging studies (Munro, 1974; Olsen and Koblic, 1975; Clairovin, 1980; Waugh, 1981; Lozano et al., 1991; Muller et al., 1997) and length frequency analysis from commercial fishery data (Baez et al., 1991; Phillips et al., 1992; Haughton and King, 1992; Leon et al., 1995). However, estimating growth rates of *P. argus* by length frequency analysis has been unsuccessfully attempted for USVI (Bohnsack et al., 1992). 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 and USVI commercial fishery. However, they could not get reliable estimates of growth parameters such as L_∞ (asymptotic length) and K (body growth coefficient) 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.

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

METHODS

Information of historical landings, harvest rates, and fishing effort data (i.e. number of boat trips, number of traps) was obtained through the National Marine Fisheries Service (NMFS) Cooperative Statistics Program. Biostatistical data of *P. argus* were collected by port agents from 1995 to 1999. Each lobster was weighed to the nearest 25g. Carapace length (CL) was measured to the nearest 0.1 mm and sex was determined. The sample size per month ranged from 0 to 636 individuals per month. 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 for each year. Differences on length frequency distributions by sex and by years were examined using Kolmogorov-Smirnov test (KS) (Sokal and Rohlf, 1981).

Estimation of Growth Parameters and Mortality

Analysis of growth parameters assumes Von Bertalanffy growth:$L_t = L_\infty$ (1-Le$^{k(t-t_0)}$), where L_t is the carapace length at time t, L_∞ is the asymptotic length an individual would reach if it lived indefinitely, and k is the rate at which L_∞ is approached. The growth parameters L_∞ and K were estimated using ELEFAN I from the FISAT software package (Gayanilo et al., 1995). Comparisons of different estimates of growth parameters were done using the empirical equation of Pauly and Munro (1984):phi= Log_{10} K + 2 Log_{10} (L_∞).

Instantaneous total mortality (Z) (Beverton and Holt, 1957), fishing mortality (F) and length at first capture (Lc) were calculated using length-converted catch curve (Ricker, 1975; Pauly, 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 in the USVI 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. Jones' length cohort analysis (Jones, 1984) was used to estimate stock size biomass, as well as total and fishing mortalities and exploitation ratios. 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). Maximum sustainable yield (MSY) for *P. argus* was calculated using Fox (1970) and Schaefer (1954) surplus yield models. Catch data and effort data, which could be used to calculate MSY, were available for 1993-1998 fishing seasons.

RESULTS

Commercial Landings Data

Spiny lobster landings increased steadily from 1978 to 1998, from landings of 3400 kilograms (kg) to more than 17700 kg. Average landings during the 1980's were 3550 kg while in the 1990's averaged 13732 kg (Figure 1). Divers accounted for approximately 85% of the total landings throughout the years from 1990 to 1998 (Figure 2). Fishing effort for 1993-1998 fishing seasons (as defined by number of fishing trips) has averaged about 4690 trips per year (Figure 3) while number of fish traps per year averaged about 1488 traps (Figure 4). Mean total catch per unit effort (CPUE) for 1993-1998 fishing seasons varied from 2.9 kg per trip in 1993 to 4.5 kg in 1998 (Figure 5). The number of kilograms landed per fishing trips by gear for 1993-1998 fishing seasons has averaged 7.2 kg per trip for divers and 0.7 kg for fish traps. Mean CPUE by trap averaged 1.3 kg per trap (Figure 6).

Size Distribution

During the period of 1995-1999, 2862 lobsters were measured, of which 1734 were males and 1128 females. The male:female sex ratio was skewed toward males (1.5) most likely because females with eggs were not landed and this caused to bias the ratio. The size range was from 75 mm to 190 mm of CL. The mean CL for males and females were 108.44 mm and 103.42 mm, respectively. The average modal lengths for males and females were 100 mm and 93 mm, respectively. CL for males was significantly larger than those of the females (KS, p=0.014) (Figure 7). Less than 4% of the lobsters measured from 1995 to 1999 were under the legal size limits. When average lengths were compared by years there was a significant decline in mean CL in males from 1995 to 1999 (KS, p=0.01) but not in females (KS, p=0.16).

Growth and Mortality Parameters

The estimated values of L_∞ for females ranged from 170 to 177 mm CL (Table 1), and K values ranged from 0.20 to 0.23. For males the L_∞ values ranged 185 to 197 mm CL, and K values ranged from 0.23 to 0.28. These results showed that males had a faster growth rate and attained their maximum size more quickly than females. Females had higher good fitness indices (Rn) of ELEFAN I.

The length-converted catch curve and Beverton and Holt Z estimates ranged from 1.24 to 1.91 for males and 0.8 to 1.58 for females (Table 1). Length at first capture (Lc) for males ranged from 94.8 to 108.6 mm and 89.3 to 93.3 mm for females. The Z estimated from Jones length cohort analysis ranged from 0.835 to 1.15 for males and 0.65 to 0.83 for females (Table 2). The exploitation ratios from length converted catch curve ranged from 0.73 to 0.82 for males and 0.58 to 0.76 for females. Whereas, exploitation rates from Jones length cohort analysis ranged from 0.59 to 0.70 for males and 0.475 to 0.64 for females. Average exploitation ratios from the two different methods were well above the optimum exploitation rate (E=0.5) suggesting that the St. Croix spiny lobster is overfished.

Estimates of stock size and fishing mortality were obtained using Jones length cohort analysis (Table 3). The results suggest that approximately 91530 lobsters in the 82 to 84 mm range were recruited to the fishery for 1999. The total catch for 1999 was approximately 57300 lobsters. Estimate of total biomass was 87 metric tons (t). The total number of survivors was 33200. The mean fishing mortality and exploitation ratio for fully recruited length groups was 0.472 and 0.581 for females while 0.663 and 0.670 for males, respectively. Due to the tendency of length catch curve methods to overestimate mortality parameters due to variable recruitment and migration of larger specimens we decided to use the results from Jones length cohort analysis for the yield per recruit analysis.

Yield Estimates

The Beverton relative yield per recruit model for males in 1999 implies that with values of E =0.66 and Lc =95.4 mm the current lobster fishery is harvesting approximately 98% of the potential yield (Figure 8a). Likewise, the analysis for females show that with a value of E= 0.58 and Lc= 89.36 mm the fishery is harvesting 95% of the potential yield in females (Figure 8b). 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 (0.71 and 0.72, respectively) have not been surpassed by the current exploitation ratios (0.66 and 0.58).

Estimates of MSY varied from 15300 to 15500 kg within the two models. The number of trips required to harvest the MSY ranged from 5688 to 7644 trips.

DISCUSSION

The estimation of growth and mortality rates for *P. argus* by any presently known method is quite troublesome in nature. The adequacy of Von Bertalanffy (1938) growth functions as a reliable description of growth rates in *P. argus* depends on the validity of the assumption that growth rate is constant throughout the year (Leon et al., 1995). However, this is not the case for *P. argus* where molting frequency varies seasonally (Lipcius, 1985). Previous works by Munro (1974) and Lipcius (1985) state that lobster growth is a function of two processes:molting frequency and change in size during molting. Munro (1974) stated that *P. argus* had an average of four molts per year with length increment between 5 and 8 mm in each molt. Molting frequencies do not remain constant and change throughout life. Therefore, *P. argus* juveniles have successive molts till they reach sexual maturity, and individuals of larger size molt once a year and they reproduce twice during spring-summer season.

Overall, the growth curves estimated using ELEFAN I represented a rather poor fit to the peaks in the restructured data. The goodness of fit (Rn), that can reach to a maximum of 1, was generally low ranging from a minimum of 0.142 to a maximum of 0.182. The relatively poor fit of the growth curves was probably a result of spawning year all round and the effects of seasonal growth. Previous studies on estimates of growth parameters indicate that *P. argus* is long lived, slow growing and has low rates of natural mortality (Munro, 1974; Olsen and Koblic, 1975; Clairovin, 1980; Waugh, 1981; Lozano, et al., 1991; Baez et al., 1991; Phillips et al., 1992; Haughton and King, 1992; Leon et al., 1994; Leon et al. 1995). However, comparisons of growth rates by females and males found on different areas have several discrepancies. While authors such as Cruz and de Leon (1991), Baez et al. (1991), Lozano et al. (1991), Phillips et al. (1992) Castano and Cadima (1993), Haughton and King (1992) and Ivo (1996) give higher K values for females, other workers found that females had lower growth rates than males (Olsen and Koblic, 1975; Clarovin, 1980; Waugh, 1981; Evans, 1981; Gonzalez-Cano, 1991; Leon et al., 1994; Leon et al., 1995; Gonzalez-Cano and Rocha, 1995). These differences may be due to the sample size used and the different methods used to estimate growth. Furthermore, in some of these studies data on smaller sizes or larger sizes above 120 mm are scarce, therefore, diminishing diminish the precision and accuracy of L_∞ as well as K values. Nevertheless, Kanciruk (1980) states that *P. argus* males attain larger sizes at a faster growth rate than females similar to other species from the Panuliridae family (*P. guttatus*). This is explained because female lobsters need to allocate their metabolic energy between growth and reproduction. 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_∞ have been reported to vary from 154 to 225 mm. Our estimate of growth performance index (3.96) from *P. argus* males lies well within a 95% confidence interval (3.86-4.03) of phi (φ) based on a mean of 3.97 (SE=0.03). Similarly, for females our estimate of growth performance index (3.86) lies well within a 95% confidence interval (3.78-3.97) of phi based on a mean of

3.85 (SE=0.03). In brief, the results from this study are in agreement with other growth studies of *P. argus.*

Estimation of mortality parameters in *P. argus* is also difficult due to the lack of accurate age-based data and the migratory behavior of this species (Baisre and Cruz, 1994). Shifts in length frequency distributions toward larger sizes in deeper waters are known for many marine organisms including the spiny lobster (Kanciruk and Hernkind, 1976; Lyons et al., 1981; Baisre and Cruz, 1994), reflecting ontogenetic migrations from inshore/shallow areas to offshore/deeper areas. This can produce a major problem. If migration of larger individuals into deeper waters had an effect on the length frequency distribution data from this study, it is expected that the mortalities derived from the catch curve and Beverton and Holt formula would be overestimated. The amount of bias will depend on the magnitude of K and L_∞ values and will increase if K values are low and L_∞ are high.

Total mortalities (Z) from length catch curves and Beverton and Holt (1957) formula ranged from 1.24 to 1.91 for males and 0.8 to 1.58 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). However, average Z from Jones length cohort analysis for males ranged from 0.83 to 1.16 while females average instantaneous mortalities ranged from 0.72 to 0.83. These values were in agreement 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).

Exploitation rates from males and females calculated from all methods were greater than the accepted optimum level of 0.5 and suggest that the lobster populations in St. Croix are being overfished. MSY calculated from Schaeffer and Fox model were around 15500 kg per year. Lobster landings in St. Croix have exceeded this figure in 1990-91, 1993-94 1997-98 and 1998-99 fishing seasons. Given the limited data these calculations should be treated cautiously. The implication is that the fishery is fully exploited.

The reliability of Beverton yield per recruit analysis and its application to lobster populations is limited by the quality of the input parameters (Baisre and Cruz, 1994). This model does not consider the effect of variable recruitment, it also assumes that spiny lobster growth conforms a Von Bertalanffy growth function, and total mortality estimates are greatly affected by growth and natural mortality rates. It is known that mortality estimations by length catch curves and Beverton and Holt formula are often overestimated by growth parameters affected by different factors such as variable recruitment and migration (Baisre and Cruz, 1994). We decided to calculate yield per recruit using estimates of mortalities from Jones length cohort analysis because age and length structured models assume neither constant recruitment nor constant mortalities across ages or size classes (Muller et. al., 1997). Consequently, they effectively model the patterns of the fishery because of their high precision.

According to the yield per recruit analysis, increasing length at first capture Lc with the current level of effort will not result in an increase of Y/R. Likewise, no gain in Y/R would be expected if effort were increased with the current length at first capture. Species that are slow growing and long lived such as *P. argus* can be susceptible even at low levels of exploitation. By maintaining the fishery at the present level or barely lower it, it will permit the harvest of most of the potential yield but might potentially affect the spawning stock. A more conservative approach would be warranted given the Beverton model does not account for the effect of fishing pressure on the spawning stock.

Although the mortality estimates may be subject to considerable errors as consequences of the biases in the data collected from the commercial fishery and the violations of assumptions made during analyses, the present level of fishing mortality appears to be much greater than the optimum required level for the lobster fishery. The results of the yield per recruit analysis show that fishing pressure should be decreased considerably in St. Croix. Possible management options include implementation of catch quotas, seasonal closures or limitation the number of fishermen or traps.

Based on the *P. argus* life history characteristics and the present results from the yield per recruit analysis and surplus production models, the most promising of the various management options for the reduction of fishing pressure on the spiny lobster would be to create a seasonal closure of the fishery. Given the current law enforcement limitations around St. Croix, this option has the best chance to be implemented. Enforcement requirements would be limited on a temporal and spatial scale and the closure would have little impact on other sectors of the fishery.

Finally, it is very important for all fishery agencies in the US Caribbean to reevaluate the status and conditions of the spiny lobster stocks and the definitions of overfishing around this economically important resource. According to the SAFE report (Bohnsack et al., 1992) the assessment team concluded that St. Croix lobster populations appeared to be healthy at the levels of fishing effort based on data from 1987 to 1989, and recommended increased compliance with the minimum size regulation. Our present results indicate that lobster populations in St. Croix are apparently overfished. Besides the enforcement of fishery regulations, successful management of the US Virgin Islands spiny lobster fishery will depend on more intensive biological research together with new approaches to stock assessment in order to improve the management decisions.

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Table 1. Estimates of length (L¥), body growth rate (K), goodness of fit index (Rn), age at birthday (T0), fishing mortality (F), exploitation ratio (E=F/Z), and length at first capture (Lc) by sex for the spiny lobster, St. Croix, USVI.

Sex/Parameters	L_∞	K	Rn	T_0	Z_1	Z_2	F	E	Lc
Male									
1995	197	0.28	0.155	0.35	1.84	1.82	1.48	0.81	94.80
1996	195	0.26	0.182	0.38	1.91	1.84	1.50	0.82	108.67
1997	185	0.24	0.142	0.42	1.43	1.24	0.90	0.73	100.10
1998	193	0.25	0.141	0.40	1.41	1.44	1.10	0.76	96.12
1999	191	0.23	0.144	0.44	1.60	1.90	1.56	0.82	99.18
Female									
1995	172	0.23	0.142	0.45	1.17	1.22	0.88	0.72	91.38
1996	172	0.20	0.161	0.52	0.80	0.87	0.53	0.61	91.63
1997	177	0.23	0.176	0.45	1.28	1.58	1.24	0.78	93.34
1998	170	0.20	0.142	0.52	0.83	0.81	0.47	0.58	90.10
1999	173	0.22	0.180	0.47	1.25	1.41	1.07	0.76	89.30

Z_1= Beverton and Holt,Z

Z_2=Length Catch Curve Z

Table 2. Estimation of abundance (N), biomass (T), fishing mortality (F), exploitation ratio (E), and instantaneous total mortality (Z), by sex using Jones length cohort analysis for the spiny lobster at St. Croix, USVI.

Sex/Parameter	N	T	F	E	Z
Male					
1995	41862	37.53	0.82	0.71	1.16
1996	40805	34.84	0.61	0.64	0.95
1997	91036	83.31	0.50	0.59	0.84
1998	47440	43.92	0.59	0.63	0.93
1999	49299	42.35	0.67	0.66	1.01
Female					
1995	37208	32.08	0.54	0.62	0.88
1996	45561	42.54	0.31	0.48	0.65
1997	38487	32.99	0.60	0.64	0.94
1998	63984	56.25	0.38	0.53	0.72
1999	51450	45.05	0.47	0.58	0.81

Table 3. Comparison of length (L¥) 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_∞)**	**K**	**φ (phi)**	**Source**
Brasil	M	141	0.34	3.82	Dos Santos et al., 1964
	F	148	0.38	3.92	
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	165	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	Haughton 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	M	192	0.25	3.96	Mateo and Tobias, 2000
	F	172	0.22	3.81	(this study)

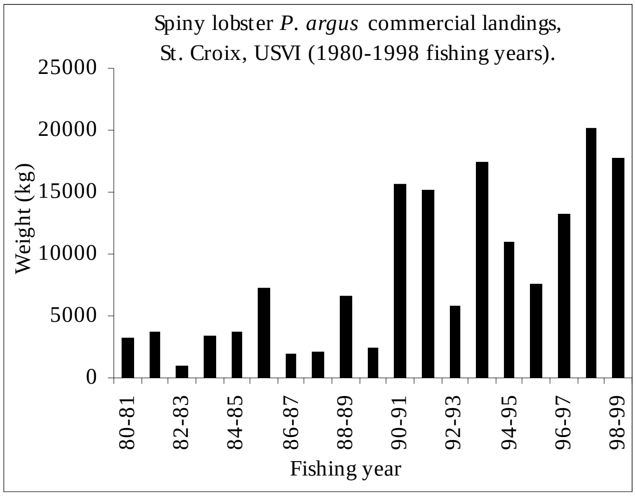

Figure 1. Spiny lobster landings for St. Croix by fishing season 1980-81 through 1998-1999.

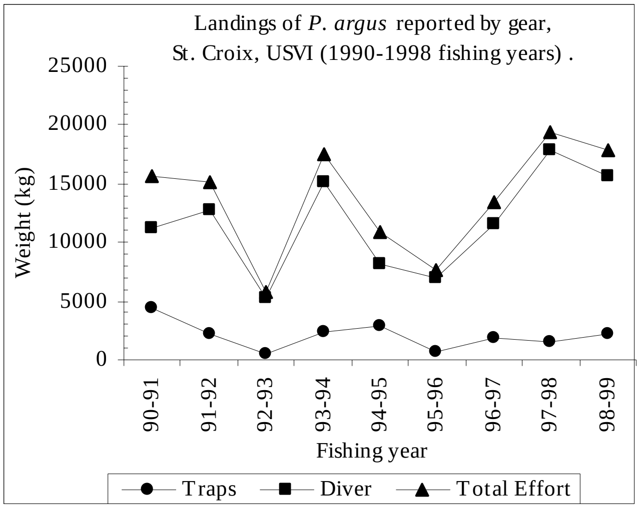

Figure 2. Landings of P. argus reported by gear and all gears combined (total effort) for St. Croix, USVI, 1990-1998 fishing years.

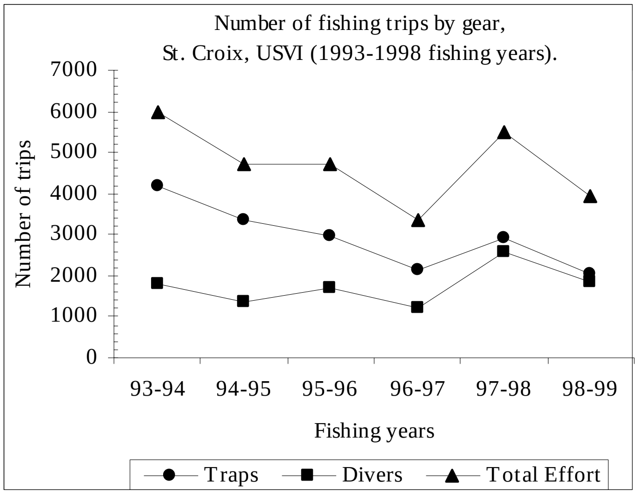

Figure 3. Number of fish trips by gear and all gears combined (total effort) for St. Croix, USVI, 1993-1998 fishing years.

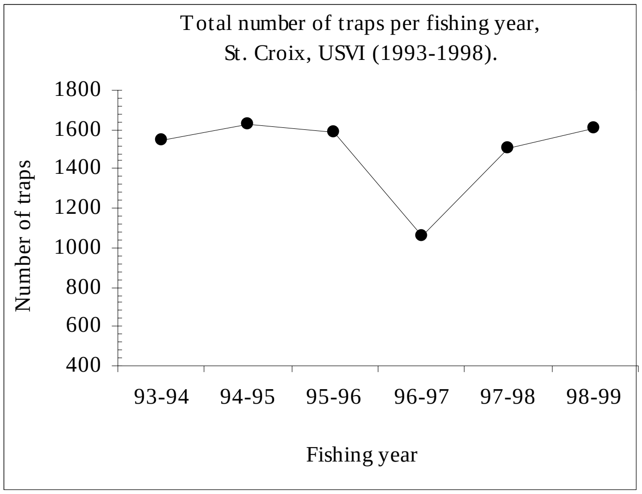

Figure 4. Number of traps per fishing year (1993-1998) for St. Croix, USVI.

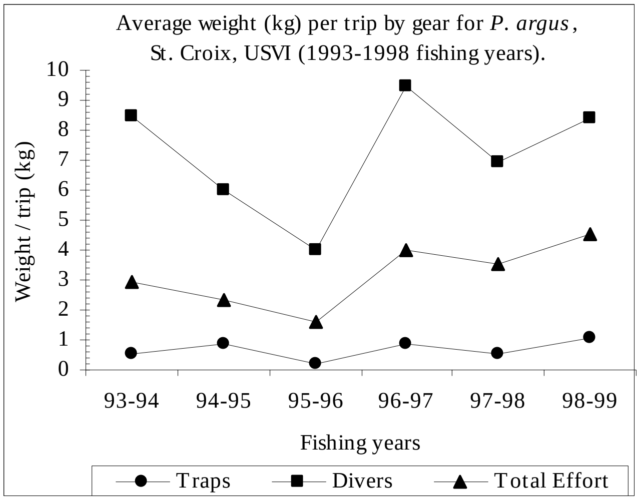

Figure 5. Average weight (kg) per trip by gear and all gears combined (total effort) for P. argus, St. Croix, USVI, 1993-1998 fishing years.

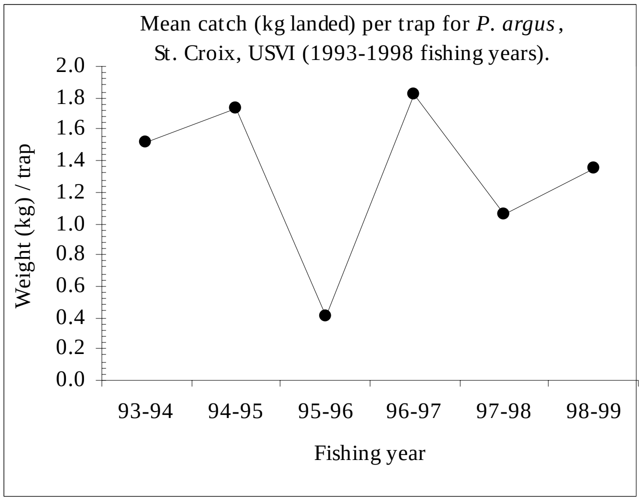

Figure 6. Mean catch (kg landed) per trap for P. argus, St. Croix, USVI for 1993-1998 fishing years.

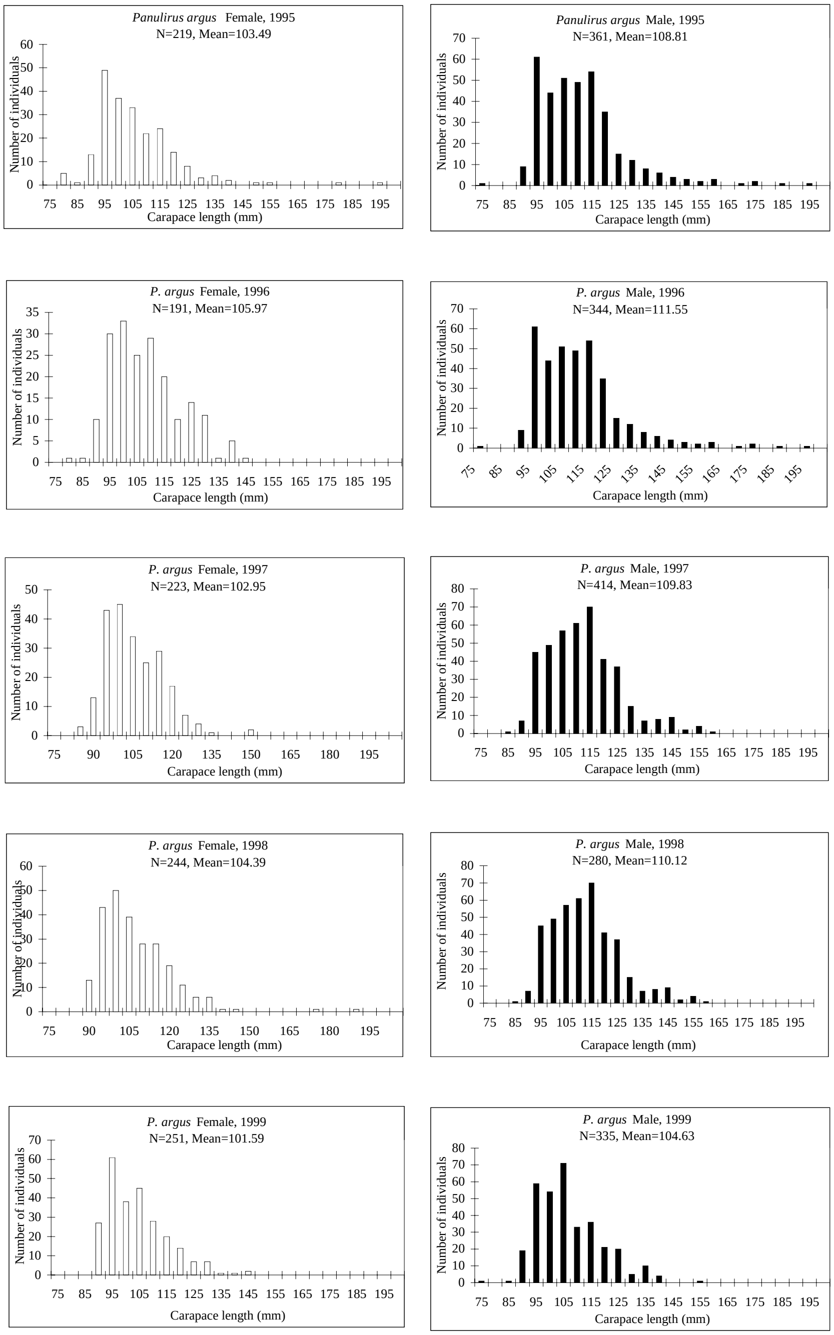

Figure 7. Length frequency distributions for male and female spiny lobster P. argus for St. Croix, USVI, for 1995-1999 fishing years.

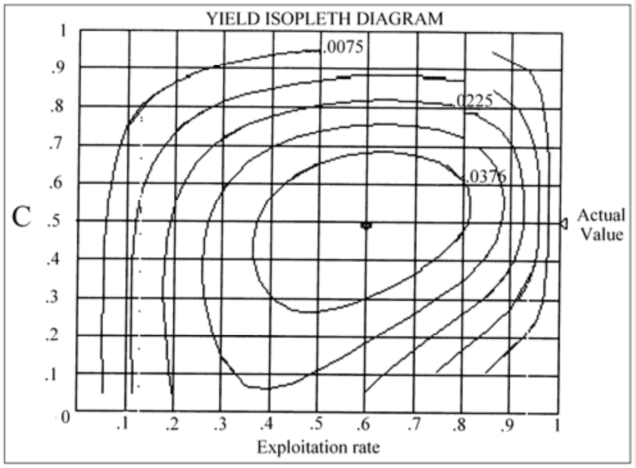

Figure 8a. Yield per recruit isopleth for male *P. argus* as a function of exploitation ratio (E) and size at first capture relative to asymptotic length (C).

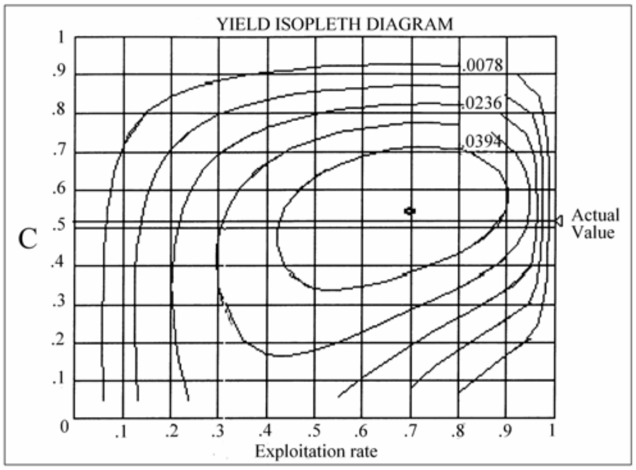

Figure 8b. Yield per recruit isopleth for female *P. argus* as a function of exploitation ratio (E) and size at first capture relative to asymptotic length (C).