CARIBBEAN LOBSTER REPRODUCTION: A REVIEW

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ABSTRACT

This review of the reproduction of the spiny lobster *Panulirus argus* aims to provide information that will improve the management decisions, the study in population dynamics and on spiny lobsters aquaculture research. We update the reader on this topic with studies carried out by decades in Cuban archipelago, Florida, Bermuda, Mexico and Brazil. In particular, it was discussed the results of fieldwork studies on reproductive cycle, fecundity, brood size and population egg production. It is pointed out the need to undertake studies in captivity for understanding of the reproductive mechanism and maturation in this specie. Despite the increasing number of experimental studies on reproductive system, courting, copulation and spawning of lobsters, laboratory trials carried out have proven to be not enough to get a detailed knowledge of the reproductive process of *P. argus*, which it is considered necessary to increase the experimental research. Factors affecting reproduction (seasonality and temperature) have not been fully understood. The impact of fishery and hydro-meteorological event at the level of the interface between shelf edge and the ocean water, where reproductive performance and egg production is high, needs special research attention. The fraction of stock inhabits deep (30-50 m) region with a carapace length more than 90 mm, perhaps ensure the size of the spawning stock and the reproductive capacity of the specie.

Key words**:** review; reproduction; fecundity; *Panulirus* spp.; ASW, Cuba.

RESUMEN

Esta revisión de la reproducción de la langosta *Panulirus argus* tiene como objetivo proporcionar información para mejorar las decisiones de gestión, el estudio de la dinámica poblacional y en la investigación de la acuicultura de langostas espinosas. Actualizamos al lector en este tema a partir de los estudios realizados durante décadas en el archipiélago cubano, Florida, Bermuda, México y Brasil. En particular, se discuten los resultados de los estudios de campo sobre el ciclo reproductivo, fecundidad, tamaño de la freza y producción de huevos en la población. Se enfatiza la necesidad de efectuar estudios en cautiverio para comprender los mecanismos de maduración reproductiva en esta especie. A pesar de que ha habido un número creciente de trabajos experimentales sobre el sistema reproductivo, cortejo, copulación y desove de las langostas, los experimentos realizados han sido insuficientes para obtener un conocimiento detallado del proceso reproductivo de *P. argus*, por lo que se considera necesario incrementar la investigación experimental. Los factores que influyen en la reproducción (estacionalidad y temperatura) no han sido comprendidos plenamente. El impacto de la pesca y eventos hidro-meteorológicos, en la interfase entre el borde de la plataforma y el agua oceánica, donde el éxito reproductivo y la producción de huevos son elevados necesita de una especial atención investigativa. Se plantea la posibilidad de en la región profunda entre los (30-50 m), la fracción de la población de langostas con una longitud de carapacho superior a los 90 mm, contribuya a garantizar la talla del stock desovador y la capacidad reproductiva de la especie.

Palabras claves: revisión; reproducción; fecundidad; *Panulirus* spp.; ASW, Cuba

Efficient management decisions and achieving sustainable aquaculture of spiny lobsters require deep knowledge of the reproduction and life cycle of the exploited species. Considering the commercial importance of lobsters stocks in the Gran Caribbean, it is amazing how little knowledge exist about the reproductive ecology and biology of this resource.

Over the last 50 years in five locations: Bermuda, Cuba, Florida Keys, Mexico Caribbean and Brazil the cycles of reproduction behavior, spawning, fecundity, brood size and population egg production has been studied from data on the lobster fisheries resources, basically on *Panulirus argus* and *Panulirus laevicauda*. While the knowledge on physiology of oogenesis, spermatogenesis and fertilization, like integral components of maturation and mating, is lacking and need special attention.

Given the importance of this resource for the fisheries in the Caribbean region and considering the methods used and the intense fishing pressure that has caused reduction of spiny lobster population size structure and size at maturity (Acosta and Robertson, 2003), the aim of this

review is to synthesize available information on reproductive dynamics of lobster *P. argus* throughout the Atlantic area. In particular, we discuss the results of field and experimental studies, emphasizing the many questions which remain unanswered yet. Since experiments in captivity conditions are still insufficient, we argue that more laboratory researches and detailed observations are needed to address the gaps on the knowledge on reproductive behavior of *P. argus*.

STUDIES FROM THE FIELD

Reproductive maturity of *P. argus* female ovaries generally occurs one or two months before the spawning season (March-May) in the Cuban archipelago (Cruz and León, 1991) and Brazil (Soares and Cavalcante, 1985).

The annual ovigerous female cycle of *P. argus* on the shelf of south and northeaster of Cuba (Cruz *et al.*, 1987), Mexico Caribbean (Cruz *et al.*, 2001), Florida (Lyons *et al.*, 1981), Bahamas (Smith, 1951) and Brazil (Soares and Cavalcante, 1985) was markedly seasonal, approximately 85% of all reproduction occurred during March – May. Cruz (1975) and Douglas *et. al.* (1982) suggested that spawning frequency depends on seasonal trends on latitudinal range.

Taking this into account and keeping in mind that all lobster fisheries are considered fully exploited or overexploited, Cruz and Bertelsen (2009) have recommended to legislate a four-month closed season for all countries in the Western Atlantic that have a lobster *P. argus* fishery, between February 1st to June 30th to protect the peak of the reproductive cycle (maturity and ovigerous female) and the major recruitment pulse (March to May). Cruz and Bertelsen (2009) determined the relationship between carapace length and reproductive activity. They showed that as in other spiny lobster species, large females mature between 90 and 119 mm of CL (carapace length), mate and lay eggs early in the breeding season, while smaller females (70-89 mm, CL) develop and spawn towards the end of the breeding season, allowing a molt to a large size (Fig. 1).

In Cuban waters, multiple spawning appears to be less frequent in females at sizes 67-89 mm CL, but egg-bearing females ranging in size between 90 and 107 mm CL can also have mature ovaries and fresh spermatophores; this reproductive conditions allows these females to produce at least two broods separated by three or fourth weeks (Cruz and León, 1991).

Reproductive activity of *P. argus* in Bahamas (Kanciruk and Herrnkind, 1976), Florida Keys (Gregory *et al.*, 1982) and Cuba archipelago (Cruz and Bertelsen, 2009) decreases from outer reefs area (near to open ocean) toward near shore area and within 10 km of the interface between ocean water and the shelf edge (Fig. 2), reproductive success is highest helping to assure oceanic larval recruitment.

Factors that affected reproduction, such as seasonality and temperature were described by Cruz (1975). He observed that when the average air temperature between October and December was 24°C, the highest percentages of mature females appears in March (following year) and when the average temperature is higher or lower, maturation rates decrease. The effect of temperature and climatic conditions on lobster's egg development has not received much attention though Shields (1991), in crustaceans reported that low temperatures decrease and high temperature increase the rate of embryogenesis.

Fecundity, brood size and population egg production

Lobster eggs were categorized 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). The eggs are carried on the pleopods for three to four weeks before hatching depending on water temperature (Crawford, 1921).

The relationship between carapace length and egg clutch size (fecundity) is best described through the non-linear equation from the type $\mathbf{y=aX^b}$ expressed like $\mathbf{F=aCL^b}$. It is evident from the trends in Fig. 3, that in general larger females brood more eggs than the smaller ones; while size-specific fecundity is greater in lobsters from *Panulirus* genera.

While in *Panulirus* the body size of the specimens is generally smaller, the fecundity is superior compared to *Jasus* and *Palinurus* genera; probably explained by a smaller individual egg size and prolonged larval phase of *Panulirus* (MacDiarmid and Sainte-Marie, 2006). Only the enormous size of *Jasus verreauxi* allows it to produce as many eggs as *P. argus* (MacDiarmid and Sainte-Marie, 2006). Female brood size depends on the amount of sperm transferred by the male (MacDiarmid and Butler, 1999). This is often a function of male size,

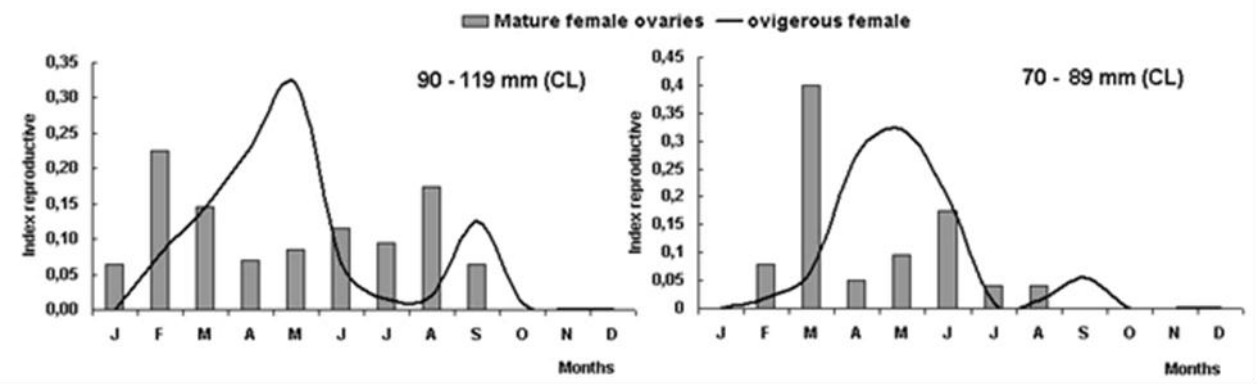

Fig. 1. Reproductive cycle for spiny lobster *Panulirus argus* by length composition on Cuba archipelago, modified of Cruz and Bertelsen (2009).

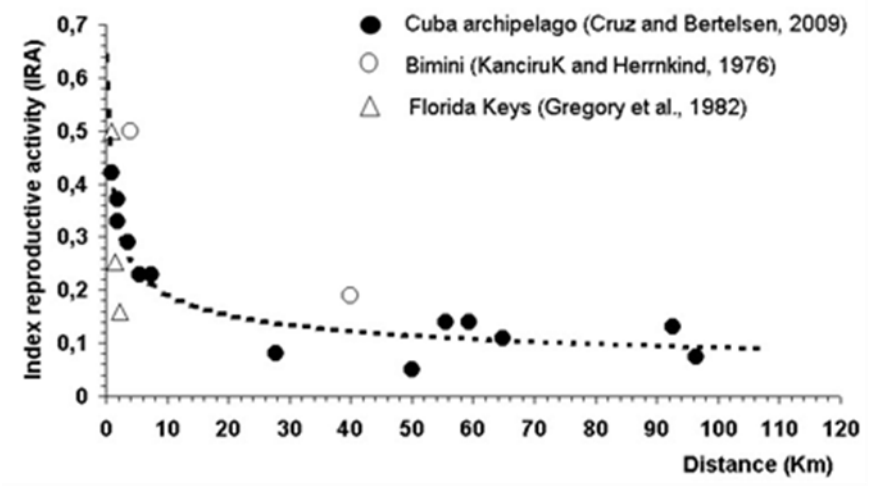

Fig. 2. Reproductive activity of *Panulirus argus* in different locations of the Western Central Atlantic. The index of reproductive activity (IRA) was defined as: Total females in any reproductive stage / Total females collected (Cruz *et al.*, 1987).

but the number of recent previous mating can also be important. In at least two species of spiny lobster, *J. edwardsii* and *P. argus*, small males generally do not transfer enough sperm to fertilize all eggs that a large female can extrude, resulting in reduced rates of fertilization (MacDiarmid and Butler, 1999).

A way to assess the egg production of a population is the reproductive efficiency expressed as the number of eggs that a female produces per gram of body weight. Bertelsen and Matthews (2001) examined the reproductive efficiency of female lobsters in south Florida and found that the highest reproductive efficiency occurred between carapace lengths of 80 to 110 mm CL. When these calculations were performed on additional data collected in Mexico and Cuba (Cruz, 1980; Ramírez, 1996), greatest reproductive efficiencies (> 800 eggs per gram body weight) was observed on females between 80 and 114 mm CL.

Cruz and Bertelsen (2009) proposed a relationship between egg clutch size and carapace length (mm) for female *P. argus* on the Greater Caribbean region using the data from Cuba (Cruz, 1980), Florida (Bertelsen and Cox, 2001) and Mexico Caribbean (Ramírez, 1996). Female lobster size between 57 to 150 mm CL, which functions is described as floow:

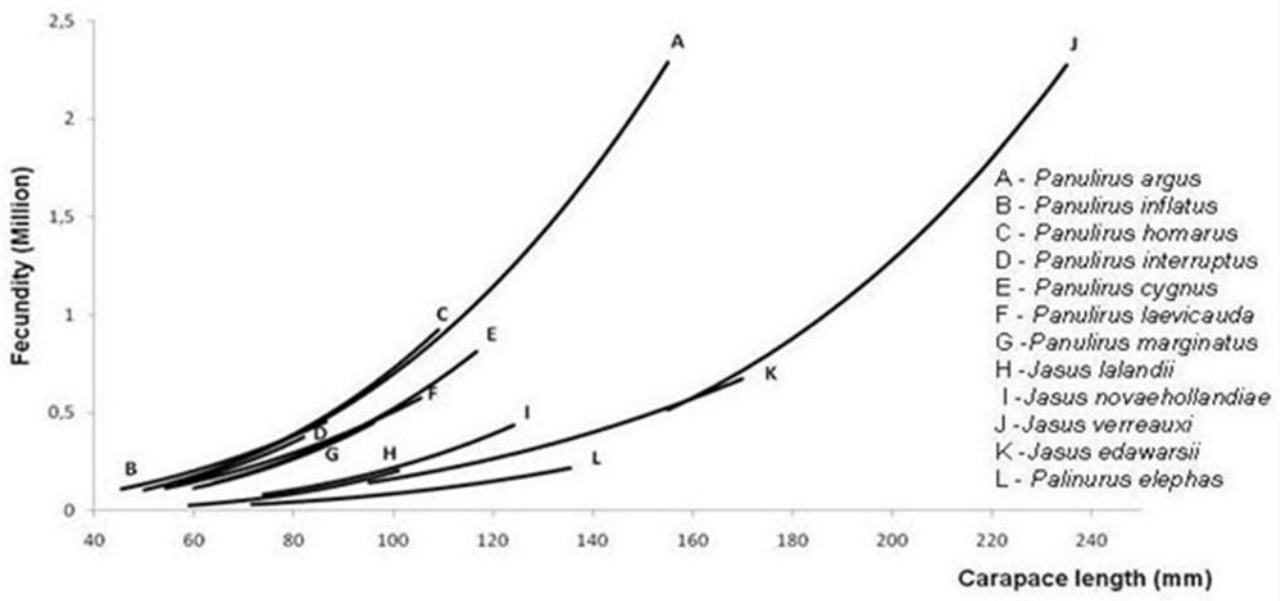

Fig. 3. Egg clutch size as a function of carapace length (mm) in a range of lobster species, modified of Cruz (1980). The relationship is described through equation used for A- *Panulirus argus* (Cruz and Bertelsen, 2009), B- *Panulirus inflatus* (Gracia, 1979), C- *Panulirus homarus* (Berry, 1971), D- *Panulirus interruptus* (Tapia-Vázquez and Castro-González, 2000), E- *Panulirus cygnus* (Morgan, 1972), F- *Panulirus laevicauda* (Nascimento,1976), G- *Panulirus marginatus* (DeMartini *et al*, 2003), H- *Jasus lalandii* (Heydorn, 1965), I- *Jasus novaehollandiae* (Hickman, 1946), J- *Jasus verreauxi* (Kennsler, 1967), K- *Jasus edawarsii* (Kennsler, 1968) and L- *Palinurus elephas* (Goñi *et al*, 2003).

Egg count = 2.668CL2.709 (n = 658; R2 = 0.7913; p << 0.00001).

It is proposed her that this general equation for *P. argus* can be used to study the stock-recruitment relationship and in the assessment of egg production population. For example, Cruz and Bertelsen (2009) discussed different indices and their sensitivity used by different authors (Kanciruk and Herrnkind, 1976; Cruz, 2000; Cruz *et al*, 2007) to estimate the index of reproductive potential.

Reproduction and recruitment are two major events in the life cycle of lobster species. The relationship between the number of eggs fertilized and the cohort to which they gave rise, commonly called stock recruitment, is an unsolved problem although it has been discussed by different authors for *P. argus* (Pérez *et al.*, 1978; Herrnkind and Butler, 1997; Medley and Ninnes, 1997; Cruz, 2000).

EXPERIMENTAL STUDIES

Reproductive system

Male functional maturity is very difficult to assess in the field but is often assumed to be associated with a change in the dimensions of the second and third walking legs in spiny lobsters in connection with the carapace length. It is assumed that a bigger size of these structures is an adaptation that facilitates them to take out the females of the hollows of the refuges for the mating (MacDiarmid and Sainte-Marie, 2006).

In the case of *P. argus* females it has been defined phases of gonadal development according to the spermatophore or the clutch presence (Ramírez, 1996). The long setae specialized to carry eggs during the incubation period (Lipcius and Herrnkind, 1987), were also used as indicators of maturity in species like *P. cygnus* (Chittleborough, 1976), *J. edwardsii* and *P. argus* (MacDiarmid, 1989). However, Fielder (1964) points out the presence of these setae in animals with immature ovaries, what indicates that some females are potentially capable to carry eggs at least a molt before their ovaries begin to mature. Thus, although the detailed morphology of reproductive structures in lobsters has been well described, the histological analysis is indispensable to determine clearly the level of gonadal maturation.

Males

The spermatophore of *Panulirus* and *Jasus* is a continuous coiled tubule which contains sperms. This spermatophore is part of the spermatophoric mass and at copulation, the entire mass - spermatophore plus matrix- is extruded by peristaltic contraction of the distal portion of the *vas deferens* (Aiken and Waddy, 1980). Dávila, (2007) pointed out that once placed the spermatophore to the female *P. argus*, this keeps in the same disposition observed by Aiken and Waddy (1980) in *P. homarus*; a protector matrix originated from the secreted matrix of the "typhlosole", the spermatophoric matrix in which the spermatophoric ducts are observed with sperms in the interior and the basal adhesive matrix whose origin is the secreted matrix by the peripheral epithelium.

In *P. argus*, the male gonads do not change in colour along the gonadal development, for that reason this cannot be used as an indicator of maturity, only the consistency and the development of the half portion of the *vas deferens* is notorious as macroscopic indicator of the maturation phase (Dávila, 2007); however, as already mentioned, the histological analysis is in them necessary.

Females

In immature condition the ovaries are very thin and difficult of locating in some size classes to be small and flabby. With the progress of the gonadal development, the gonads change from pale orange to a very intense colour orange; they become very big and turgid, and the previous and the ends lobes are expanded more deeply in both the cephalothorax and in the first segments of the abdomen respectively (Dávila, 2007).

Buesa and Mota-Alves (1970), for *P argus* in accordance with the colour of the female gonad proposed a scale of colours to classify the phase of gonadal development and it was implemented in 1965 in Cuba and since 1966 in Brazil. This classification is very useful in the field work but it can offer doubts when being observed, since in the regression stage, gonads colour is similar to recently spawned gonads or in half development stage. The same problem is presented in the stage I (immaturity) and the stage II (beginning of the development). With the purpose to unifying the macroscopic and microscopic characteristics Dávila *et al.*, (2009a; 2009b) reported stages of gonadal development based on haematoxylin-eosin histological preparations from ovary and testis of *P argus* according to the cellular types (Table 1).

Dávila *et al.*, (2009a; 2009b) reported diameter of the cellular types similar of the proposed interval by Mota-Alves and Tomé (1965), but in primary oocytes with advanced phase of the growth - defined by the presence of accessory nucleolus, the diameters are very variable according to the carapace length. The initial cause of these differences can be due to the technique of paraffin inclusion; the cells during the inclusion process depending on the vitellogenic vesicles content (that in a same way they are related with the stage of gonadal development), can absorb with more or less difficulty this substance (see discussion in Dávila, 2007). But, if we take into account that the number of larvae that hatching successfully increases with female sizes (*P. interruptus*; Báez-Hidalgo *et al.,* 2004); the egg diameter increases with female size (*Palinurus elephas*; Goñi *et al*, 2003) and larger eggs hatch larger larvae that survive longer under condition of low food supply (*Jasus edwardsii;* A. B. MacDiarmid, unpublished data). Hince is likely that the largest females of *P. argus* have a more mature gonadal development and they are able to produce oocytes that give place eggs having more vitelo and probably will be born larvae with better conditions for the survival.

Courting, copulation and spawning

The references about the mating are based mainly on experiences in laboratory; it is insufficient the knowledge of this process in the natural conditions. Lipcius *et al.,* (1983) present the only documentation in situ of this process for *P. argus* and they describe a polygynous mating system with the largest males doing the most mating. Females may become less selective in their choice of mate if they near the time of egg extrusion and no reproductively active male have been provided (Lipcius and Herrnkind, 1987).

In controlled laboratory conditions like a photoperiod of 12:12 (light:dark), a temperature of 25°C, a salinity (of 35°/$_{oo}$) and squid feeding, mating and spawn of *P. argus* have shown to be successful (Dávila, 2007). A distinct pre-copulatory courtship phase may be from several minutes to days (MacDiarmid and Kittaka, 2000; Dávila, 2007). The size of the spermatophore varies in dependence of different factors like the size of the female, the size of the male that places and the frequency of multiple copulation (MacDiarmid and Sainte-Marie, 2006), for such a reason the males need careful management to ensure that they have time

Table1. Lobster male and female (*Panulirus argus*), stages of gonadal development and cellular types according to the morphology and diameter (Dávila 2007 and Dávila *et al.*, 2009a; 2009b).

	Cellular Types	Stages of Gonadal Development
Males	Spermatogonia (19.45 ± 1.02µm)	Stage I (not developed)
	Primary spermatocytes (15.25 ± 0.92µm)	Stage II (in development)
	Secondary spermatocytes (10.75 ± 1.25µm)	Stage III Initial maturity
	Spermatids (6.8 ± 0.6µm)	Advanced maturity
	Sperms (3.5 ± 0.3µm)	
Females	Oogonias (19.70 ± 0.63µm)	Stage I (Immaturity)
	Primary oocytes at the initial phase of the growth (54.80 ± 1.81µm)	Stage II (Beginning of the development)
		Stage III (Half development)
	at advanced phase of the growth (the diameters are very variable according to the CL)	Stage IV (Final development pre-ovigerous)
	Mature oocytes (427.3 ± 28.43µm)	Stage V (Regression or phase post-spawning)

to recover sperm supplies after repeated mating. However, up to now this approach has not taken like a restrictive factor in the populations.

For the egg extrusion the female forms a brood chamber by flexing her abdomen forwards beneath her body, extending the exopodite of the pleopods, and spreading her telson and uropods into a fan covering the genital apertures. Fertilization occurs externally, in the brood chamber eggs and spermatozoa are swirled around by the beating of the pleopods (MacDiarmid and Kittaka, 2000).

The duration of egg bearing varies greatly among species and with temperature, in *P. argus* egg bearing lasts between 20 and 30 days (Kanciruk and Herrnkind, 1976). Hatching occurs as the female violently beats the pleopods for a few seconds, releasing a "swarm" of larvae which typically are strongly photopositive and swim towards the brightest light source (MacDiarmid and Kittaka, 2000).

CONCLUSION

This review of the reproduction of the spiny lobster *P. argus* aimed to provide information that will improve the knowledge on these resource and furthermore it can aid in management decisions, the research in population dynamics and perhaps successful progress of lobster aquaculture. Dissemination of information about lobsters can also serve as reference for educators and researchers working in this field.

Knowledge on the reproductive dynamics of the Caribbean spiny lobster *P. argus* comes from the fields work in artificial or natural refuges. However, in the short term, more experiments are needed to unravel the mating system of *P. argus*, particularly, those aspects regarding the effect of male size on reproductive success. Issues as the effects of male size on fecundity, stock-recruitment relationship, the relationship of oocytes, egg quality and larval size with maternal size and reproductive experience (primiparous *vs* multiparous) are still not well understood.

Factors affecting reproduction, such as seasonality and deep variation of the temperature have not been fully understood. In addition, the impact of harvest and hydro-meteorological event on the interface between shelf edge and the ocean water, where reproductive success and egg production is high, needs special research attention. After this review, it is contended that the fraction of the stock with a carapace length more than 90 mm that inhabits deep region, could ensures the size of the spawning stock and the reproductive capacity of the specie.

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