Preliminary Application of a State-Space Age-Structured Production Model to the Spiny Lobster (*Panulirus argus*) Fishery of the U.S. Caribbean

By

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ABSTRACT

This document illustrates an application of a state-space age-structured production model (Porch, 2002) to Caribbean spiny lobster. A review of the fisheries, the data available for assessment, and the biological parameters and assumptions needed to implement the model are presented. As fishery data for spiny lobster in the U.S. Caribbean are sparse, variable among islands, and relative abundance indices do not show consistent trends, it was difficult to fit the model without placing a suite of constraints on initial parameter values. Despite constraints, reasonable fits to the indices and the catch series could not be obtained simultaneously, and in all cases results were very unrealistic. Under all the scenarios tested, the model tended to overestimate SSB and underestimate F. At this time, it is not possible to draw a conclusion about the stock status from this age-structured production model.

COMMERCIAL FISHERY

The commercial fisheries of the U. S. Caribbean are characterized by being multi-specific and by using a variety of gears to harvest reef fish, shellfish, and pelagic species. Commercial landings statistics have been collected in this region since the early seventies. In 1983, Puerto Rico and the United States Virgin Islands entered a cooperative agreement with the National Marine Fisheries Service to enhance data collection and reporting. Biostatistical sampling from trip interviews also became part of this agreement, through the Trip Interview Program (TIP).

Catch report forms differ between Puerto Rico and the U.S. Virgin Islands. In Puerto Rico, the information collected is at the species or gender level, while in the U.S. Virgin Islands catch has been reported by gear type (pots, lobster pots, lines, dive, etc.), by type of fish (snapper, grouper, or other), and more recently by species groups. Since the program's inception, catch of queen conch and spiny lobster have been reported in separate fields, which allows for better examination of these fisheries as those landings can be disaggregated from the multi-specific catch.

Annual landings of spiny lobster from the U.S. Virgin Islands, including St. Thomas, St. John, and St. Croix are available since 1974-75, and since 1983 from Puerto Rico. In the present study, expanded landings from the Virgin Islands were used, but only reported landings (without expansion) were available from Puerto Rico (Table 1, Figure 1). Initial model applications attempted to use landings by sector and island with their corresponding index; final trials used the combined landings for the whole U.S. Caribbean (i.e., total reported) and only one of the abundance indices.

COMMERCIAL CATCH RATES

Selected standardized CPUE indices developed by Valle-Esquivel (2005) for the Virgin Islands and by Mateo and Die (2004) from Puerto Rico were used to calibrate an age structured production model (Table 2, Figure 2). To facilitate comparison, relative indices of abundance were scaled to the mean of the overlapping years in each series. Scaled standard index values were incorporated as inputs of the assessment model. The indices selected were those that had a corresponding, fairly complete catch series, that encompassed a sufficient period of time, and that were deemed representative of trends in the respective fisheries. Under these premises, trap and dive CPUE indices from the U.S. Virgin Islands and an overall (multi-gear) index from Puerto Rico were used in all trials, either simultaneously or one at a time.

POPULATION MODEL

A state-space, age-structured production model was used to evaluate the status of spiny lobster in the U.S. Caribbean. A state-space model can facilitate parameter estimation by separately estimating observation and process error. The present formulation can accommodate Bayesian priors, and allows for interannual variations in parameters such as recruitment and catchability. An age-structured production model is advantageous because it allows fecundity and vulnerability of the fishery to vary with age. The theory and implementation of the model is described in detail in Porch (2002).

Required inputs to run this age structured production model include: a time series of catch and effort (or CPUE) for each fishery, a length-weight relationship, a length-at-age equation, and a maturity schedule. In addition, parameters for the stock-recruitment function are specified in terms of virgin recruitment and α, the maximum rate of reproduction at low stock sizes (Myers et al. 1999). Parameters estimated by the model include a catchability coefficient for each fishery, annual effort, historical average fishing mortality, abundance, spawning biomass, and equilibrium statistics corresponding to MSY, Fmax and various other benchmark statistics (Porch 2002).

POPULATION PARAMETERS

Length-Weight Relationship

A morphometric relationship was estimated from Puerto Rico TIP data (1986-2003), after a thorough examination of outliers and after performing a conversion of units into millimeters (carapace length) and grams (weight) (Saul and Chormanski 2005). The estimated equation is:

$$W_T = 0.00921\, L_C^{\,2.4804}$$

where W_T is total weight in grams and L_C is carapace length in millimeters. The estimated parameters and 95% confidence intervals are given in Table 3 and the fit is illustrated in Figure 3.

Natural Mortality

The mortality estimates used were obtained from literature values for the Virgin Islands and the Turks and Caicos Islands (FAO 2001, Olsen and Koblic 1975; Medley and Ninnes 1996). The median value of 0.36 for adult lobsters was used for all ages.

Growth

Growth in carapace length (CL) was assumed to follow a von Bertalanffy growth model, with parameters taken from León et al. (1994) for Cuba. The estimates for males were used for all age calculations, and mean parameter values for both sexes combined were used to estimate a maturity schedule (Table 4, Figure 4). The SEDAR8 group decided to use the parameters for the U.S. Virgin Islands, estimated by Olsen and Koblic (1975) as an alternative (Table 4).

Maturity

A logistic maturity schedule for spiny lobsters in the U.S. Caribbean was estimated by Die at the SEDAR8-AW (Die 2005) based on a re-examination on data from

Bohnsack et al. (1992). Parameters for Model A from Die (2005) were applied in this study, and are shown in Table 5 and the fitted curves are reproduced in Figure 5.

Model A is:

$$m = \frac{1}{1 + e^{-kL-\gamma}}$$

$$L_{50\%m} = \frac{\gamma}{k} - \frac{1}{k} Ln(1)$$

Fecundity

A fecundity schedule was calculated from a relationship between carapace length and fecundity from Cuba (FAO 2001):

$$E = 0.5911 * L_C^{\ 2.9866}$$

where E= number of eggs and L_C= carapace length (mm). Length was converted to age and fecundity values were scaled to the maximum value. Fecundity estimates by age are shown in Table 6 and Figure 6. Some trials used weight as a surrogate of fecundity, but this did not alter results.

Stock-Recruitment Relationship

In initial trials of the ASPM model an ad-hoc stock-recruitment relationship was used to derive starting values for the stock-recruitment parameters. The scaled CPUE series from Puerto Rico was lagged by 4 years, the approximate time from spawning to maturity, when lobsters are assumed to be recruited to the fishery. A Beverton-Holt (1957) model was adjusted to the lagged abundance series using non-linear regression.

$$R = \frac{\alpha * STOCK}{\beta + STOCK}$$

where the Stock is the CPUE series and Recruitment (R) is the lagged CPUE series. Only years 1983 to 1997 could be used for stock-recruitment estimation. Data and estimated parameters for this model are given in Tables 7 and 8 and the fit is illustrated in Figure 7.

This approach did not provide good information regarding α, and it was difficult for the model to calculate this parameter, and no convergence was achieved. An alternative starting point was derived from a steepness value 0.8. This corresponds to α=16. A fairly flat prior was put on α (lognormal with mean 16 and CV of 70%) to reflect our uncertainty in this parameter. A starting point for virgin recruitment (R_0 in numbers) was obtained by assuming that it was approximately 10 times the largest catch observed (e.g., 4 million pounds). An additional assumption was that each lobster weighs on average one pound,so the initial value for R_0 was 4 million fish.

Number of Age Classes and Selectivity

Based on the spiny lobster length distribution from Puerto Rico TIP data (1983-2003) (Table 9 and Figure 8), the range 20.9 to 180 mm corresponds to an age distribution between 1 and 16 years of age. This age was used as the longevity estimate for the ASPM model. However, this distribution includes data from years prior to the implementation of the minimum size (CL=75 mm) regulation. Therefore the main size classes targeted in the fishery can be considered those within this length limit and the upper 99.5% quantile of the distribution (75-150mm). This range corresponds approximately to ages 2.7 to 7.68. This indicates that the fishery is centered around five main ages classes (3 to 8). Ages 1-10 are included in the model; age 10 is a plus group.

Initial trials used distinct selectivities for Puerto Rico and the U.S. Virgin Islands. The Puerto Rico selectivity was modeled with a logistic function, with 3.6 as the age of 50% recruitment and the curve was essentially knife-edged. Knife-edge selectivity at 4 years was assumed for the U.S.V.I. dive and trap fisheries, as size and age of entry to the fishery has been consistent over time, even before the size regulations were introduced. Final trials used only the Puerto Rico value (50% selectivity at 3.6 years) because Puerto Rico takes the largest proportion of the catch.

MODEL SET-UP

For initial ASPM model runs, the total Caribbean spiny lobster landings were divided into three catch series: Puerto Rico, USVI-Dive and USVI-Traps. Each fishery was linked to an appropriate abundance index (Puerto Rico commercial index, Dive index from St. Croix, and a Trap index from St. Thomas/St. John) and was assigned different selectivity, catchability and effort patterns, with their respective variance parameters.

Initial trials at fitting the age-structured production model with all three indices were unsuccessful. In general, the model tended to fit the catch very well while the fits to the indices showed great bias. Subsequent trials were constrained to one catch series (overall U.S. Caribbean lobster landings) and focused on fitting the models to only one index, and these results are discussed below. In the three base models constructed, effort was allowed to vary interannually, the catchability coefficients were estimated as constant (time-independent), and the catch and effort series were allowed to have a lognormal error distribution. Even fitting one index at a time, the model still tended to favor greatly a fit to catch rather than the index, so constraints were imposed to force the model to fit the indices better, typically 2.0-3.5 times better than the catch series.

Natural mortality was given a lognormal prior with a mode of 0.36. A very tight distribution was imposed (CV=0.10) as the model tended to go to the upper bound of 0.8 without this constraint. In constrast, very wide bounds and flatter distributions were specified for R0 and α (virgin recruitment in numbers and the maximum reproductive rate, respectively): R0 was in the range [2.00E+03, 6.50E+09] and α was in the range [2,90]. Initial parameter starting values were 4.00E+07 for R0 and 16 for α (this value for α corresponds to a steepness of 0.8). Point estimates for R0, α, and M for each model are given in Table 10.

MODEL RESULTS

Puerto Rico Index

The index constructed from Puerto Rico commercial landings (Mateo and Die, 2002) was fairly flat overall, and the model fit a trend through the middle of the observations; catch was fit very well (Figure 9). Given the lack of trend in the index, and the lack of information prior to 1975, estimated fluctuations in F and SSB were driven by the catch series. A plot of the relative management benchmarks F/F_{MSY} and SSB/SSB_{MSY} suggest that the stock is not overfished and there is no overfishing occurring. In fact, it suggests that fishing mortality has been, on average, about 400 times less than the level that would achieve MSY, while SSB is close to 4 times greater than the level that would produce MSY. F in 2002 (last year of data) is estimated to be 8.42E-04 while SSB is estimated to be 4.47E+08 (20% greater than the estimate of virgin SSB). These results are very unrealistic.

St. Croix Dive Index

This index had no observations for the period 1987-1992, and attempts to fit both catch and CPUE led to a very poor fit to the second half of the time series (generally the bias was positive). In an attempt to force the model to fit the entire index, it was split into two time periods, and a separate catchability parameter was estimated for each period. This successfully eliminated the bias, although the estimated fit was flat (Figure 10). It was also necessary to constrain the model to fit the index 2 times better than the catch index, which still provided a decent fit to catch (Figure 10). A plot of the relative management benchmarks F/F_{MSY} and SSB/SSB_{MSY} suggest that the stock is not overfished and there is no overfishing occurring. On average, the level of fishing mortality has been 10% of the rate that would achieve MSY, while SSB has been about 3.7 times the level that would yield MSY (Figure 2). F in 2002 (last year of data) is estimated to be 0.035 while SSB is estimated to be 9.4E+6 (about 95% of virgin SSB). These results seem intuitively unrealistic. Forcing the model to fit the index trend (which gave a really poor fit to catch in some years) suggested that the stock is at 80% of virgin levels in 2002, but overall there is no overfishing and the stock is not overfished (Figure 11).

St. John Trap Index

The Trap index has a trend which is very similar to the Dive index, so the results from this model exercise were not very different from the results described for the previous model runs.

CONCLUSIONS

Although the results across all model runs were consistent in their estimate of stock status (i.e., no overfishing and not overfished), their resemblance to reality was questionable, mainly because they estimated that the stock was currently at or above virgin levels and that impacts from fishing were practically nil. A possible explanation for these results is the lack of contrast in the data. The Puerto Rico index in particular is flat, and while the Trap and Dive indices show some trend (downward overall), there are no index values for the years 1987-1992 when the catches were lowest.

At this time, it is not possible to draw a conclusion about the stock status from this age-structured production model.

LITERATURE CITED

Die, D. 2005. Maturity of spiny lobsters in the US Caribbean. CIMAS/CUFER University of Miami. SEDAR8-AW Document.

Bohnsack, J., S. Meyers, R. Appledoorn, J. Beets, D. Matos-Caraballo, and Y. Sadovy. 1991. Stock Assessment of Spiny Lobster, *Panulirus argus*, in the U.S. Caribbean. Miami Laboratory Contribution No. MIA-9C91-49, National Marine Fisheries Service - Southeast Fisheries Science Center.

FAO. 2001. Western Central Atlantic Fishery Commission. Report on the FAO/ DANIDA/CFRAMP/WECAFC Regional Workshops on the Assessment of the Caribbean Spiny Lobster (Panulirus argus) Belize City, Belize, 21 April-2 May 1997; Merida, Mexico, 1-12 June 1998. FAO, Rome.

León, M.E. de, Puga, R. y Cruz, R. 1994. Estimación de los parámetros de crecimiento de *Panulirus argus* en el Golfo de Batabanó, Cuba. *Rev. Cub. Inv. Pesq.* 18(1):9-12.

Mateo, I. and D. Die. 2004. The Status of Spiny Lobster *Panulirus argus* in Puerto Rico: Based on Commercial Landings Data. Rosenstiel School of Marine and Atmospheric Science,Cooperative Institute for Marine and Atmospheric Studies.

Medley, P.A.H. and Ninnes, C.H. 1997. A recruitment index and population model for spiny lobster (*Panulirus argus*) using catch and effort data. Can. J. Fish. Aquat. Sci., 54: 1414-1421.

Myers, R.A., K.G. Bowen, and N.J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. 56:2404-2419.

Olsen, D. A. and I. G. Koblic. (1975). Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John. U. S. V. I. Growth and mortality. Results of the Tektite Program. Bull. Nat. Hist. Mus. L. A. County, (20):17-22.

Porch, C. E. 2002. A preliminary assessment of Atlantic white marlin (*Tetrapturus albidus*) using a state-space implementation of an age-structured model. SCRS/02/68 23pp.

Valle-Esquivel, M. 2005. Standardized catch rates of spiny lobster (*Panulirus argus*) estimated from the U.S. Virgin Islands Commercial Landings (1976-2003). SEDAR8-AW3. Univ. Miami, RSMAS-CIMAS.

Table 1. Reported commercial landings (in pounds) from the U.S. Caribbean. Puerto Rico (1983-2002) are reported landings, U.S. Virgin Islands (1975-2002) are expanded reported landings. Landings from historic documents (1969-1982) are included.

Year	Puerto Rico Historic	Puerto Rico	USVI-Dive (Expanded)	USVI-Traps (Expanded)	TOTAL Reported
1969	354000				
1970	417000				
1971	258000				
1972	237000				
1973	250000				
1974	244000				
1975	311000		5233	27054	32286
1976	384000		4145	23036	27181
1977	421000		17672	54785	72457
1978	451000		30293	123196	153489
1979	512000		7824	62352	70176
1980	474000		16211	81303	97514
1981	481000		11575	79118	90693
1982	359000		10802	76414	87216
1983		273700	8104	74315	356119
1984		248000	15987	53889	317876
1985		211100	11981	53833	276914
1986		210100	18919	42837	271856
1987		153400	6193	18317	177910
1988		141200			141200
1989		185800			185800
1990		168700			168700
1991		211600			211600
1992		160500	9316	38744	208560
1993		168900	37294	91095	297289
1994		192100	29374	69411	290885
1995		279200	24072	92863	396134
1996		280600	30533	119744	430878
1997		283300	33651	83338	400289
1998		298500	40196	59089	397784
1999		327100	50724	53494	431318
2000		258400	86407	47198	392005
2001		280600	117959	48912	447471
2002		300400	124221	56587	481208

Table 2. Scaled relative indices of abundance selected for use in the ASPM assessment model. The Puerto Rico index is from a Delta-Lognormal standardized index estimated by Mateo and Die (2002) from the commercial landings. The St. Croix (STX) and St. Thomas/St. John (STT/STJ) are standardized indices from the commercial landings calculated with a GLM approach by Valle (2005).

Year	PR	STX-DIVE	STT/STJ-TRAPS
1969			
1970			
1971			
1972			
1973			
1974			
1975			
1976		1.000	0.629
1977		0.619	0.636
1978		0.515	0.762
1979		0.322	0.737
1980		0.399	0.916
1981		0.381	1.000
1982		0.407	0.636
1983	0.496	0.273	0.638
1984	0.529	0.204	0.591
1985	0.606	0.189	0.552
1986	0.885	0.404	0.677
1987	0.732		
1988	0.830		
1989	0.872		
1990	0.684		
1991	0.704		
1992	0.839		
1993	0.740	0.267	0.637
1994	0.777	0.241	0.550
1995	0.858	0.164	0.603
1996	0.790	0.195	0.638
1997	0.825	0.187	0.650
1998	1.000	0.211	0.570
1999	0.996	0.227	0.544
2000	0.792	0.245	0.527
2001	0.843	0.259	0.493
2002		0.259	0.523
2003		0.233	0.563

Table 3. Parameters and 95% confidence intervals for a length –weight relationship for Puerto Rico spiny lobster estimated from TIP data (1986-2003). The form of the equation is: $W_T = a\, L_C^{\,b}$

Parameter	Estimate	StdError	Lower CL	Upper CL
a	9.21E-03	3.07E-04	8.63E-03	9.83E-03
b	2.480418	7.10E-03	2.466591	2.494236

Table 4. Growth parameters for Caribbean spiny lobster taken from FAO (1998).

Zone	Sex	Linfinity	K	T0	References
Cuba	Male	185	0.23	0.44	León et al. (1995)
	Female	155	0.19	0.37	
	Average	**170**	**0.21**	**0.405**	
Virgin Islands, USA	Male	153	0.44		Olsen and Koblic (1975)
	Female	133	0.32		
	Average	**143**	**0.38**		

Table 5. Estimates of parameters for logistic models of proportion mature of female lobsters in the US Caribbean (taken from Table1, Die 2005).

Model	k	λ	m_{oo}	SSQ
A	9.4	-2.59	n/a	103,610
B	19.58	-5.69	0.74	23,939

Table 6. Estimated fecundity by age and length for Caribbean spiny lobster with a model for Cuba taken from FAO (2001).

Fecundity by Age and Carapace Length

Age	LC(mm)	Fecundity	Scaled F
1	22.4	6.34E+03	0.00
2	55.8	9.72E+04	0.04
3	82.3	3.11E+05	0.13
4	103.4	6.14E+05	0.25
5	120.2	9.62E+05	0.39
6	133.5	1.32E+06	0.54
7	144.1	1.65E+06	0.67
8	152.5	1.96E+06	0.80
9	159.2	2.23E+06	0.91
10	164.5	2.46E+06	1.00

Table 7. Lagged CPUE data from Puerto Rico used to develop a Beverton-Holt stock-recruitment curve.

Year	S(CPUE)	R(CPUE 4yr Lag)	Recruitment (Beverton-Holt)
1979		0.496	
1980		0.529	
1981		0.606	
1982		0.885	
1983	0.496	0.732	0.797
1984	0.529	0.830	0.802
1985	0.606	0.872	0.810
1986	0.885	0.684	0.828
1987	0.732	0.704	0.819
1988	0.830	0.839	0.825
1989	0.872	0.740	0.827
1990	0.684	0.777	0.816
1991	0.704	0.858	0.817
1992	0.839	0.790	0.826
1993	0.740	0.825	0.820
1994	0.777	1.000	0.822
1995	0.858	0.996	0.826
1996	0.790	0.792	0.823
1997	0.825	0.843	0.825
1998	1.000		
1999	0.996		
2000	0.792		
2001	0.843		

Table 8. Parameters of a Beverton-Holt stock-recruitment relationship developed for Caribbean spiny lobster based on lagged CPUE data from Puerto Rico.

Parameter	Estimate	ApproxStdErr	Lower CL	Upper CL
Alpha	0.8700216244	0.15188853	0.64106204	1.42622406
Beta	0.0452258161	0.13284315	-0.1487098	0.54578244

Table 9. Descriptive statistics for the overall carapace length distribution of Caribbean spiny lobster from Puerto Rico TIP data (1983-2003).

Quantiles

100.0%	maximum	180.00
99.5%		148.78
97.5%		132.00
90.0%		115.57
75.0%	quartile	104.00
50.0%	median	93.98
25.0%	quartile	85.00
10.0%		76.20
2.5%		67.56
0.5%		57.21
0.0%	minimum	20.90

Moments

Mean	95.27
Std Dev	16.1
Std Err Mean	0.119
upper 95% Mean	95.498
lower 95% Mean	95.033
N	18447

Table 10. Point estimates (standard deviation) for natural mortality (M), virgin recruitment (R0) and maximum reproductive rate (α) for models which attempted to fit an index derived from Puerto Rico TIP data, St. Croix Dive data, or St. John Trap data.

Parameter	Puerto Rico	Dive	Trap
M	0.44 (0.04)	0.54 (0.05)	0.52 (0.05)
R0	6.2E+5 (3.5E+5)	2.6E+4 (1.2E+4)	6.1E+4 (2.5E+4)
α	14.8 (6.5)	15.9 (6.2)	15.9 (6.2)

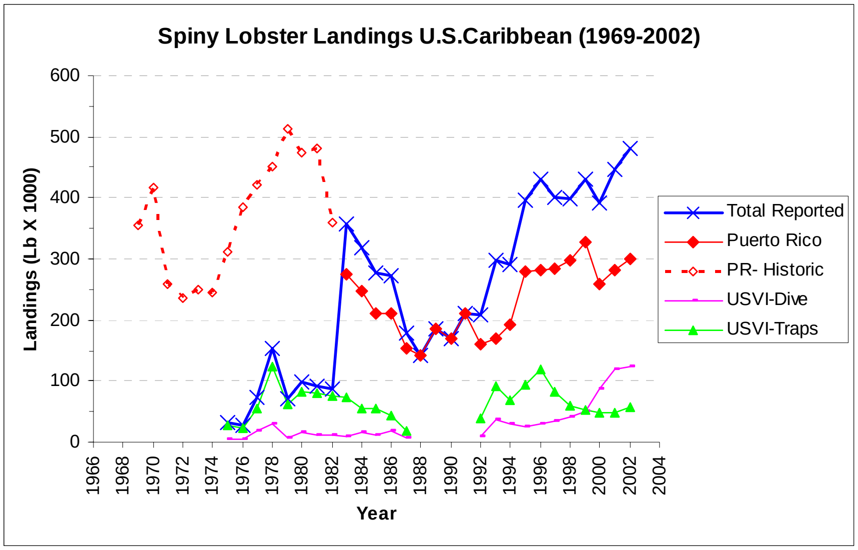


Figure 1. Reported commercial landings (in pounds) from the U.S. Caribbean. Puerto Rico (1983-2002) are reported landings, U.S. Virgin Islands (1975-2002) are expanded reported landings. Landings from historic documents (1969-1982) are included.

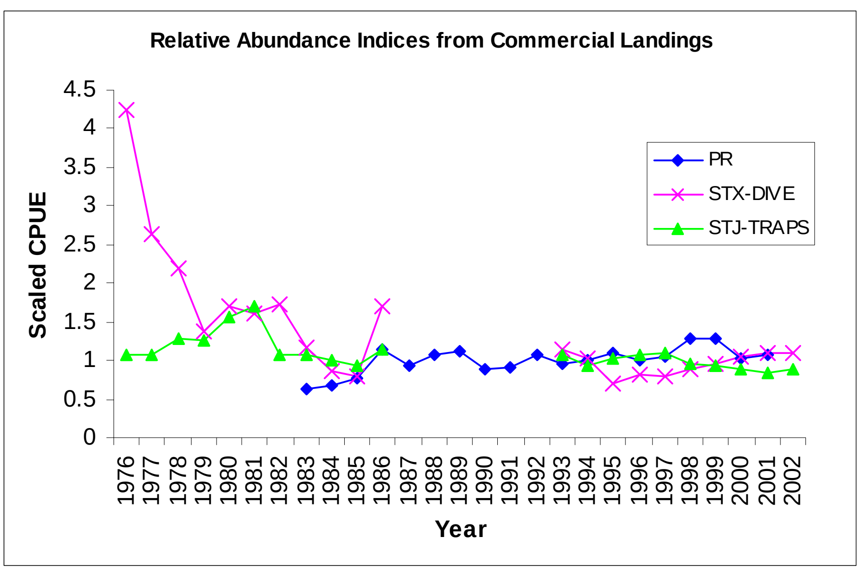


Figure 2. Scaled relative indices of abundance selected for use in the ASPM assessment model. All indices are standardized and were estimated from commercial landings. The Puerto Rico index used the Delta-Lognormal model, and was estimated by Mateo and Die (2004); the St. Croix (STX) and St. Thomas/St. John (STT/STJ) were calculated with a GLM approach by Valle (2005).

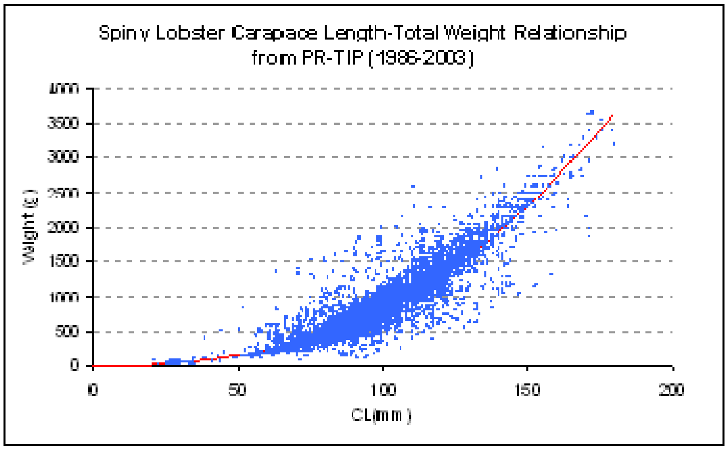


Figure 3. Length –weight relationship for Puerto Rico spiny lobster estimated from TIP data (1986-2003). The model is $W_T = 0.009\ L_C^{2.48}$

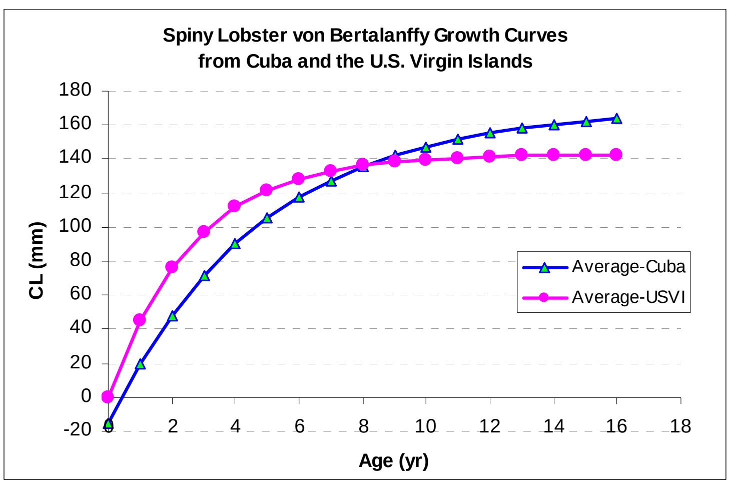


Figure 4. Growth parameters for Caribbean spiny lobster taken from FAO (2001).

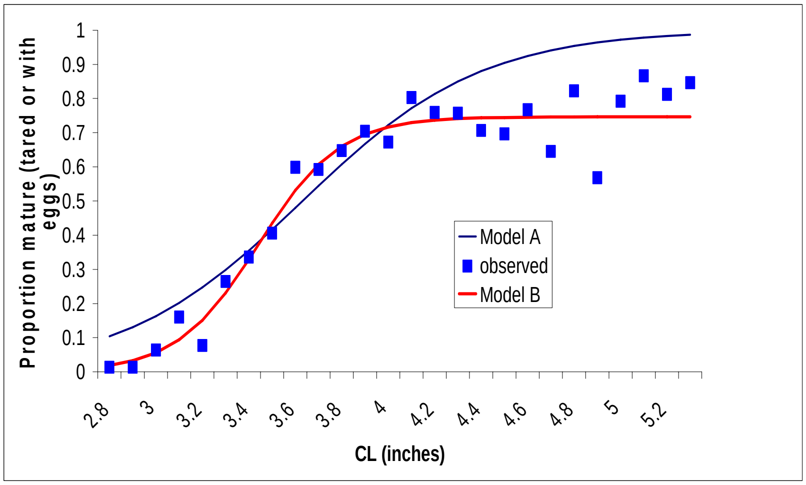


Figure 5. Observed proportion mature of female lobsters as a function of length for the US Caribbean and fits of logistic models to the data (taken from Figure 2, Die, 2005).

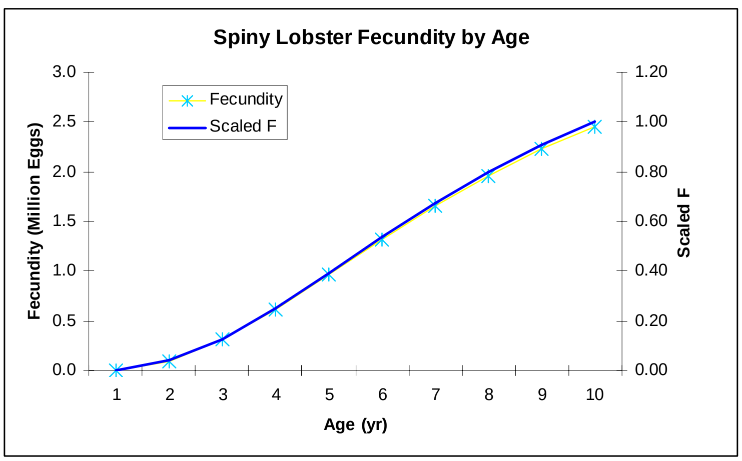


Figure 6. Fecundity schedule for spiny lobster using the model $E = 0.5911 * L_C^{2.9866}$ from Cuba (FAO, 2001).

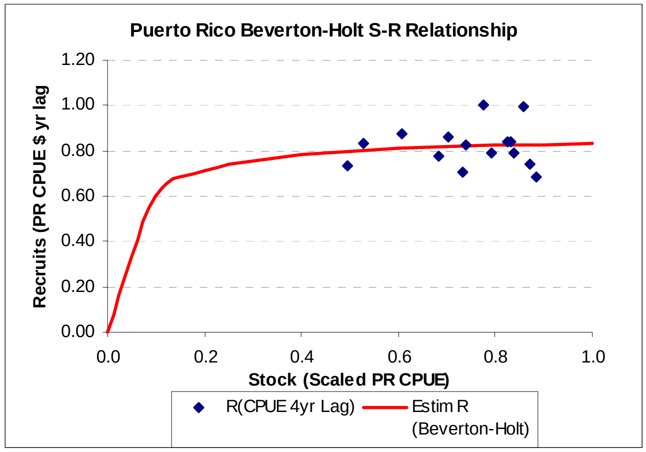


Figure 7. Beverton-Holt stock-recruitment relationship for Caribbean spiny lobster fit to CPUE data from Puerto Rico lagged by 4 years.

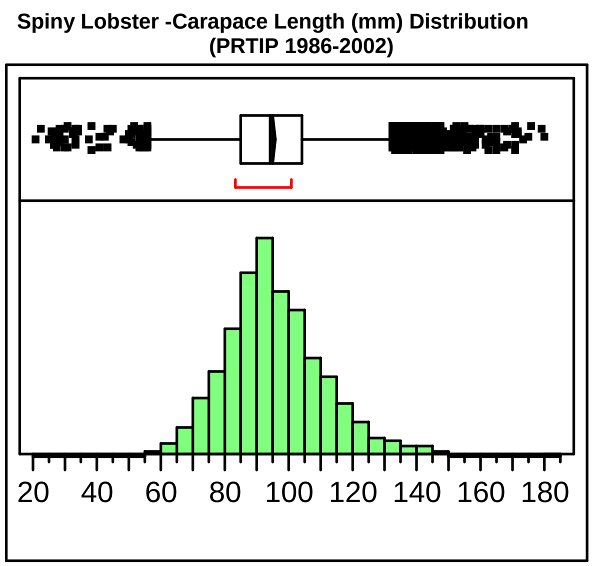
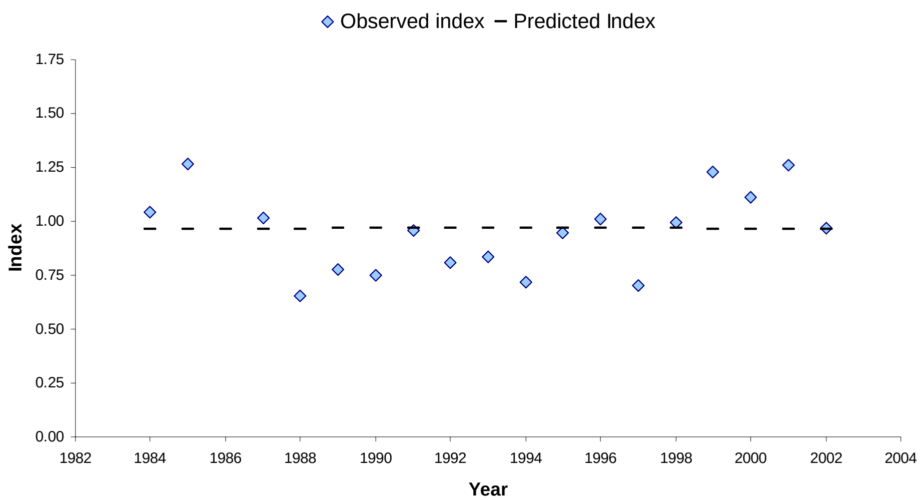
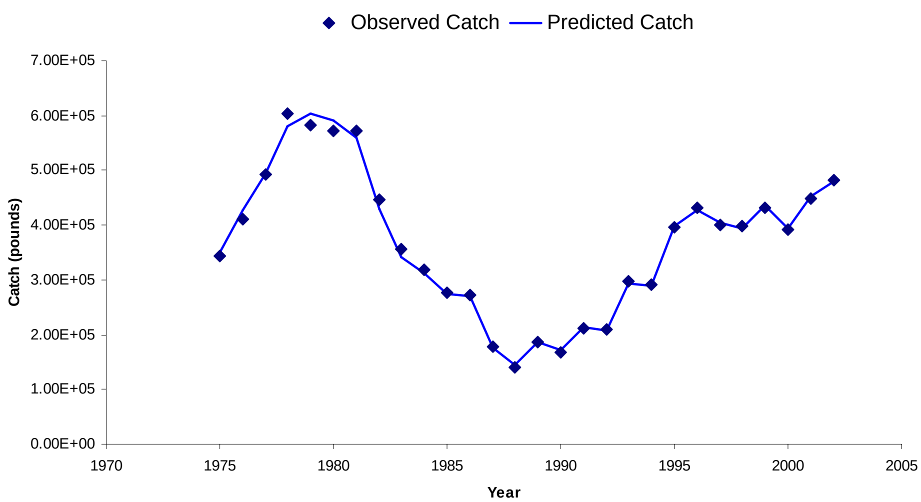


Figure 8. Carapace length distribution (mm) of Caribbean spiny lobster from Puerto Rico TIP data (1983-2003).





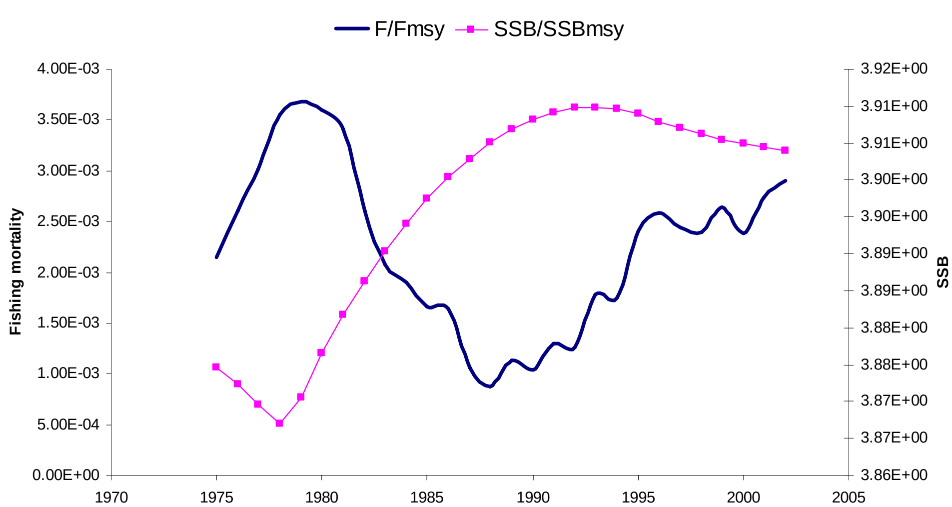
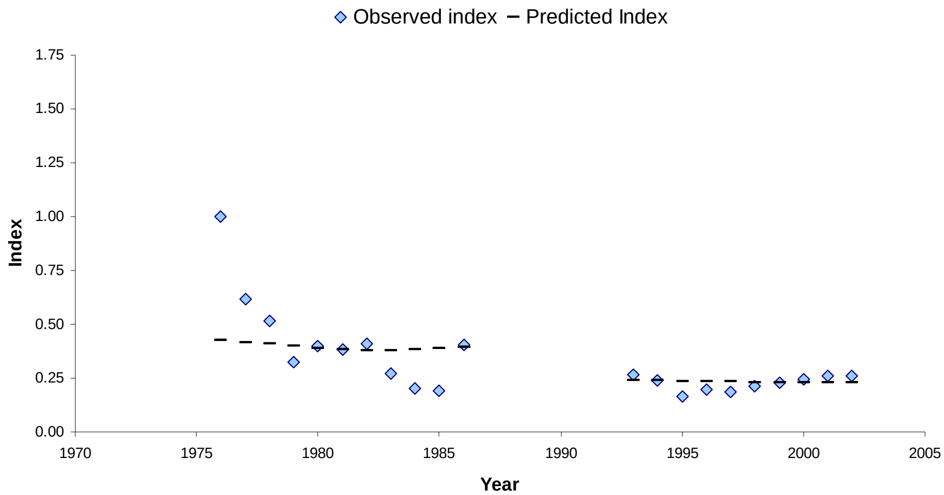
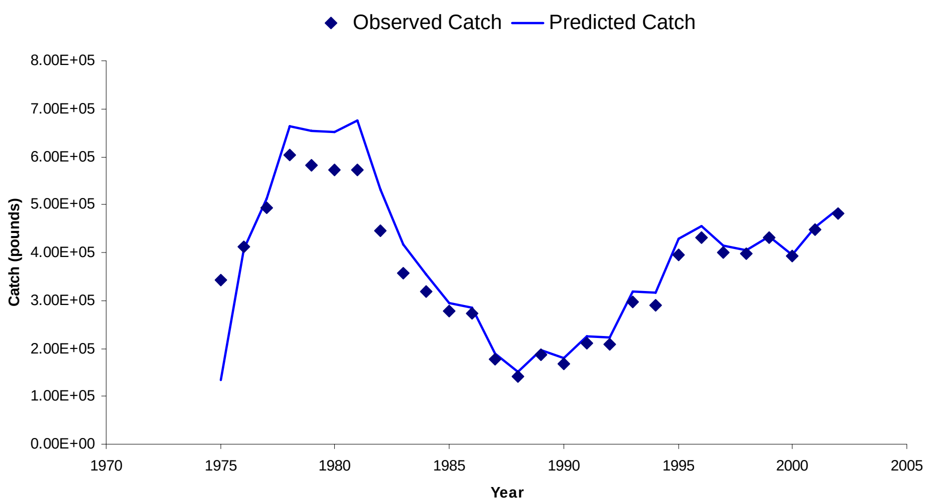


Figure 9. Model fit to the Puerto Rico index (top), total reported (expanded) catch of spiny lobster (middle), and relative benchmarks (bottom).





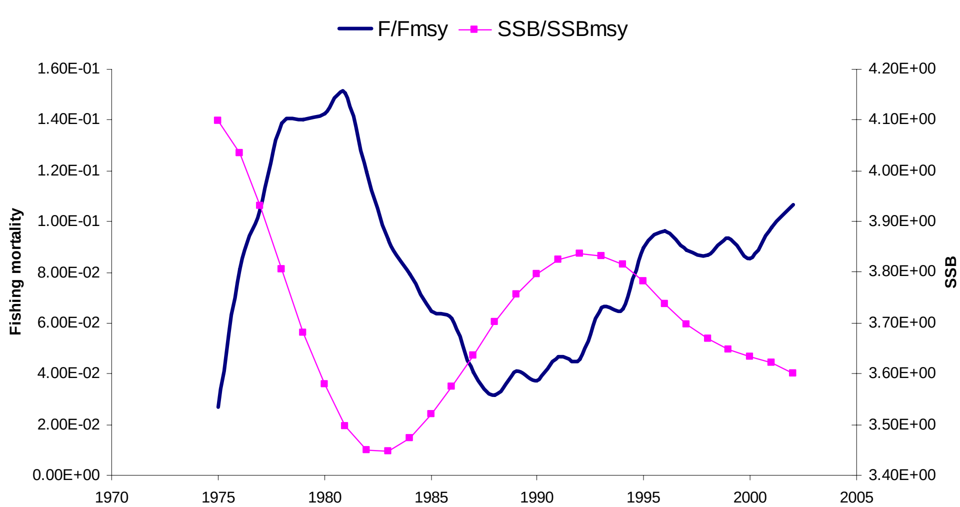


Figure 10. Model fit to the St. Croix Dive index (top), total reported (expanded) catch of spiny lobster (middle), and relative benchmarks (bottom).

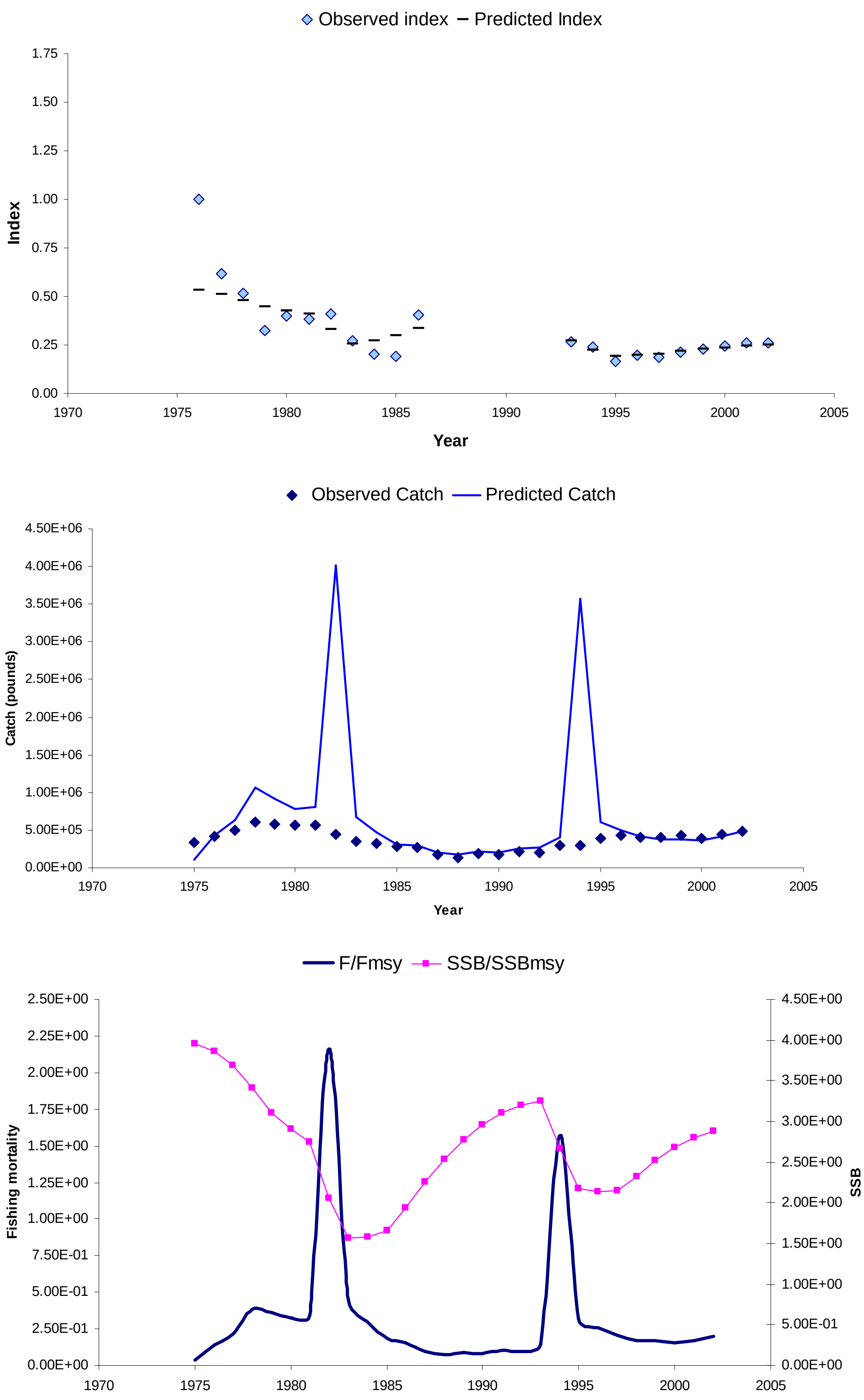


Figure 11. Model fit to the St. Croix Dive index (top), total reported (expanded) catch of spiny lobster (middle), and relative benchmarks (bottom) when model was constrained to fit the trend in the index.