The Spiny Lobster (*Panulirus argus*) in the Wider Caribbean: A Review of Life Cycle Dynamics and Implications for Responsible Fisheries Management

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ABSTRACT

The spiny lobster *Panulirus argus* (Latreille, 1804) is the most important fishery resource in the western central Atlantic and north-eastern Brazil. The complex life cycle has been studied over the last 50 years in five locations in the wider Caribbean: Cuba archipelago, Florida Keys, Bermuda, Mexico and Brazil. Field studies have increased our understanding of variations in the reproductive season by location and depth, size at first maturity, fecundity, and relative magnitude of egg production as indicated by an index of reproductive potential. This review of the life cycle dynamics of spiny lobster suggests that new regulatory measures for the western Atlantic population should be adopted to increase the reproductive potential and ensure sustainable recruitment. A regional focus is therefore needed in investigations of the life cycle and the fisheries to assist in improving responsible fisheries management

KEY WORDS: *Panulirus argus*, life cycle, reproduction, Caribbean

La Langosta Espinosa (*Panulirus argus*) en el Gran Caribe: Una Revisión de la Dinámica del Ciclo de Vida e Implicaciones en el Manejo Responsable de la Pesquería

La langosta espinosa *Panulirus argus* (Latreille, 1804) es el recurso pesquero más importante en el Atlántico centro occidental y en el nordeste del Brasil. El complejo ciclo de vida se estudió durante los últimos 50 años en cinco localidades del Gran Caribe, en el archipiélago cubano, cayos de la Florida, Bermudas, México y Brasil. Los estudios de campo han incrementado nuestra comprensión sobre la actividad reproductora, la variación de la reproducción por localidad-profundidad, la talla de primera madurez, fecundidad y la magnitud relativa de la producción de huevos como un indicador del índice del potencial reproductor. Sin embargo, ésta revisión de la dinámica del ciclo de vida de la langosta sugiere que nuevas medidas regulatorias deben ser adoptadas para toda la población. Por consiguiente, se necesita realizar un enfoque regional de las investigaciones del ciclo de vida y la pesquería para asistir en el mejoramiento del manejo responsable de la pesquería.

PALABRAS CLAVES: Ciclo de vida, *Panulirus argus*, Caribe,

INTRODUCTION

Spiny lobster (*Panulirus argus)* is a common tropical and sub-tropical species in the western Atlantic ocean, and its distribution ranges from Bermuda and North Carolina to north-eastern Brazil. It supports a large commercial and recreational fishery in the Wider Caribbean. Increased consumer demand, higher market value, expanding fishing fleets, and perhaps, climate variability, has led to the *P. argus* resource being fully or over-exploited over much of its range (Cochrane and Chakalall 2001). The complex life cycle has been studied over the last 50 years in five locations: Cuba, Bermuda, Florida Keys, Mexico (Yucatan), and Brazil. The study of the reproductive biology and recruitment was identified as a priority because 84% of the countries that have commercial or small-scale artisanal fisheries lack information on the process that determines recruitment and its relationship with the fishery and climate variability.

The first observations of sexual dimorphism and the breeding of the spiny lobster in Bermuda were carried out by Creaser (1950) and Sutcliffe (1952). Smith (1951) provided evidence of the percent of lobsters breeding by month in Bahamas. The smallest berried females by length were reported by Smith (1948), Buesa y Mota-Alves (1971), Cobo de Barany (1972) and Davis (1975). Buesa (1965) carried out an integral study of lobster reproduction in the Cuban archipelago. Cruz (1975) expanded this study by including water temperature information. Buesa and Mota Alves (1971) proposed an ovary colours scale for the study of the reproductive cycle. The autumnal reproduction and potential larval production by female size was investigated in Bimini (Kanciruk and Herrnkind 1976). In 1975, a study of spiny lobster biology was begun in the Florida Keys (Warner *et al*. 1977). Since 1980, field studies of spiny lobster have increased our understanding of reproductive activity, variations in the reproductive season by location and depth, size at first maturity of females, fecundity and relative magnitude of egg production as indicated by an index of reproductive potential (Cruz 1980, Lyons *et al*. 1981, Gregory *et al*. 1982, Munro 1983, Cruz and León 1991, Quackenbush 1994, Ramírez 1996, Cruz and Phillips 2000, Bertelsen and Cox 2001, Bertelsen and Matthews 2001). However, there is no information on the reproductive cycle and size at first maturity for males.

Understanding recruitment to the fishable stock of a species depends on knowledge of oceanographic and biological factors that operate during the different phases of the life cycle. For *P. argus,* only limited data exist on the puerulus and juvenile phases and their relationship to environmental variables. The long larval period of *P. argus* in the ocean (between 6 and 12 months in the Caribbean; Lewis *et al*. 1952, Farmer *et al*. 1987, Kittaka 1994) and the complex oceanographic currents that can transport larvae many hundreds of kilometres, as well as genetic evidence suggest a single pan-Caribbean stock (Silberman and Walsh 1994) and that recruitment of pueruli to any given location probably originates from any number of different sources (Briones-Fourzán *et al*. 2008). The arrival of pueruli to coastal regions occurs throughout the year but shows a seasonal pattern that is very similar within the Caribbean and in Bermuda (September-December) but quite different in Florida (February–March) (Acosta *et al*. 1997). The variation in settlement at the different sites is probably attributable to the variability in the local environmental factors controlling water flow and retention (Cruz *et al*. 2001b).

Many aspects of the ecology of the younger juveniles has been assessed to evaluate the sources of the pueruli and obtain a better understanding of recruitment variability and limitations, catch prediction, and mortality rates during the juvenile phase (Forcucci *et al*. 1994, Butler and Herrnkind, 1997, Cruz and Adriano 2001, Cruz *et al*. 2001a, Cruz *et al*. 2006, Cruz *et al*. 2007b). The use of artificial shelters made of concrete blocks (Cruz *et al*. 1986a) is proving to be of great value in investigations of the juvenile phase, in particular to estimate the abundance of recruits in nursery areas. The high concentration of juveniles in the shelters has made it possible to carry out a marking program that has provided excellent estimates of population density, distribution, and residential and migratory behaviour of the juvenile stage in the Gulf of Batabanó (Cruz *et al*. 1986b).

The aim of this review is to compare the reproductive and recruitment dynamics of the spiny lobster in the Wider Caribbean. In particular, we discuss new regulatory measures for the lobster population should be considered to increase the reproductive potential and ensure sustainable recruitment.

METHODS

Main Study Areas

The review was carried out based on data from the following locations:

i) Cuba archipelago: Gulf of Batabanó (22º 21´ N 82º 32´ W), South-eastern (20º 43´ N 78º 43´ W) and North-eastern (22º 33´ N 79º 06´ W)
ii) Florida State: Florida Keys reef tract (25º 30´ N 80º 10´ W), Florida Bay (25º 00´ N 80º 49´W) and Dry Tortugas (24º 38´ N 82º 52´ W).
iii) Bermuda: 32º 14´ N 64º 46´ W
iv) México: Caribbean coast (19º 45´ N 87º 22´ W)
v) Colombia: Providencia and Santa Catalina (13º 26´ N 81º 20´ W)
vi) Brazil: North-east coast (2º 30' N - 18º S and 35º W 47º W)

Life-history Phases of *P. argus*

The spiny lobster (*P. argus*) is able to utilize a variety of habitats and undergoes several habitat shifts during its ontogenetic development. The major phases are:

i) The adult (> 80 mm, CL),
ii) Eggs (~ 0.5 mm diameter) with a colour ranging from bright orange to brown (Cruz 1980) carried by female lobsters and released near open ocean waters,
iii) Planktonic phyllosoma (1.2 - 19.6 mm CL) with 11 larval stages (Baisre 1964),
iv) Puerulus (4 - 6 mm CL) which transits from oceanic to nearshore habitats (Acosta and Butler 1999),
v) Post-puerulus or solitary juvenile algal phase (6 - 16 mm CL) living in relatively shallow hard bottom with typically with structurally complex algae (Herrnkind *et al*. 1994),
vi) Gregarious juvenile (16 - 50 mm CL) shifting from algal to crevice shelters (Childress and Herrnkind 1997), and
vii) Older juvenile or pre-recruit phase (50 - 79 mm CL) which migrates from nearshore hard bottom habitats to deeper offshore hard dbottom adult habitats (Cruz *et al*. 2001a).

Reproduction Cycle

In the Cuban archipelago, a total of 483,529 lobsters were caught in an extensive area of 42 stations with artificial shelters (pesqueros or casitas cubanas) during the period 1982 - 1987. The data collected were used to characterize different aspects of the reproductive dynamics of lobsters (Cruz and León 1991). The maturity of the ovaries was estimated using the colour scale of Buesa and Mota Alves 1971. Evidence of mating was determined by observing a spermatophore on the thorax of a female. Evidence of spawning was made by observing the presence of fertilised eggs on the abdomen of a female.

Reproductive maturity of female ovaries generally occurs one or two months before the spawning season (March - May) in the Cuban archipelago (Cruz and León 1991) and in Brazil (Soares and Cavalcante 1984). The relationship between size and reproductive activity (Figure 1) shows that for sizes 90 - 99 and 100 - 119 mm CL ovaries begin to mature in January and peak during February-March then decline during August. The sizes at 70-79 and 80-89 mm CL have the same pattern, but with a peak in March. Mating takes places during all months and the female carries the black spermatophore on the sternal plates of the cephalothorax. Mating activity peaks during June-July (Cruz and Phillips 2000) and is lowest during February. This timing compares well with Lyons *et al*. (1981) for the Florida Keys. During August mating activity declines and a few female may retain spermatophores until they moult.

In the western Caribbean (Mexico and south coast of

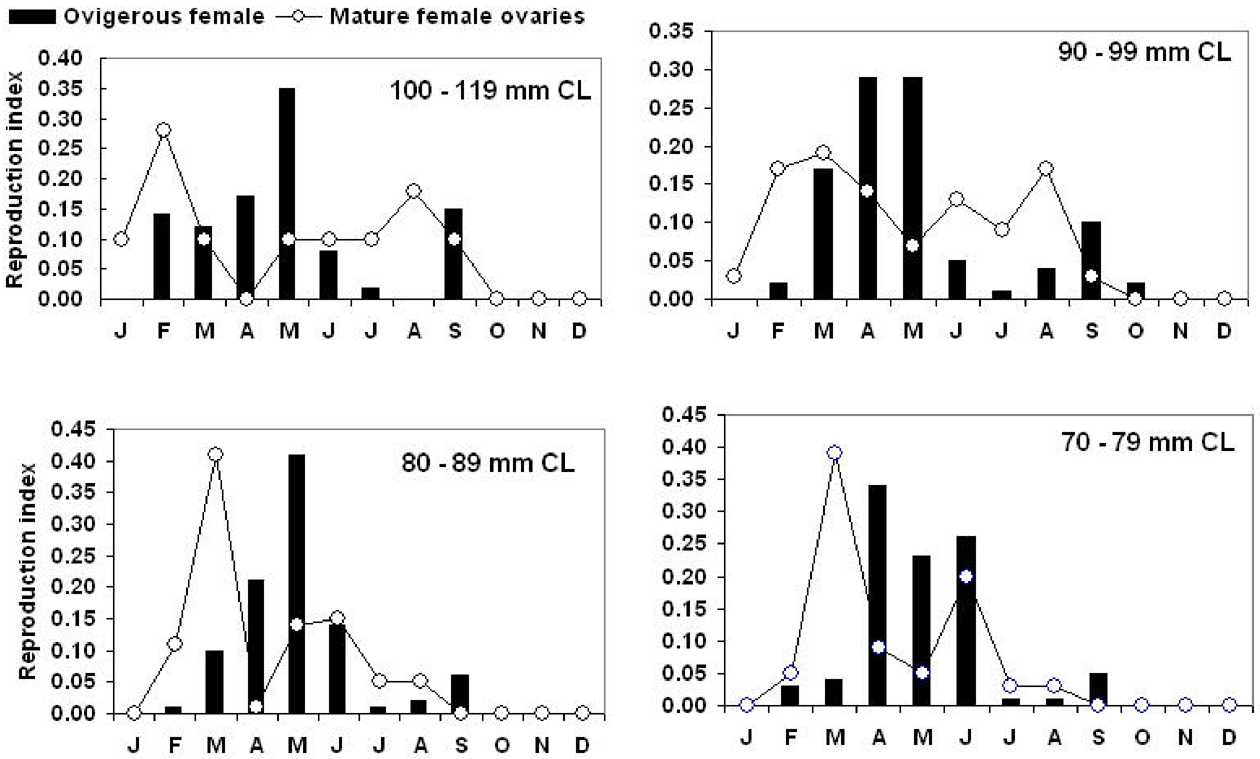

Figure 1. Reproductive cycle for the spiny lobster *Panulirus argus* by length composition on the shelf of Cuba.

Cuba), the principal spawning season is between March and May (Cruz and León 1991, Cruz *et al*. 2001b) for lobsters larger than ~70 mm CL). A secondary peak occurs in September for lobsters between 90 - 119 mm CL (Figure 1). The peak of spawning season for very large egg-bearing females (> 120 mm CL) residing on the deep reef of Providencia occurs during October - November (Cruz *et al*. 2007a). The peak of spawning season in the Bahamas occurs in April (Smith 1951). The principal spawning season in the Florida Keys, north-eastern coast of Cuba and the archipelago of San Andrés-Providencia-Santa Catalina is between April and June (Gregory *et al*. 1982, Cruz *et al*. 2001b, Bertelsen and Cox 2001, Cruz *et al*. 2007a). The peak of the spawning season in the south Florida is estimated to occur in early May for lobsters larger than 90 mm CL (principally the Dry Tortugas) and late May for lobsters smaller than 80 mm CL (principally in the Florida Keys) (Bertelsen and Matthews 2001). In northeast Brazil, the principal spawning season is between March and April (Soares y Cavalcante 1984).

The annual ovigerous female cycle of *P. argus* for various regions in the Atlantic is summarized in Figure 2. The overall pattern was markedly seasonal, approximately 85% of all reproduction occurred during March - May and is related to lobster size and water depth. The regional variation of this pattern depends on the seasonal trend in water temperature with each region (Cruz 1975, Gregory *et al*. 1982).

Lobster eggs were categorised as brilliant orange (recently spawned), dark orange (embryo eyes appear as oval black points), and brown (near hatching) with egg size diameters of 509 ± 4.16 µm, 578 ± 7.10 µm and 618 ± 6.80 µm (Mean and 95% confidence limits) respectively (Cruz 1980). Mota-Alves and Tomé (1967) in Brazil reported egg size diameters ranging from 480 to 660 µm. The eggs are carried on the pleopods for three to four weeks before hatching depending on water temperature (Sutcliffe 1952, Crawford 1921). Eggs capsule remnants have been observed on females after the eggs have hatched.

Field evidence has shown that the frequency of multiple spawning for *P. argus* in Cuba (Cruz and León 1991) and *P. laevicauda* in Brazil (Mota-Alves and Paiva 1976) reaches 53% and 43%, respectively. In Cuban waters, egg-bearing females ranging in size between 90 and 107 mm CL, can also have mature ovaries and fresh spermatophores. This reproductive condition allows these females to produce at least two broods separated by three or fourth weeks (Cruz and León 1991). Multiple spawning appears to be less frequent in females at sizes 67 - 89 mm CL. In the Florida Keys, Gregory *et al*. (1982) reported multiple spawning in females at sizes 74 - 103 mm CL. Sutcliffe (1953), and Buesa (1965) reported two spawnings in *P. argus* in the same season. In tropical species, MacDiarmid and Kittaka (2000) suggested that spawning frequency depended on latitudinal range. Full understanding of lobster multiple spawning and mating behaviour

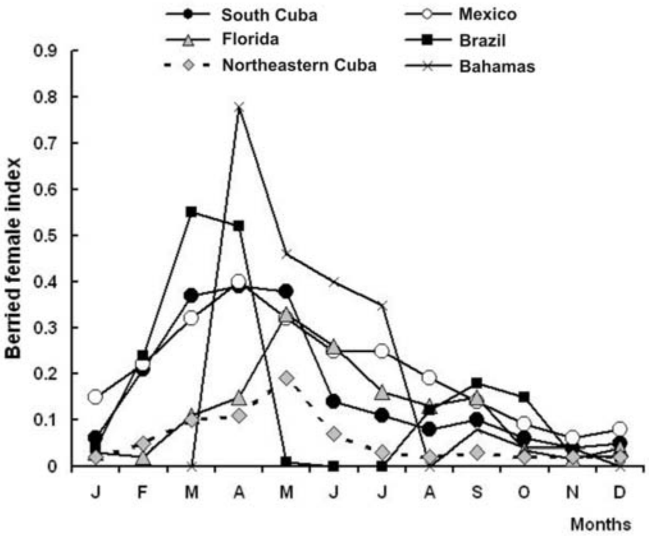

Figure 2. Summary of the ovigerous females cycle for the spiny lobster *Panulirus argus* on the shelf of south and northeaster of Cuba (Cruz *et al*. 1987), Mexico Caribbean (Cruz *et al*. 2001b), Florida (Lyons *et al*. 1981), Bahamas (Smith 1951) and Brazil (Soares and Cavalcante 1984).

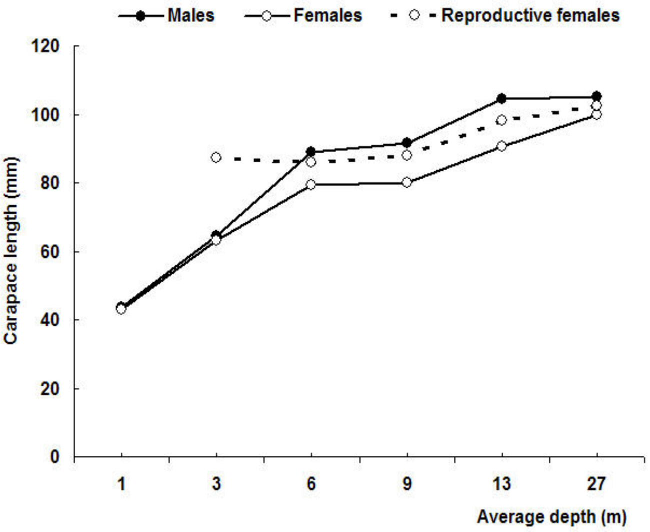

Figure 3. Relationship between mean carapace length of the spiny lobster *Panulirus argus* and the mean depth of catch. Data on the shelf of Cuba (Cruz and Phillips 2000) and in the barrier reef of Providencia-Santa Catalina, Caribbean Colombia, (Cruz *et al*. 2007a).

could have been examined. Perhaps, these require the link with the environment and fisheries.

Reproductive Activity by Depth and Location

The mean size of lobsters increases with depth ($R^2 = 0.9722$, $p < 0.05$, $n = 18$), with the mean carapace length of males being significantly higher ($p < 0.05$) than that of females, from 6 m to 13 depth (Figure 3). The mean size of reproductively active females remains relatively constant, averaging 87 mm CL, in depths from 3 to 9 m, but increases to greater than 95 mm CL from 13 to 27 m depth (Figure 3). Kanciruk and Herrnkind (Bimini; 1976) and Bertelsen (Florida; 1999) found similar positive relationships with the size of reproductively active females and depth.

The index of reproductive activity (IRA) was defined as the total number of females in any reproductive stage divided by the total number of females collected (Cruz *et al*. 1987). A highly significant relationship ($n = 11$, $R^2 = 0.7068$, $p < 0.001$) was observed between the IRA of lobsters residing in the Gulf of Batabanó and distance to the continental shelf edge (Figure 4). The IRA increases dramatically within 10 km of the interface of ocean water and the shelf edge. During March and April, lobsters inhabiting the Gulf of Batabanó are relatively small (between 69 to 82 mm CL) and are sexually immature or sexually inactive (Cruz 2000). In the shelf edge, the unfished proportion of ovigerous females constitutes 40% to 79% of the total females collected and receives periodic migrations from the shallow waters (González-Sansón *et at*. 1991), but the contribution to total egg production by size class is unknown. Similar patterns of *P. argus* reproductive activity increasing from nearshore area to outer reefs near the open ocean have been described in Bermuda (Evans *et al*. 1995, Sutclife 1952, 1953), Bahamas (Kanciruk and Herrnkind 1976), and Florida Keys (Gregory *et al*. 1982). These areas perhaps constitute an "optimal environmental window" (Cury and Roy 1989) where the reproductive success is highest helping to assure oceanic larval recruitment.

Size at Onset of Female Breeding

Knowledge of the size at onset of breeding (SOB) is important for determining the percentage of females which contribute eggs to the population pool. SOB is defined as the size where 50% of females carry eggs. In Cuba, SOB varied between 79 to 81 mm CL (Figure 5). Similar estimates of SOB have been reported from Brazil (79 mm CL; Soares and Cavalcantes 1984), Bermuda (81 mm CL; Evans, 1990), the Dry Tortugas (85 mm CL; Bertelsen and Matthews 2001), Florida Keys (75 mm CL; Bertelsen and Matthews 2001), and the Bahamas (81 mm CL; Ehrhardt, 1996). An inverse relationship between water temperature and size at sexual maturity has been hypothesized by Bradstock (1950), Sutcliffe (1952) and Street (1969), to explain changes in SOB for different areas of the Caribbean. However, Lyons *et al.* (1981) do not support this hypothesis. Chittleborough (1976) also rejected this idea for *Panulirus cygnus* in Western Australia. Therefore, it is possible that these discrepancies in adjacent populations of the same species may be due to sampling methodologies.

In Belize (Weber 1968) and Jamaica (Munro 1974) reported the SOB 95 mm CL, however; because these studies employed traps they may have underestimated the number of female lobsters and the composition of the breeding female (24% of the total) due to trap avoidance

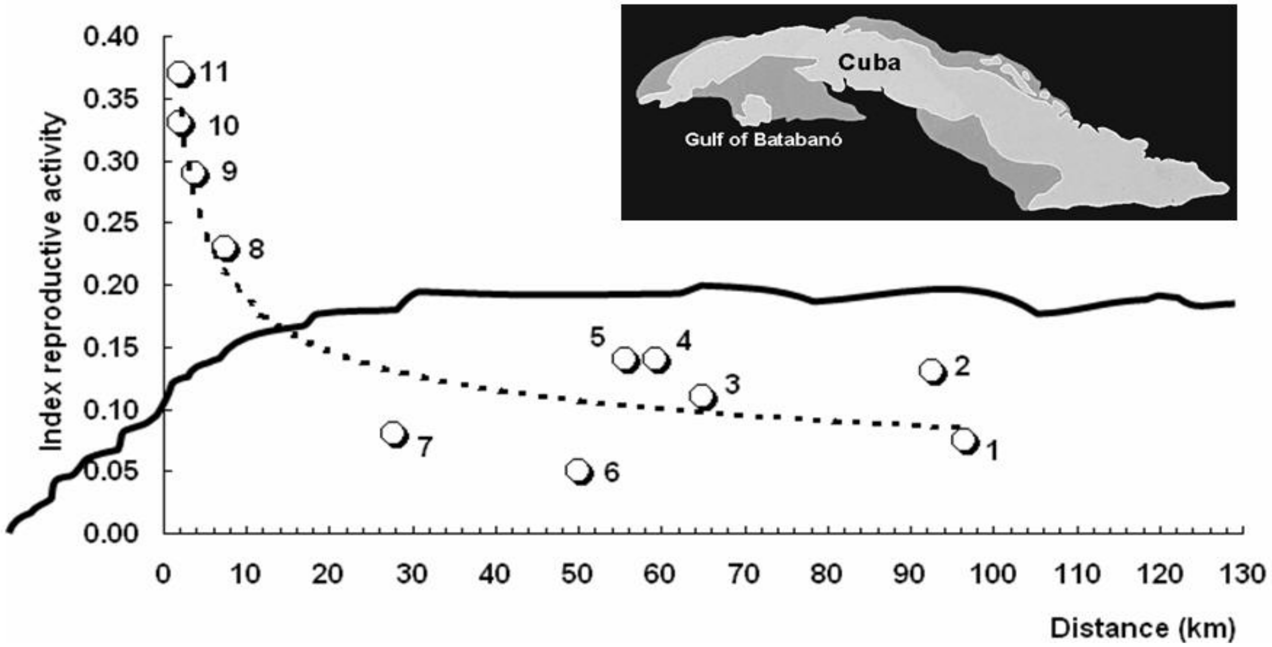

Figure 4. Relationship between the index of reproductive activity of the spiny lobster *Panulirus argus* and the distance from the locations to the edge border habitats shelves in the Gulf of Batabanó. Localities: 1- Ensenada de la Broa (22° 27' 56 N 81° 53' 33 W), 2- La Gata (22° 23' N 82° 25' W), 3- El Verde (22° 11' 14" N 83° 23' 31" W), 4- Rabihorcado (22° 17' 54" N 82° 45' 37" W), 5- Cayo Redondo (22° 02' N 82° 51' W), 6- La Traviesa (21° 58' N 81° 50' W), 7- Cayo Dios (22° 02' N 83° 10' W), 8- Cantiles (21° 34' 40" N 82° 14' 55" W), 9- Cayo Sigua (21° 52' 31 N 81° 23' 08" W), 10- Sur Matías (21° 33' 31" N 83° 22' 02" W), 11- Sur San Felipe (21° 56' 46" N 83° 22' 28" W).

(Chittleborough 1970, Morgan 1974, Kanciruk and Herrnkind 1976). For similar reasons, the estimated SOB (90 mm CL; Sutcliffe 1952) in Bermuda maybe due to the deep water placement of traps and that small females are seldom found at these depths. The SOB of female lobsters was estimated at 80 - 89 mm CL in Jamaica (Aiken 1977) and 86 - 95 mm CL in Dry Tortugas (Davis 1975). These estimates are difficult to evaluate due to very low precision of the sampling design.

Some studies that have reported SOB, unfortunately are based on small sample sized. These include 80 - 89 mm CL in Antigua and Barbuda (Peacock 1974), 96 - 100 mm CL in Bimini (Kanciruk and Herrnkind 1976) (also not conducted during peak breeding season), 91 - 95 mm CL in Florida (Lyons *et al.* 1981), 78 mm CL (Paiva and Costa 1963), 69 mm CL (Nascimento and Santos 1970), and 92 mm CL (Anonymous 1979) reported in Brazil

The presence of setae on the pleopods is sometimes used to indicate sexual maturity of females. Gregory and Labisky (1981) used this character to estimate an SOB at 85-90 mm CL in Florida Keys; however, Chittleborough (1974) observed that *P. cygus* females became setose 5 to 15 months before spawning, so caution may be in order when using this character.

The slowing in growth rate of female lobsters may signify a shift in energy use at onset of maturation. Hunt and Lyons (1986) reported that a decrease in growth rate of females occurred between 71 - 75 mm CL and 76 - 80 mm CL size classes and suggest that the size of first spawning is about 75 mm CL. However, Munro (1974) pointed that growth rates are quite divergent among authors and Cruz *et al*. (2001a) show with a mark-recapture study, that the 71 - 75 size range corresponds to when sub-adults migrate (recruit) to adult habitats (lobster fishing grounds). Therefore the slowing of growth rate in females should not be considered as an indicator of the size at first maturity.

Unusually small sizes of SOB reported: 57 mm CL (Buesa 1965), 60 - 69 mm CL (Cruz 1980), 45 - 69 mm CL (Smith 1948; Paiva y Costa 1963, FAO 1965, Butler and Pease 1965, Cobo de Barany *et al*. 1972, Costa and Gesteira 1974) in the Caribbean, but these are exceptional cases. These cases should not be considered as an indicator of the size at first breeding because this size is an attribute of the lobster population and not of the individuals sampled. They are individuals who due to metabolic issues (Hunt and Lyons 1986) or reduced growth, they mature at a smaller size than normal.

Fecundity

Some early estimates of the fecundity of *P. argus* females were made in Florida (Crawford and Smith 1922, Smith 1948), Bermuda (Creaser 1950), Cuba (Buesa 1965) and Brazil (Mota-Alves and Bezerra 1968, Nascimento, 1976). Because egg counts were only made for a few individuals for very few sizes, a size-fecundity predictive curve could not be estimated.

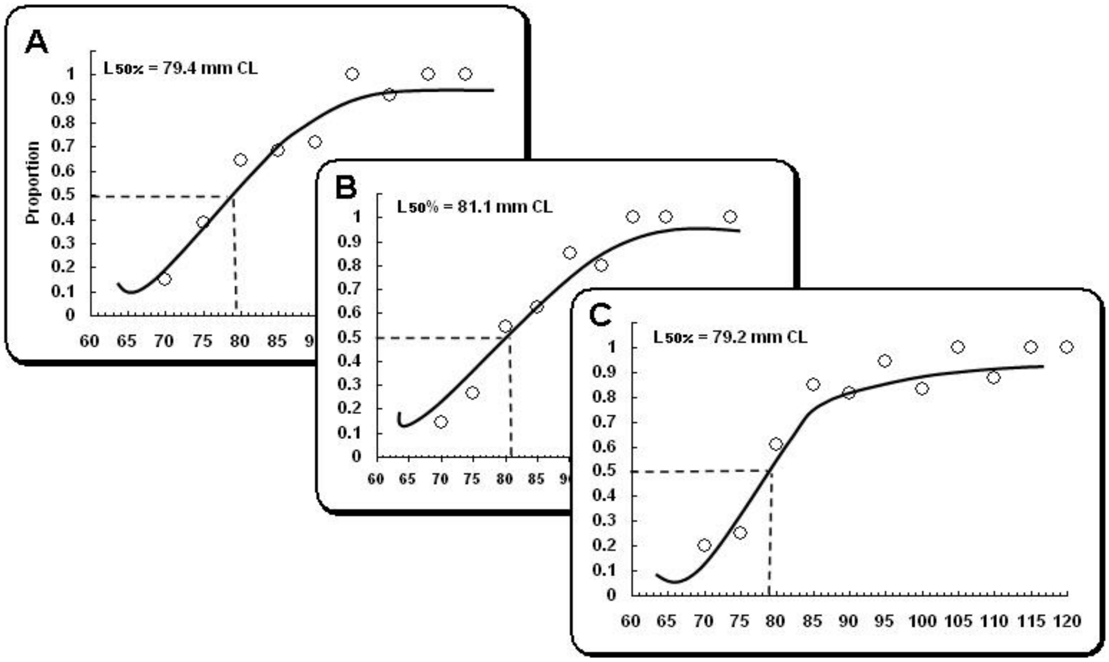

Figure 5. Curves of retention of ovigerous female for the spiny lobster (*Panulirus argus*) in different areas on the south coast of Cuba. (A)- Sur Juan Garcia-Cayo Coco (21° 57' N 82° 32' W), (B)- Peralta-Boca Rica (20° 03' N 77° 39' W) and (C)- Bretón-Machos de Afuera (21° 33' N 79° 39' W).

The carapace length to brood size or mass relationship for spiny lobsters is best described through the power relationship ($y = ax^b$ or $y = a + bx^c$; Systat, 2002) and has been used, for example, to describe this relationship for *Jasus edwardsii* (Annala and Bycroft 1987, Linnane *et al.* 2008), *Panulirus marginatus* (DeMartini *et al.* 2003), *Panulirus guttatus* (Acosta and Robertson 2003), *Panulirus elephas* (Goñi *et al*. 2003), and *Panulirus argus* (Bertelsen and Matthews 2001). For *P. argus* data collected from Cuba: Ensenada de la Broa, Punta del Este and south eastern (Cruz 1980); Florida Keys and Dry Tortugas (Bertelsen and Cox 2001) and Mexico Caribbean (Ramírez, 1996), the eggcount to carapace relationship was found as Egg Count = $2.668CL^{2.709}$ (n = 658; F = 3373; p << 0.00001) (Figure 6).

Subsequent observations of fecundity across a range of sizes have shown that brood size (number of eggs) is a function of carapace length (Figure 6); large females brood more eggs that smaller females. For example the fecundity was estimated between 159000-1727775 at 62 - 135 mm CL respectively on the south coast of Cuba (Cruz 1980), 280400-1308200 at 77 - 145 mm CL respectively in México Caribbean (Ramírez 1996) and 147000-1952000 at 72 - 141 mm CL, respectively in Florida Keys (Bertelsen and Matthews 2001). The mean fecundity (mean egg count ± 95% confidence limits) is 414176 ± 29808 (Florida), 467481 ± 25413 (Cuba archipelago), and 732626 ± 82031 (Mexico Caribbean). The female lobster mean size is 83.08 ± 1.62 mm CL (Florida), 92.42 ± 1.47 mm CL (Cuba archipelago), and 110 ± 5.49 mm CL (Mexico Caribbean). The *P. argus* size-fecundity relationship is relatively independent from geographical position (Cruz 1980). Morgan (1972) reported similar results for *P. cygnus*.

Female lobsters larger than 100 mm CL produce at least two spawnings that are separated by three to four weeks (Cruz 1980, MacDiarmid and Kittaka 2000). Within a given size class, variation in the egg count can range between 40 to 70% (Figure 6). Bertelsen (1999) tested whether egg counts declined in the field during the spawning season by regressing the observed egg count minus expected egg count (standardized residual) with time. For south Florida data collected from 1995 through 1998, egg counts were found to be consistent throughout the season (slope = 0.00083 Std. Res./day; F = 0.259; p = 0.611) (Figure 7). Nonetheless, variability in fecundity in a lobster population is one of the major obstacles to understanding the relative contributions of the population to total egg production and defeats attempts at stock-recruitment prediction. Lobsters larger than 140 mm CL show the highest fecundity variation but all female lobsters produce > 1 million eggs.

Assessment of Population Egg Production

The index of reproductive potential (IRP) by female size class was developed by Kanciruk and Herrnkind (1976) in Bimini to estimate the contribution of overall fecundity by different size classes of female lobsters. This index is sensitive to the methodology used to collect the data (e.g. traps, artificial shelter observation, and diver census) and whether the data were collected near the peak

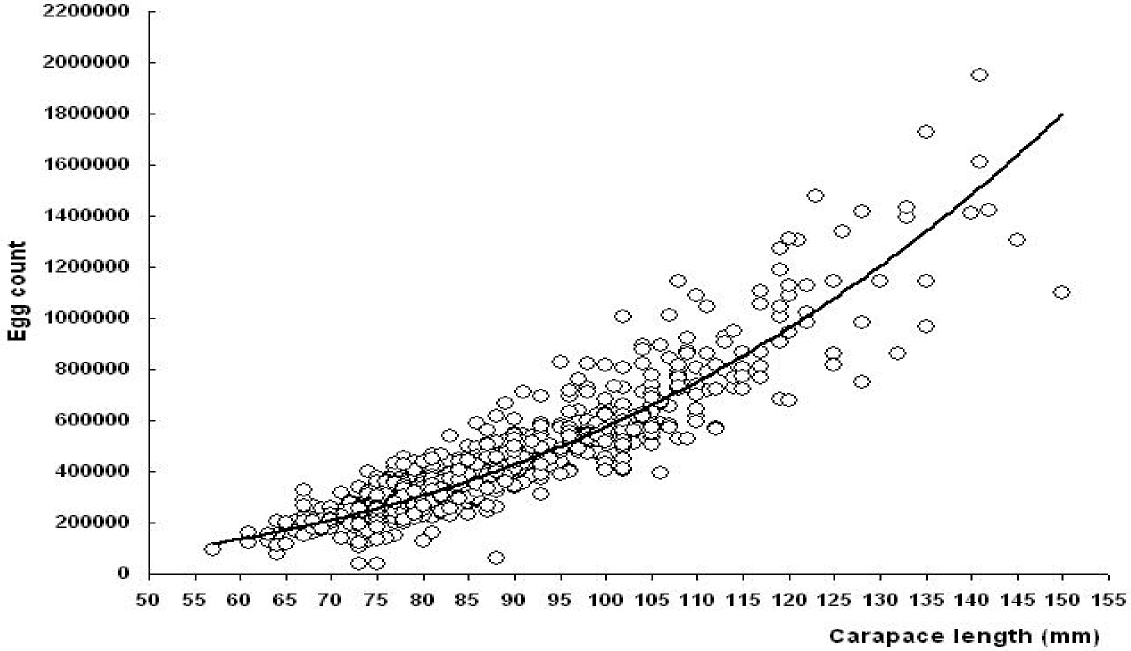

Figure 6. Relationship between egg clutch size and carapace length (mm) for female *Panulirus argus* on the Greater Caribbean region using the data from Cuba: Ensenada de la Broa (22° 27' 56 N 81° 53' 33 W), Punta del Este (21° 33' N 82° 33' W) and south eastern (Cruz, 1980); Florida Keys and Dry Tortugas (Bertelsen and Cox, 2001) and Mexico Caribbean (Ramírez, 1996). N = 658, $R^2 = 0.7913$, F = 3373, P << 0.001, female lobster size between 57 to 150 mm CL and equation: egg count = $2.668CL^{2.709}$.

spawning season because larger lobsters tend to begin and end spawning sooner than small lobsters (Lipcius 1985, Bertelsen and Matthews 2001). The data were obtained by SCUBA diving at the western edge of Bahamas Bank using the average fecundity by size of Mota-Alves and Bezerra (1968) in Brazil. Gregory (1979) and Lyons *et al.* (1981) in Florida and Cruz and León (1991) in Cuba, used the same equation. The first two studies obtained data only by trapping while the data from Cuba were obtained from artificial shelters (casitas cubanas or pesqueros). Other analyses estimate IRP by using the combination of the number of mature females per kg of catch from monitoring lobster catch in the area with pesqueros (Ni), the catch (kg) of female per number of pesqueros checked for the region (Ci), the average fecundity in the region (Fi) and the spawning area (Ai - km^2) in the region (Cruz 2000, Cruz *et al.* 2007a). These data are applied to the spawning stock index model recommended by Chubb (1994) in *Panulirus cygnus.*

The review of the data of spawning female recorded in pesqueros, showed that ovigerous females constitute 80% of the total females collected near the shelf edge. Lobsters sampled by trapping and diving probably introduce an error through selective sampling. Diving areas are occasionally influenced by the amount of fishing effort there and large egg-bearing females establish solitary dens and seldom feed, probably biasing catch in the large size classes. Kanciruk and Herrnkind (1976) suggest that trapping underestimates the number of gravid females. However, Davis (1975) and Lyons *et al.* (1981) relied on traps to collect most of their data and rejected Kanciruk and Herrnkind (1976) observations. The early years of data (1976-1996) using different sampling methods, making them difficult to compare with data from 1996 onwards.

Relative magnitudes of egg production as indicated by the IRP and size of spiny lobsters on the south coast of Cuba (Gulf of Batabanó) is greatest by females in the range 90-100 mm (CL). This is the most (74%) productive size while representing 38% of all females caught with a productivity rating of 1.84 % (IRP / % of total female). The size class 70-80 mm CL represented 50% of all females collected but produced only 11% of the estimated egg production and a productivity rating of 0.4. However, females larger than 110 mm CL produced 19% of the egg production while representing 11 % total females. On the shelf of Providencia and Santa Catalina, the IRP (Cruz *et al.* 2007a) the size class 100 - 110 mm CL produced the greatest percentage of egg production (67%) with a reproductive rating of 1.53%. The females ≤ 90 mm CL produced 41 % of the total egg production, < 16% (IRP) and a productivity rating of 0.39 (Figure 8). Although, the two regions are ecologically quite different in lobster size frequency and in depth distribution of habitat, the difference in egg production by size class suggests overfishing of large lobsters (Cruz *et al.* 2007a). Fishing larger lobster in deep water (≥ 20 m) reduces the most reproductively important individuals, depresses the population and the reproductive potential of species. The IRPs calculated are comparable because they were produced using the same

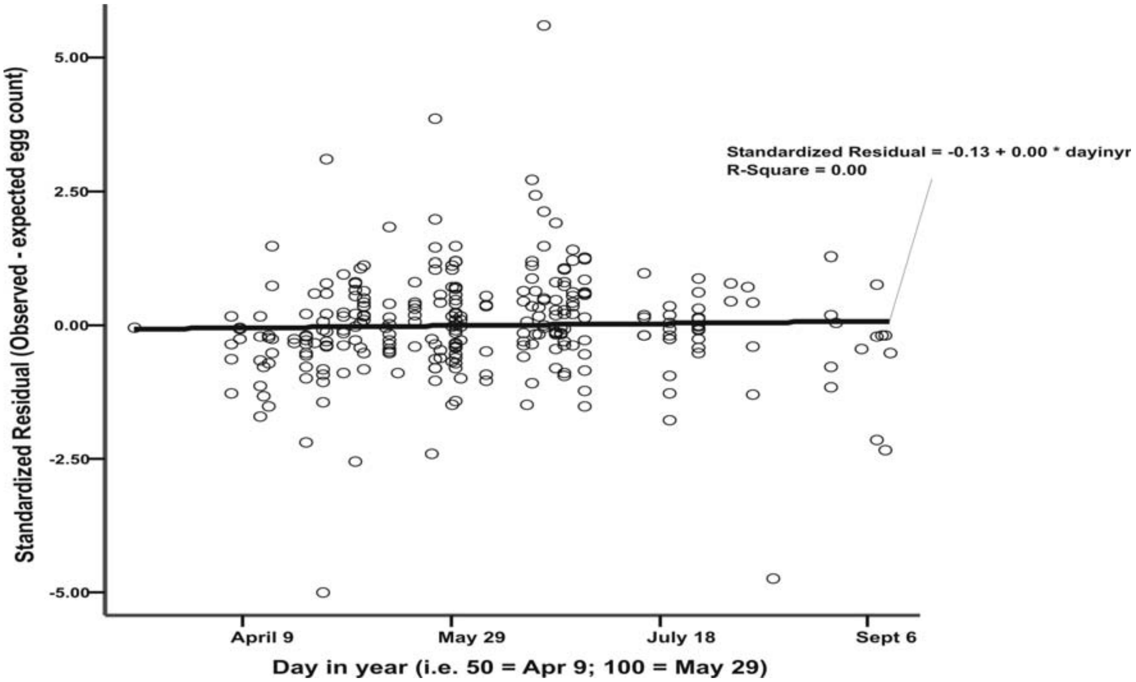

Figure 7. The standardized residual of egg counts (observed – expected) regressed by time for south Florida spiny lobsters observed from 1995 to 1998. The lack of any slope (+0,000083 Std. Res./day; F = 0.259; p = 0.611) indicates that egg counts by individual lobsters remain consistent through the spawning season. The x-axis represents the day in year where for example, Jan 1 is the first day and April 9 is the 50th day.

methodology. The average of values for each region probably indicate the length composition and magnitude of potential spawning index contributions for all the Wider Caribbean regions (Figure 8). Absolute densities of spawning lobsters must also be considered when comparing relative spawning contributions between regions.

The fishing of the largest lobsters can reduce the overall quality of the eggs in a population. The largest females have eggs with more yolk granules which results in larger larvae, perhaps containing more lipids at hatching (MacDiarmid and Sainte-Marie 2006). This finding is corroborated by Dávila *et al.* (2007) who found that the oocytes of lobsters sized between 97 - 127 mm CL were larger (oocytes IIA average 135.79 ± 5.96 µm) than the oocytes of lobster sized between 61 - 96 mm CL (oocytes IIB of 95.29 ± 3.98 µm). Larger females also produce more clutches per breeding season than do smaller females and large males are also capable mating more often and produce larger spermatophores than smaller males perhaps resulting in improved fertilization rates. Therefore, a management plan that protects both large female and male lobsters impacts the reproductive output of lobster stock at many levels.

Another measure that can assess the egg production of a population is reproductive efficiency as given by the number eggs a female produces per gram of her body weight. Bertelsen and Matthews (2001) examined the reproductive efficiency of female lobsters in south Florida and found that the highest level of eggs per gram of body mass occurred between a carapace length of 80 to 110 mm CL. When these calculations were performed on additional data collected in Mexico and Cuba (Cruz, 1980; Ramírez, 1996), we found the greatest reproductive efficiencies (greater than 800 eggs per gram body weight) for females between 80 and 114 mm CL. In south Florida, when fisheries independent size distributions of lobsters from adult lobster habitat were plotted against reproductive efficiency (Figure 8: Bertelsen and Matthews 2001), they found that 75% of the female population was below 80 mm CL. At carapace lengths above 114 mm, reproductive efficiency began to decline but only by approximately 12% from peak effienciency to the maximum sized females (144 mm CL) (Figure 9). Goñi *et al.* (2003) found a similar relationship in *Panulirus elephas* in the western Mediterranean.

Recruitment

Through its complex life cycle, the Caribbean spiny lobster *P. argus* lives in a wide variety of environments and changes of habitat during its ontogenetic development. The pueruli arrive at the coast every month and settle in complex substrates, especially hard-bottom habitat covered by the red macroalgae, *Laurencia* spp. (Marx and Herrnkind 1985, Herrnkind and Butler 1986, Lalana *et al.* 1989) and others species of algae (Brito and Suáres 1994). The yearly periodicity of settling pueruli is very different geographically and all the processes involved are not yet completely understood. For example, Florida Keys showed a larger peak in February-March with the lowest

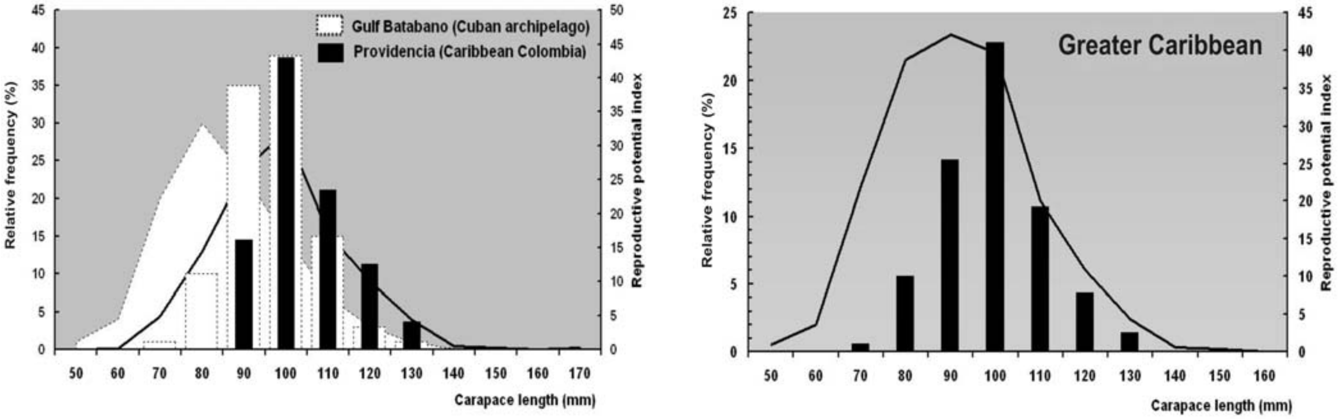

Figure 8. Relative frequency (bars) and Reproductive potential index (lines) by carapace length. (A)Contribution of female size classes to population egg production (Reproductive potential index) in *Panulirus argus* stock of Gulf of Batabanó (1 to 6 m) in Cuba (Cruz, 2000) and barrier reef of Providencia-Santa Catalina (10 to 27 m), Caribbean Colombia, (Cruz *et al*., 2007a). (B) Combination of the average size classes and egg production (RPI) was useful as a first approximation of the *Panulirus argus* population in the Greater Caribbean.

settlement occurring in August, but other studies in Cuba archipelago and Mexican Caribbean have found a larger peak in October. In Bermuda settlement is concentrated in August and September (Cruz *et al*. 2001b). However, in most other Caribbean locations, yearly settlement patterns are unknown.

Approximately eight months after hatching, the pueruli become juveniles, settling into shallow nursery areas for the next 6–8 months. Lobsters between 45 and 50 mm CL become nomadic generally moving away from nursery areas towards deeper hard-bottom areas closer to the open ocean and ultimately recruit to the fishery, as supported by mark-recapture results in the Florida Keys (Forcucci *et al*. 1994, Butler and Herrnkind 1997) and Cuba (Cruz *et al*. 1986b, Cruz *et al*. 2001a). The direction of movement of lobsters tagged in the nursery area of Florida Bay and Bocas de Alonso (Cuba) is generally toward the south and recruitment to the fishing grounds was at a mean size of 76.2 mm CL (Davis 1978, Davis and Dodrill 1980, Davis 1985) and 76.8 mm CL (Cruz *et al*. 1986b, Cruz *et al*. 2001a), respectively (Figures 10 and 11). These results are very consistent, no additional fieldwork on the directed offshore movement of juvenile has been published and this recruitment size offers a new perspective on the regulation of pre-recruit lobsters.

Recruitment to the fishing grounds exhibits a pronounced seasonal cycle. From March to May the average size of lobsters decreases corresponding with the arrival of the small lobsters (pre-recruits) into the fishery (Cruz *et al*. 2001a). These data concur with the results of Cruz (2001) in Brazil (February - May). Lyons *et al*. (1981) reported a decrease in the average size in the months of February - March in the sampling stations at Matacumbe (24° 53' N 80° 44' W) and Fat Deer Key (24° 39' N 80° 59' W), Florida. No other seasonal pre-recruit studies are available for any Caribbean spiny lobster (*P. argus*, *P. guttatus* and *P. laevicauda*).

Management Implications

The Caribbean fishery has been regulated for more than a half century in some regions, but control measures are inconsistent in the fishery and law enforcement is often ineffective. The existing principal management regulations include a minimum legal size, a closed season, and a prohibition on the taking of egg-bearing females. Where large recreational fisheries are present (e.g. Florida and Bahamas), a personal daily bag limit is added to the regulations.

This review of the life history of the spiny lobster (*P. argus*) aims to provide information that will improve the management of this valuable resource and suggests that new regulatory measures for all the population should be adopted to increase the reproductive potential and ensure sustainable recruitment, keeping in mind that all the lobster fisheries are considered fully exploited or overexploited.

The closed seasons for spiny lobster vary remarkably in each country: Brazil (1 January to 30 April); Cuba and Belize (15 February to 15 June); Mexico Caribbean and República Dominicana (1 March to 30 June); Nicaragua (1 April to 2 June); Archipiélago San Andrés-Providencia y Santa Catalina and Jamaica (1 April to 30 June); Bermuda (April 1 – August 31st); Bahamas, Honduras and Turks and Caicos (1 April to 31 July); Florida (1 April to 5 August); Saint Lucia (1 May to 31 August); and Venezuela (1 May to 31 October). The first recommendation those managing lobster fishery was to legislate a closed season for all the countries in the western Atlantic that fish lobster (*P. argus*) between the months of 1 February to 30 June to protect the highest reproductive cycle (maturity and ovigerous female) and the principal recruitment peak (March to May) to the

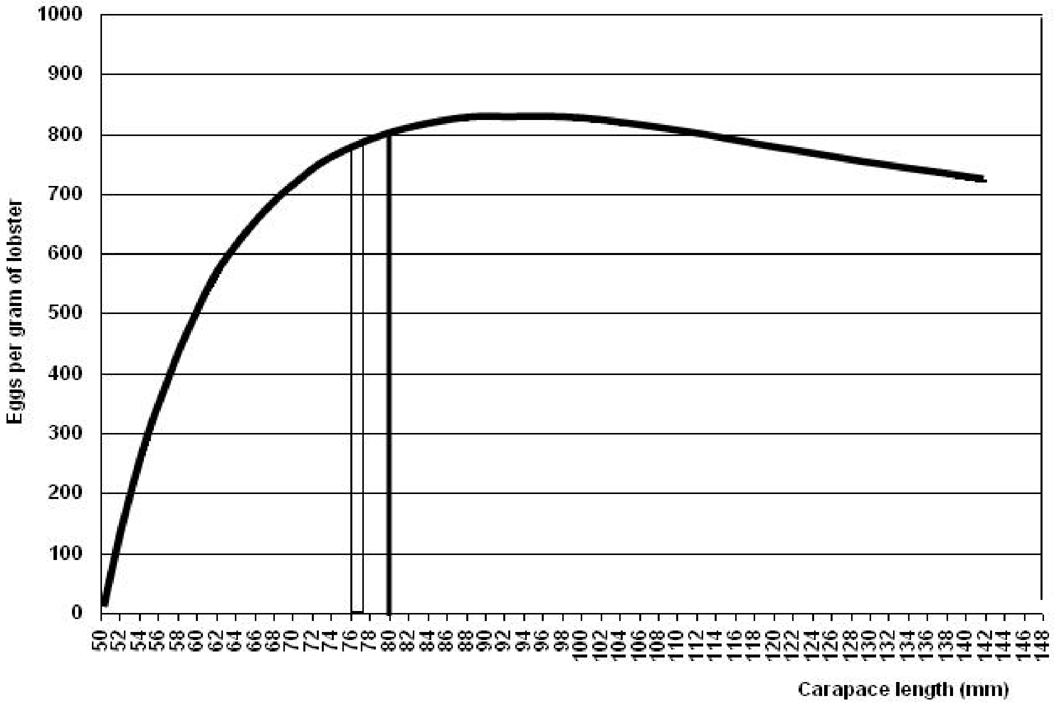

Figure 9. Reproductive efficiency in units of eggs per gram of body mass by carapace length (modified from Bertelsen and Matthews, 2001) for the spiny lobster *Panulirus argus* in the Greater Caribbean. The open and dark line represents the size of the pre-recruit between Florida, 76.2 mm CL (Davis and Dodrill, 1980) and Cuba, 76.8 mm CL (Cruz *et al*., 2001a). and the optimum minimal legal size (80 mm CL), respectively.

fishing grounds (Figure 12); it coincides with the decrease in the average size of lobsters and the arrival of the smallest lobsters (pre-recruits) into the fishery. These regulatory measures reduce the total effort indirectly, reduce the capture of berried females and pre-recruits, and diminish the mortality of undersized lobster through reduced handling. The second recommendation was to situate escape gaps in the traps to allow the escape of the juvenile and sublegal lobster. The third recommendation was to eliminate the use of undersized lobsters (decoys or shorts) in fishing gear. This will significantly improve the survival of pre-recruits and will increase the total yield from the stock.

The high densities of lobster juveniles in nursery areas, their gregarious behaviour, their territorial migratory habits, and the evidence of decreasing recruitment to nursery areas in the Gulf of Batabanó from 1988 onwards (Cruz *et al*. 2007a) suggest that placing artificial shelters to improve the habitat might help diminish natural mortality, increase the local abundant of lobsters and increase recruitment to fishing areas (Eggleston *et al*. 1990). The establishment of marine reserves or a total closed season to protect the juvenile nursery areas, decrease human impact (diminish commercial and recreational fishing) since, as a result, the fishing mortality is null, the injure mortality decreases (Parsons, 2006), and the recruitment and population could increase (Cruz *et al*. 2006). As the fishery currently stands, it is not advisable to introduce artificial shelters for juveniles in countries that have an open access fishery and a huge contraband of sub-legal lobsters. In Guajira (Colombia), for example, most (70%) of the lobster catch (number) is sub-legal (Nieto and Barreto, unpublished data) and is from unregulated artificial shelters.

The minimal legal size (MLS) in Belize, Cuba, Florida and Jamaica (76 mm CL), Quintana Roo-Mexico (74 mm CL) and Brazil (75 mm CL) fisheries is less than the size at onset of female breeding calculates (79 to 81 mm CL). Though this legal size is highest in the regions of Mexico (others areas), República Dominicana and Honduras (80 mm CL), archipelago San Andrés (Colombia) and Bahamas (82 mm CL), Turks & Caicos and Nicaragua (83 mm CL), Grenada (90 mm CL), Bermuda (92 mm CL), Saint Lucia, Nevis (95 mm CL) and Venezuela (120 mm CL). However, the law enforcement is ineffective in most countries, with the notable exceptions of Cuba, Florida and Bermuda. This uncontrollable violation has internationalized the illegal trade of lobsters due to the open access and increased the overfishing of growth in the local stock.

Based on the average size at 50% first maturity and on the eggs produced per gram of lobster body mass (reproductive effiency or eggs/gm) (Bertelsen and Mathews 2001), we suggest 80 mm CL (802 eggs/gm), as the optimum minimal legal size that should be adapted in the Atlantic spiny lobster fishery. For lobster between 85 mm CL (820 EgLmCL) to 95 mm CL (828 EgLmCL) the

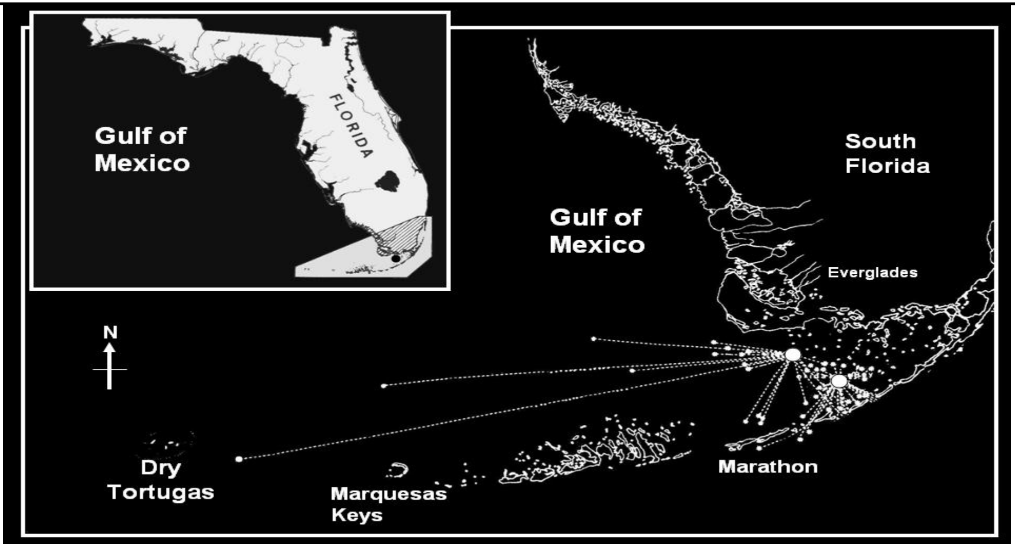

Figure 10. Summary of migratory movements by tagged spiny lobster (*Panulirus argus*) from nursery area of Florida Bay (Florida) to mature adults zone or reef sites (modified from Davis and Dodrill, 1980). The movement of the pre-recruits was generally to the southwest, with recaptures sometimes,hundreds of kilometres from the tagging site.

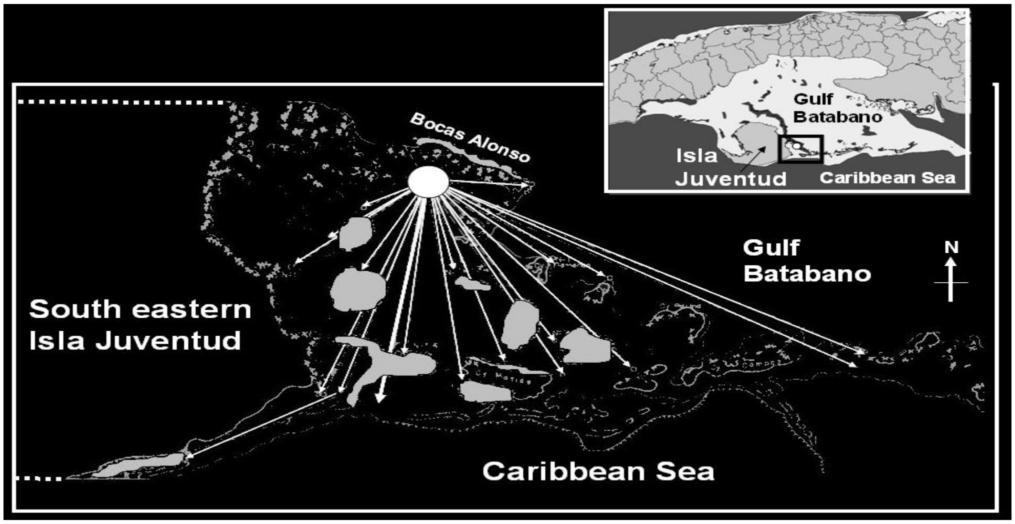

Figure 11. Summary of migratory movements by tagged spiny lobster (*Panulirus argus*) from the nursery area of Bocas de Alonso (21º 41'10.90" N 82º 28' 35" W) to the fishing grounds (grey shadow) or mature adults zone (modified from Cruz et al., 1986b). The movement of the pre-recruits to the south-western, travelling between 3 to 30 km, and are recruited to the fishery with an average size of 76.8 mm CL, range 74-79 mm CL (Cruz *et al*., 2007b).

predicted number of eggs per gram of body mass increased only between 2% to 3% respectively (Figure 9). In Cuba, Cruz *et al*. (1991) demonstrated that with an extension of the closed season and strict observance of the MLS since 1978, the sublegal catch declined which in turn resulted in an increased of the mean size of selection and an increase in harvest by approximately 3000 t. We recommend increasing the MLS at a rate of 2 mm CL per year, equivalent to 5.9 mm of total length (TL, measure of the base of the antennules to end of telson), until the MLS reaches 80 mm CL (244 mm TL).

One of the problems that law enforcements encounters in the illegal trade of lobster tails is the inconsistent tail measurements (Raymond 2006). Tail measurement was criticized more than half century ago by Creaser (1952) when he expressed that: “The abdominal length measurement is subject to considerable error as the segments are flexible allowing varied readings. The telson also becomes frayed or torn and the curvature of the abdomen is also a source of error on the abdominal measurement”. Another difficulty with using abdominal length as an enforcement tool is that the equivalent carapace length to abdominal length relationship is different between male and female lobsters (Matthews *et al*. 2003) where in adult male lobsters the abdomen grows proportionally slower with respect to the carapace length than in female lobsters. For

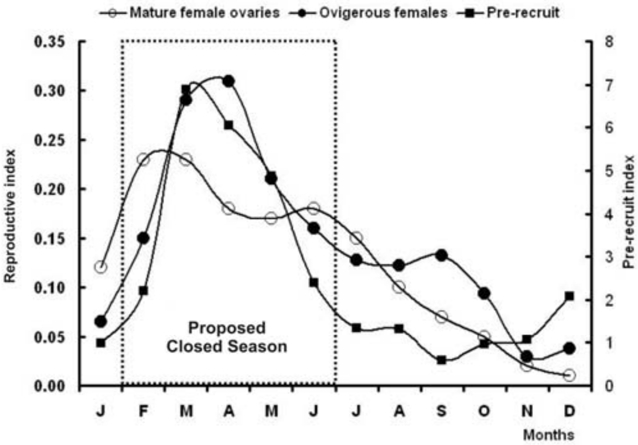

Figure 12. Summary of the mature female ovaries (Soares and Cavalcante 1984, Cruz *et al*. 1987), ovigerous females (Smith 1951, Lyons *et al*. 1981, Soares and Cavalcante 1984, Cruz *et al*. 1987) cycle and average pre-recruit index (Cruz 2000, Cruz and Phillips 2000) for the spiny lobster *Panulirus argus* in the Greater Caribbean. The rectangular dotted line show the recommended closed season.

example, in Florida a newly recruited male (76 mm CL) has an average abdomen length of 139 mm whereas the female tail length is 145 mm.

When tail has been separated from the carapace, a new measure of the tail width (TW) should be considered, measured between the spine tips on the second abdominal segment. The TW measurements is more accurately because the inflexibility of the spine. In the *Jasus* especies fishery in New Zealand, tail width was a better indicator of CL than tail length (Booth and Breen 1994). Nevertheless, Matthews *et al*. (2003) in *P. argus* suggest that the tail length is slightly more accurate as an estimator of carapace length than is tail width.

The use of tail weight as an enforcement or regulatory tool is subject to many factors that render it highly imprecise such as handling damage and other production processes in the industry. Thus, most countries' regulations require a minimum length and not weight. Regional morphometric measures do vary among local stock (Matthews *et al.* 2003), and this has undoubtedly affected harvest estimates. The use of standardized internationally accepted measurements is required to provide all countries with the means to report comparable harvests and to allow meaningful regulation of spiny lobster across its Pan-Caribbean distribution.

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