A Review of the Literature and Life History Study of the Caribbean Spiny Lobster, *Panulirus Argus*.

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Introduction

Given the economic significance of the Caribbean spiny lobster (*Panulirus argus*) to both commercial and artisanal fisheries, many individuals have sought to describe and document the life history, behavior, and general biology of this species. In order to fully devise management strategies for the efficient harvesting of *P. argus* during the upcoming Southeast Data Assessment Review (SEDAR) workshop, a review of the life history information on Caribbean spiny lobsters is provided. The following summary discusses the distribution, habitat, stock structure, morphology, feeding habits, reproductive behaviors and growth of the Caribbean spiny lobster.

Distribution, Habitat and Stock Structure

The Caribbean spiny lobster populates the Western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico ranging from Bermuda down to Brazil (Hernkind, 1980). Distribution and dispersal of *P. argus* is determined by the long planktonic larval phase, called the puerulus, during which time the infant lobsters are carried by the currents until they become large enough to settle to the bottom (Davis and Dodrill, 1989).

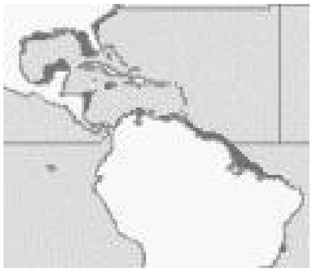

Figure 1: Distribution of *Panulirus argus*.[1]

During transformation from the puerulus to the juvenile, the lobster's ability to swim increases and they move into shallow, near shore environments to grow and develop. Young benthic stages of *P. argus* will typically inhabit branched clumps of red algae *(Laurencia sp.,)* mangrove roots, seagrass banks, or sponges feeding on local

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[1] From: Korean Ocean Science and Fisheries Information Center. Copyright 2000. Accessed 26 July 2004. < http://kosfic.yosu.ac.kr/top_memberplsql/kosfic_home.kosfic_main>.

invertebrates found within the lobster's algae microhabitat. In contrast to the social behavior of their older counterparts, the young Caribbean spiny lobster are solitary and exhibit aggressive behavior to ensure that they remain solitary. Studies suggest that the inhabitation of macroalgae by the juvenile lobsters provides protection to the vulnerable individuals from predators while providing easy access to food sources (Marx and Herrnkind, 1985).

Individuals who are from two to four years old exhibit nomadic behavior emigrating out of the shallows and moving to deeper, offshore reef environments. Once in the adult phase of life, Caribbean spiny lobsters are thigmotactic and tend to enter social living arrangements aggregating in enclosed dens. Shelter environments may include natural holes in a reef, rocky outcrops or artificially created environments (Lipcius and Cobb, 1994).

As adults in the offshore environment, Caribbean spiny lobsters support commercial, recreational and artisanal fisheries throughout their geographic range (Davis and Dodrill, 1989). Given the wide distribution of *Panulirus argus* from Bermuda down to Brazil, it is hard to determine a definitive stock structure for this species. There are a multitude of currents and other factors that influence the movement of water throughout the range of *P. argus*. The long duration that lobsters spend in the larval stage, traveling by the currents severely impairs the ability of scientists to determine a stock structure. More recent work with DNA may be useful in determining some sort of stock structure for the Caribbean spiny lobster (Lipcius and Cobb, 1994), however the extensive larval phase may also limit this tool as it takes few successful migrants to homogenize the gene pool (Silberman and Walsh 1994). Studies have also shown that the presence of local gyres or loop currents in certain locations could influence the retention of locally spawned larvae. In addition, benthic structures such as coral reef may disturb the flow of water and lead to the settlement of larvae in a particular location (Lee, et. al. 1994).

Morphology

The general anatomy of *Panulirus argus* conforms to the typical decapod body plan consisting of five cephalic and eight thoracic segments fused together to form the cephalothorax. The carapace, a hard shield-like structure, protects this portion of the body and is often the part of the lobster measured and used as a standard to determine organism length. All the segments bear paired appendages that serve in locomotion, sensory, or both (Phillips, Cobb and George, 1980). From the head of the lobster, the appendages are ordered starting with the first antennae, second antennae, mandibles, first maxillae, and second maxillae. There are five pairs of walking legs called pereiopods and a six-segmented tail. The antennae function primarily to obtain sensory information by chemoreception, as do the dactyls of the walking legs and the mouthparts involved in handling food. Lobsters have great visual ability, achieved through the use of their paired, lateral compound eyes. In addition, highly distributed superficial hairs detect water movements (Ache and Macmillan, 1980).

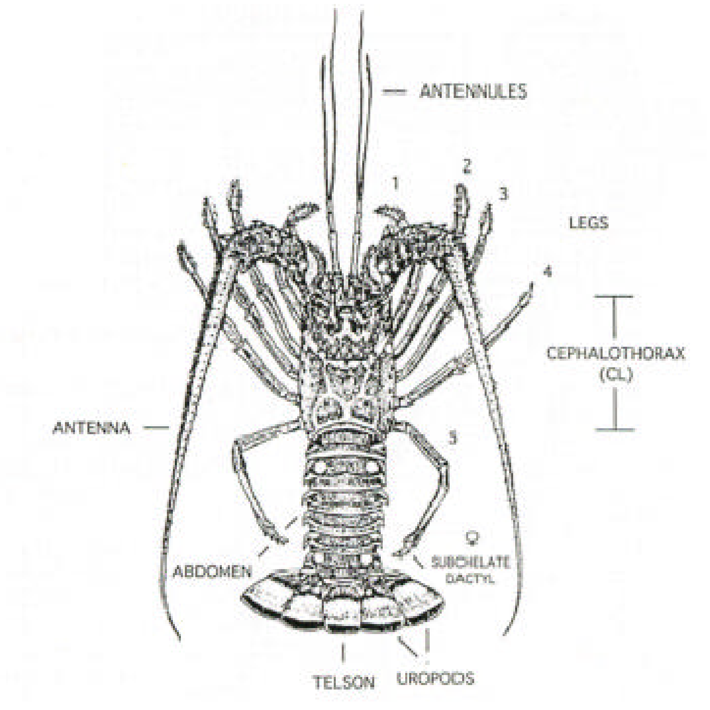


Figure 2: Morphology of *Panulirus argus* (Lipcius and Cobb, 1994).

Gills are the main organs used by lobsters for respiration. The rate of oxygen consumption in *P. argus* is dependent upon the temperature, the degree of crowding within the den, feeding and size of the lobster; oxygen consumption is not determined by the concentration of the oxygen in the water as some studies show that oxygen uptake remained the same in both hypoxic and aerated water (Phillips, Cobb and George, 1980).

Food Habits

Once *P. argus* settles out from the planktonic phase and enters the seagrass and macroalgae nursery habitat, their diet consists of small gastropod mollusks, isopods, amphipods and ostracods, most of which can be found in or within close proximity to the lobster's algal shelter. Studies suggest that as the abundance of food declines in and around their algae habitat, lobsters forage more frequently and thus have more frequent contact with conspecifics. Aggressive behavior in the juvenile lobsters, which at this time live solitarily, has been observed as a means of enforcing territoriality. The consequence of increased aggressive interactions as well as a declining food source is thought to induce the nomadic emigration from the algal nursery environment to off shore reef environments (Marx and Herrnkind, 1985).

During the adult and juvenile phases, the Caribbean spiny lobster will rest in shelters during daylight hours and emerge in the evening to forage for food. Adult lobsters are key predators in many benthic habitats with their diets consisting of slow-moving or stationary bottom-dwelling invertebrates including sea urchins, mussels, gastropods, clams and snails (Lipcius and Cobb, 1994). Juvenile lobsters also forage at night and will eat a similar diet of invertebrates, only smaller individual prey. During feeding, prey organisms are seized and maneuvered using the anterior periopods or maxillipeds, while the mandibles carry out mechanical digestion and are capable of crushing hard mollusk shell (Herrnkind, et. al. 1975). Little is known about the dietary requirements of the larval phase, plankton sized lobsters.

Larger animals such as sharks and finfish frequently prey upon adult Caribbean spiny lobsters. Studies indicate that Caribbean spiny lobsters are highly selective of the dens they choose to live in and the location of these crevices. Their evening movements away from and subsequent return to their dens illustrates the spatial orientation they have to their immediate habitats (Herrnkind, 1980).

Reproduction

Reproduction in the Caribbean spiny lobster occurs almost exclusively in the deep reef environment once mature individuals have made the permanent transition from the shallow seagrass nursery to the ocean coral reef system. Spawning season is in the spring and summer, however autumnal reproduction has been known to occur in some situations (Kanciruk and Herrnkind, 1976). The gestation period for eggs is about a month. Eggs are orange when they are fresh, and brown when they are close to hatching. Studies have found that the initiation of spawning is related to water temperature with an optimal water temperature for mating of 24 degrees centigrade (Lyons, et. al., 1981).

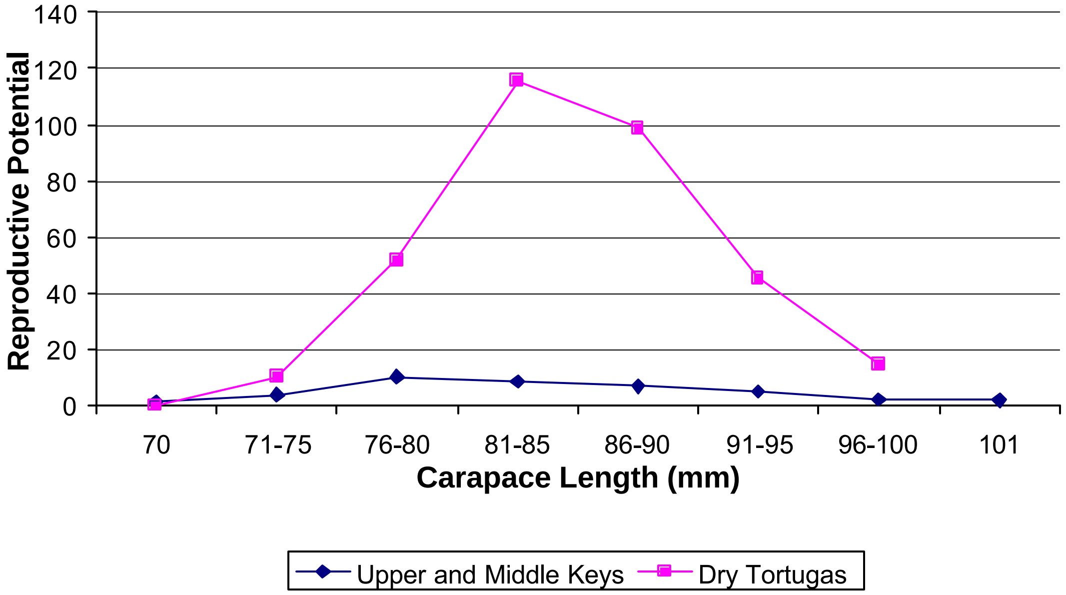
Reproductive fecundity is dependent upon the size of the individual as well as the geographic area in which the lobster lives. Reproductive efficiency for a given size in a given area can be determined using the relationship between fecundity and carapace length. A study conducted in South Florida found that differences exist between the fecundity/carapace length relationships of individuals living in the Dry Tortugas from individuals living in the Upper and Middle Florida Keys. Based on data provided from each location, an Index of Reproductive Potential was calculated using the model developed by Kanciruk and Herrnkind (1976):

$$\text{Index} = (A \times B \times C)/D$$

Where:

A = number of females in size class/total females
B = propensity of size class to carry eggs
C = egg carrying capacity of size class female
D = constant (31.27) – present to set the 76-80 mm size class index to 100 as the standard.

The graph below illustrates the reproductive potential calculated for different size classes.



Graph 1: Index of Reproductive Potential.

Individuals in the Upper and Middle Florida Keys reach maximum reproductive potential at smaller sizes than individuals in the Dry Tortugas. One possible hypothesis for this may be that larger individuals in the Keys are removed due to greater fishing pressure and thus smaller individuals must carry the population. Generally speaking, spawning in the Caribbean spiny lobster seems to begin when individuals reach carapace lengths of around 70mm while spawning declines at lengths greater than 130mm. Maximum reproductive capacity is achieved at sizes between 100 and 130 mm in carapace length (Lyons, et. al., 1981).

Choice of mate is determined by the female as well as inter-male aggression, where larger males will prevent a smaller male from courting a female (Lipcius and Cobb1994). Females mate only once during a season, while males can fertilize multiple females. During mating, the male will flick his antennules over the anterior of the female and scrape at her with the third walking legs. The male follows the female around continually trying to lift the female up and embrace her. This pattern continues until the female acquiesces and they each stand on their walking legs while the male deposits the spermatophore mass on the female sternum (Atema and Cobb, 1980). Females bearing eggs will usually live in solitary dens and infrequently forage for food (Lyons, et. al., 1981). Large adult females will produce more broods, as well as spawn eggs earlier in the reproductive period than younger females since younger individuals molt earlier in the reproductive period.

Growth and Molting

The life cycle of the Caribbean spiny lobster provides larvae with the potential to travel long distances for periods ranging from a few months to almost two years. During this time, the larval lobsters remain near the surface of the water. Maximum potential dispersal distances differ from one region to another and are primarily dependent on the currents in the area. A gyre in an area where lobster eggs have hatched may keep the larva in the same geographic area, however most of the time the larva are transported out of the area, sometimes hundreds of miles (Lee, et. al. 1994). Once the planktonic lobsters reach about 35mm they are large enough to settle down as post larval pueruli in shallow benthic environments to grow. Lobster growth in juveniles is rapid with most reaching a carapace length of 60-70mm within about two years (Hernkind, 1980). Once the lobsters reach about 70mm and begin to sexually mature, the young *P. argus* emigrate from the nursery to deeper offshore reef environments.

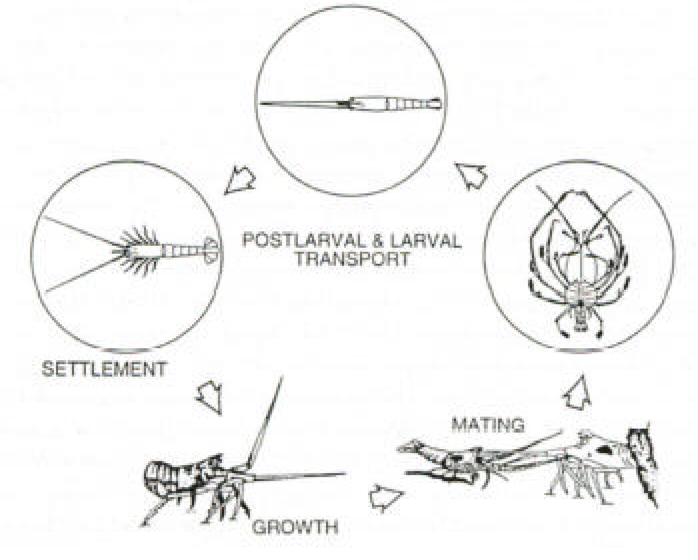


Figure 3: The Life Cycle of *Panulirus argus* (Lipcius and Cobb, 1994).

Physical growth of lobsters is achieved through molting. A thorough understanding of the molt cycle of the Caribbean spiny lobster is an important component to the management of this fishery because the catchability and captive behavior of crustaceans is directly related to the animal's proximity to molting. The molt cycle begins with the intermolt period, the time when a new cuticle is being created, tissue growth is rapid and the lobster actively forages. This period of time culminates in ecdysis, which is shedding the old cuticle or molting (Lipcius and Hernkind, 1982).

Molting occurs primarily at night. Possible reasons for nocturnal ecdysis include decreasing the risk of cannibalism by other members of this gregarious species, and decreasing diurnal predation risks. The first action to occur during molting is the rupture of the thoracoabdominal membrane followed by a rising of the dorsal part of the cephalothorax; this action frees the eyes, bases of antennae and antennules. A series of peristaltic contractions causes the removal of the abdomen from the old cuticle, while writhing motions free the cephalothorax and attached structures. A few final wriggles and contractions terminating in a tail flip completely segregates the lobster from its old cuticle. Once molted, the lobster seeks immediate shelter, as they are especially vulnerable until their new cuticle becomes hardened (Lipcius and Hernkind, 1982). For adult lobsters, molts average about two and a half times each year. The entire molting event takes approximately ten minutes. The new exoskeleton will take about 12 days from the start of the molt to harden such that it cannot be dented, however the shell is not completely formed until the 28th day (Williams, 1984).

Studies found that feeding rates significantly increase in the time preceding a molt to accommodate the increasing metabolic needs associated with new cuticle formation. About a week before ecdysis, daily food intake for the Caribbean spiny lobster decreases rapidly, in correlation with a reduction in demanding activities such as locomotion and foraging. In the few days before and the time during ecdysis, feeding ceases altogether and the lobster becomes socially reclusive. Within a week of the molting event, *P. argus* will display maximal feeding, foraging and locomotor activity rates to accommodate for the active tissue growth that occurs (Lipcius and Hernkind, 1982). The dramatic swings in feeding and foraging behavior associated with the molting cycle influences the success of fishermen when capturing this species. The highest catchability of spiny lobster is expected immediately following molting because lobsters are actively foraging at this time and will therefore be more likely to accept bait. Conversely, the lowest catachability of spiny lobster is expected before molting when foraging decreases and the lobster becomes less mobile (Lipcius and Hernkind, 1982).

Growth and Mortality Rates

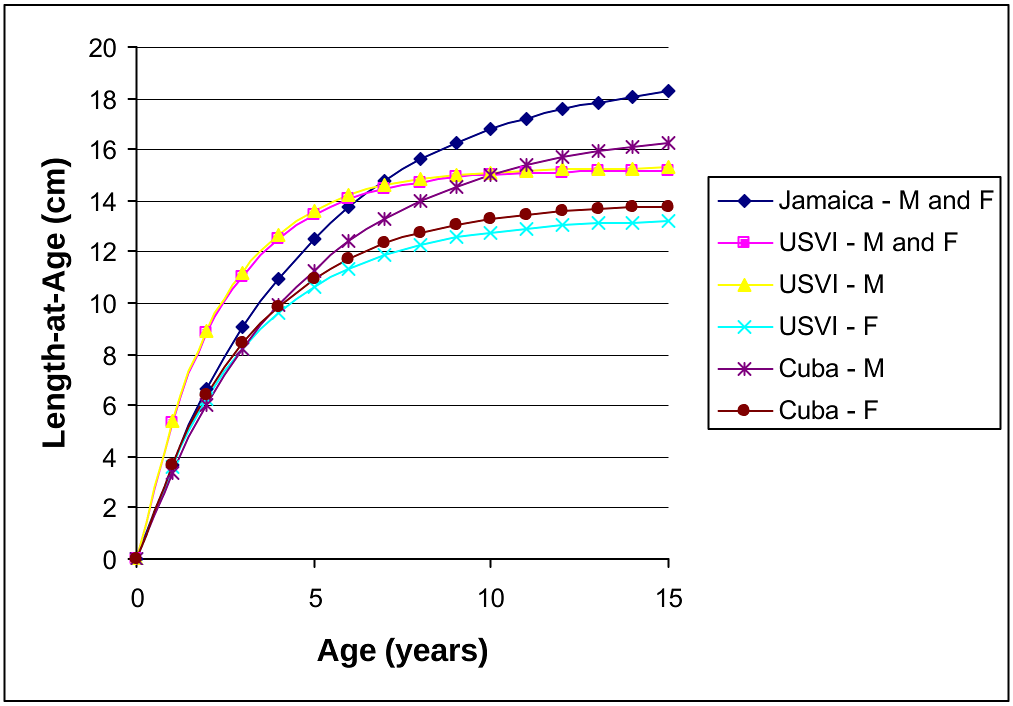
Despite the wide body of literature on this species, limited information is available on the growth and aging of the Caribbean spiny lobster due in part to the molting habits of lobsters interfering with tagging efforts. Consequently, length data, which is substantially easier and less costly to collect, has been the dominant source of information used to estimate growth in *P. argus.* The limited quantitative information that exists on growth for this species at various locations has been compiled in a doctoral thesis by Jaime Manuel Gonzalez-Cano (1991) and was graphed below using the von Bertalanffy growth model.

$$L = L_{inf}\,[1\text{-}e^{(-k(t-to))}]$$

Where:

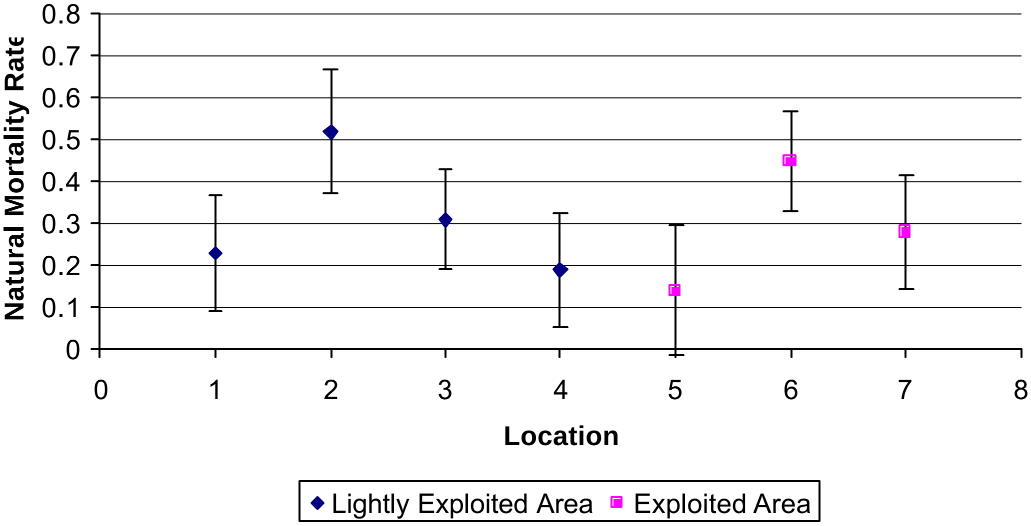
L = length of the organism at time t
L_{inf} = asymptotic average length achieved
K = growth rate with units 1/time
T_o = time when the length of the organism would be zero

The curves were derived from the available growth parameters for spiny lobster as compiled by Gonzalez-Cano (1991) from various studies assessing age and growth of spiny lobster in the Caribbean.



Graph 2: Von Bertalanffy Growth Curves for Spiny Lobster.
- Jamaica parameters from Munro (1974).
- USVI parameters from Olsen and Koblic (1975).
- Cuba parameters from Cruz, Coyula and Ramirez (1981).

As with any fished population, especially one with poor aging information, natural mortality rates for Caribbean spiny lobster populations have been difficult to isolate from fished rates of mortality. The limited data on natural mortality rate that is available has been compiled by Gonzalez-Cano (1991) and is graphed below for seven different locations. Mortality parameters compiled by Gonzales-Cano (1991) were calculated from either lightly or heavily exploited areas in Jamaica and Bermuda studied by Munro (1974) and Evans (1988).



Graph 3: Natural Mortality Rates for *Panulirus argus.*

Location 1: South Jamaica Shelf, males and females
Location 2: Pedro Cays area, Jamaica, males and females
Location 3: Argus Bank, Bermuda, males
Location 4: Argus Bank, Bermuda, females
Location 5: Port Royal Reefs, Jamaica, males and females
Location 6: Northern Fishing Grounds, Bermuda, males
Location 7: Northern Fishing Grounds, Bermuda, females

Locomotion and Migration

The Caribbean spiny lobster achieves locomotion by using the five pairs of walking legs attached to the cephalothorax and can swim (backward) for brief periods using its tail for propulsion (Lipcius and Cobb, 1994). Patterns of movement in *Panulirus argus* fall into the following categories: homing, nomadism and migration. Throughout most of their life, *P. argus* is a shelter dweller during the day and forages at night. Evening movements within the home range are directed; lobsters are apparently aware of their location at all times and can find the way back to the den of origin even if detours are caused by predators or divers. Nomadism is the movement that occurs in juvenile lobsters away from the nursery habitat and to the offshore reefs. Migration is the direct movement of an entire population or sub-population over a long distance for a given period of time (Herrnkind, 1980).

Mass movements (2-60 individuals) of Caribbean spiny lobsters occur annually throughout the geographic range of the species and are dependent on latitude and climactic factors. Observed locations for the migration include Bermuda in October, the Bahamas and Florida in late October and early November, and the Yucatan and Belize in December (Herrnkind 1985). This mass migratory behavior is thought to have evolved in response to deteriorating conditions that resulted from the periods of glaciations that occurred over the past several 100,000 years. Thus, the migration and queuing behavior became specialized by the natural selection on individuals of the harsh winters during periods of glaciations. Gonads during the migration in the fall are inactive, as they don’t begin to mature until the late winter (Herrnkind 1985).

The first autumn storm in the tropics usually brings a severe drop in water temperature of about five degrees centigrade, as well as high northerly winds of up to 40km/h and large sea swells. The shallow regions that the lobsters exploit during the summer months become turbid and cold, initiating the diurnal migration of thousands of lobsters to evade these conditions. The Caribbean spiny lobster is highly susceptible to severe winter cooling and will exhibit reduced feeding and locomotion at temperatures 12-14 degrees centigrade; molting individuals usually perish under these conditions. According to Herrnkind (1985), the behavioral changes observed in *P. argus* as well as the known biological information about the species lends credence to the idea that individuals migrate to evade the stresses of the cold and turbidity in the winter.

Caribbean spiny lobster initiate the migratory behavior by queuing, the single file formation of migrating individuals initiated by visual or tactile stimuli. Queuing is maintained by establishing contact between the antennules of one individual and anterior walking legs of another. Biologically, the queuing behavior is an important hydrodynamic drag reduction technique for the migration of individuals long distances (Bill and Herrnkind, 1976). Studies done by tagging individuals found that during the migration, individuals tended to move distances of 30-50km (Herrnkind 1985). Migratory movement lasts for variable periods of time and is believed to be dependent on the total number of migratory lobsters. One study in the Bahamas in 1971 found the migration to take six hours while another study in the same location in 1969 found the migration to take five days. It is thought that the more lobsters present, the longer the migration will last in order to avoid over crowding of shelters at their final destination (Kanciruk and Herrnkind, 1978). Once individuals reach sheltered habitats located in deeper water, such as a deep reef site, the migratory queuing behavior ends and the lobsters disperse.

Conclusion

The biological and behavioral information was researched in order to provide background on the Caribbean spiny lobster in preparation for the upcoming Southeast Data Assessment Review (SEDAR) workshop. Effective management of a species is greatly enhanced by a thorough understanding of its known biology.

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A Summary of the Biology of Caribbean Spiny Lobster *Panulirus argus*

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1. Introduction

The Caribbean spiny lobster (*Panulirus* argus) supports a primarily artisanal and semi-industrial fishery, second in economic importance only to penaeid shrimp in the Caribbean as a whole (Ehrhardt, 2001). In order to prepare for the next assessment of *P. argus* in the U.S. Caribbean, a review of its biology is provided. The following summary discusses the distribution, habitat stock structure, morphology, feeding habits, reproductive behaviors and growth of the Caribbean spiny lobster.

2. Morphology

The anatomy of adult *P. argus* conforms to the typical decapod body plan, consisting of the five cephalic and eight thoracic segments fused to form the cephalothorax and the six segments that form the abdomen or tail. The carapace, a hard chitinous shell, protects the cephalothorax, and is used as the standard measure of organism length. All segments bear paired appendages that serve in locomotion, sensory perception, or both (Bliss, 1982; Phillips et al., 1980). From the head, the appendages are ordered starting with the antennules, the antennae, the mandibles, and the first and second maxillae. Lobsters possess five pairs of walking legs, called pereiopods, and paired swimmerettes, or pleopods, on the first five tail segments, which are modified for holding eggs in females, with the sixth segment bearing the tail fan made up of the telson and four lateral uropods (Cobb & Wang, 1986). The antennae function primarily to obtain sensory information by chemoreception, as do the mouthparts and the dactyls of the walking, while lateral compound eyes provide *P. argus* with relatively acute vision. In addition, highly distributed superficial hairs detect water movements (Ache and Macmillan, 1980). Gills, located laterally under the carapace, are the lobsters' main respiratory organs (Phillips, Cobb & George, 1980).

3. Life History

The Caribbean spiny lobster populates the Western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico, ranging from North Carolina (USA) and Bermuda in the north, to Brazil in the south (Hernkind, 1980; Arce & de León, 2001; Cruz et al., 2001). *P. argus* changes habitats several times during its ontogenetic development, moving from planktonic phyllosoma larvae to pelagic swimming puerulus larvae to adults, which may utilize a variety of benthic habitats (Arce & de León, 2001; Cruz et al., 2001).

P. argus begins life as a fertilized egg, carried under the abdomen of a female lobster (Bliss, 1982). Females may migrate several kilometers toward the edges of reefs or coastal shelves in order to incubate and release larvae (Buesa, 1965). Pelagic phyllosoma larvae hatch from the eggs and may spend 6 to 10 months in the plankton, during which time they undergo 11 larval stages and are dispersed throughout the Caribbean (Alfonso et al., 1991). Maximum potential dispersal distances differ from region to region and are primarily dependent on local current regimes. Gyres may help localize reproductive output, though currents often transport larvae hundreds of miles from where they were spawned (Lee et al., 1994). The phyllosoma metamorphose into puerulus larvae, which swim to shallow, near-shore environments to settle and develop (Marx & Hernkind, 1985). Settlement peaks in September-December (Cruz et al., 1995). Young post-pueruli, or algal phase lobsters (Arce & de León, 2001), typically inhabit branched clumps of red algae (*Laurencia sp.*), submerged mangrove roots, seagrass banks, or sponges, which provide refuge from predation and easy access to food sources (Marx & Cobb, 1994). Post-pueruli lobsters grow to the juvenile stage 10-15 months post settlement (Cruz et al., 1995) and begin to move from vegetated habitats to unvegetated patches of reefs as the grow, seeking refuge in caves, coral reefs, sponges or soft corals (Herrnkind 1980). Older juveniles and sub-adults migrate offshore and recruit to the fishery when they attain minimum carapace length (89mm in the U.S. Caribbean), at about two years of age (Herrnkind, 1980; Cruz et al. 2001). Adult lobsters are thigmotactic and tend to enter social living arrangements aggregating in enclosed dens. Shelter environments may include natural holes in a reef, rocky outcrops, or artificially created environments (Lipcius & Cobb, 1994).

3.1 Feeding Behavior

Once *P. argus* pueruli settle and enter the seagrass and macroalgae nusery habitat, their diet consists of small gastropod mollusks, isopods, amphipods, and ostracods, most of which may be found within close proximity to the lobster's algal shelter. Studies suggest that food declines as lobsters forage around their territories. This leads to an increase in foraging territory and a subsequent increase in contact with conspecifics. Consequently, increased aggression between juveniles and declining food availability are thought to induce the nomadic emigration of juveniles from their algal nursery toward offshore reefs (Marx and Herrnkind, 1985).

Adult lobsters feed nocturnally, remaining in their shelters during daylight hours, with diets consisting of slow-moving or stationary bottom-dwelling invertebrates, such as sea urchins, mussels, gastropods, and clams (Lipcius and Cobb, 1994). Juveniles forage for similar items, only of smaller size. During feeding, prey organisms are seized and maneuvered using the anterior pereiopods or maxillipeds, while the mandibles, which are capable of crushing hard mollusk shells, carry out mechanical digestion (Herrnkind, et al., 1975). Little is known about the diet of pueruli or phyllosoma larvae.

The molt cycle is known to affect the feeding rates of spiny lobsters. Feeding activity increases prior to a molt, accommodating the increased metabolic needs associated with the formation of the new cuticle. About a week before ecdysis, daily food intake decreases rapidly, correlating with a reduction in locomotion and foraging. Feeding ceases altogether in the days before and during ecdysis, as the lobster becomes socially reclusive. However, within a week of the molting event, *P. argus* displays maximal foraging and locomotor activity, accommodating the active tissue growth that follows the formation of the new exoskeleton (Lipcius and Hernkind, 1982).

3.2 Migratory Behavior

Mass movements (2-60 individuals) of Caribbean spiny lobsters occur annually throughout the geographic range of the species and are dependent on latitude and climactic factors. Observed locations for the migration include Bermuda in October, the Bahamas and Florida in late October and early November, and the Yucatan and Belize in December (Herrnkind 1985). In these locations, the shallow waters that *P. argus* occupies during the summer become turbid and cold, initiating the diurnal migration of thousands of lobsters. *P. argus* is highly susceptible to severe winter cooling and will exhibit reduced feeding and locomotion at temperatures below 14ºC; molting individuals usually perish under these conditions. The lobsters migrate in single-file queues to deeper water in order to evade the stresses of the cold and turbid waters. This behavior reduces the hydrodynamic drag associated with the migration and is maintained by establishing contact between the antennules of one individual and anterior walking legs of another. *P. argus* may migrate for periods of six hours to five days and cover distances as far as 30-50km (Herrnkind, 1985).

4. Reproduction

4.1 Behavior

Reproduction in *P. argus* occurs almost exclusively in the deep reef environment once mature individuals have made the permanent transition from the shallow seagrass nursery to the ocean coral reef system. Choice of mate is determined by the female as well as by inter-male aggression, where larger males will prevent smaller males from courting females (Lipcius & Cobb, 1994). Males and females locate each other via chemical attractants released with the urine. Females mate only once during a season and are only receptive after molting, before their new shell hardens. Males may fertilize multiple females (Bliss, 1982; Atema & Cobb, 1980). During mating, the male flicks his antennules over the anterior of the female and scrape at her with the third walking legs. The male follows the female around continually trying to lift the female up and embrace her. This pattern continues until the female acquiesces and they stand on their walking legs while the male deposits the spermatophore mass on the female sternum using specially modified pleopods (Atema & Cobb, 1980; Bliss, 1982). Egg-bearing females usually seek refuge in solitary dens and infrequently forage for food (Lyons et al., 1981).

4.2 Seasonality

Spawning activity in Cuba peaks in the spring and summer (March-July) with a subsidiary peak in early autumn (September), though berried females may be found year round (Kanciruk and Hernkind, 1976; Arce and de León). More southern areas of the Caribbean may show spawning peaks that extend into October or November (Castano &

Cadima, 1993; Gallo et al. 1998). Spawning has been correlated with water temperature, with an optimal temperature of 24°C in the Florida Keys. Eggs gestate in about one month and change color from orange when freshly spawned to brown prior to hatching (Lyons et al., 1981).

4.3 Size

Fecundity is dependent upon the size of the individual as well as the geographic area in which the female lobster lives. First maturity was estimated to occur at 83mm, with 50% maturity at 93mm, and full maturity at approximately 108mm (Figure 4.1) (Arce & de León, 2001).

Reproductive efficiency for a given size in a given area can be determined utilizing a relationship between fecundity (Eggs, E) and carapace length (L_C) (Kanciruk & Herrnkind, 1976). Large adult females will produce more broods, as well as spawn eggs earlier in the reproductive period than younger females. Arce and de León (2001) present this model for the relationship in Southwest Cuba:

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

Rios (1991) presented this model:

$$E = -1031600 + 17474.2 \cdot L_C$$

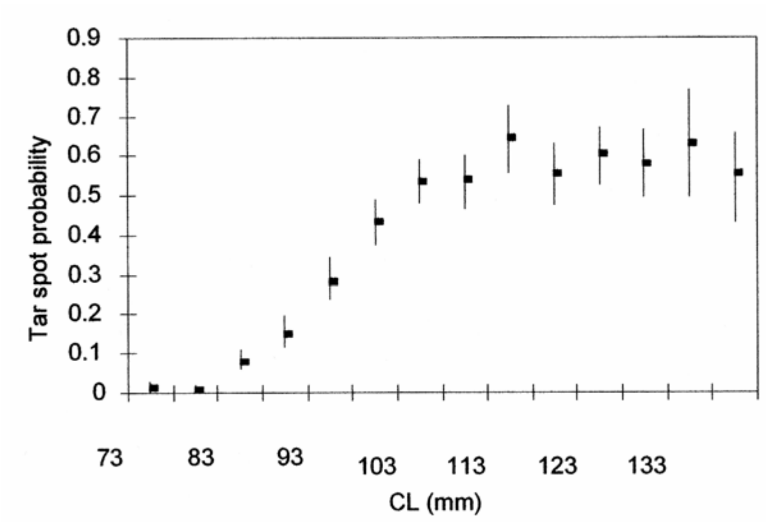


FIGURE 4.1 - Tar spot probabilities for female lobsters estimated from a logit model, Turks and Caicos Islands (Medley and Ninnes, 1997)

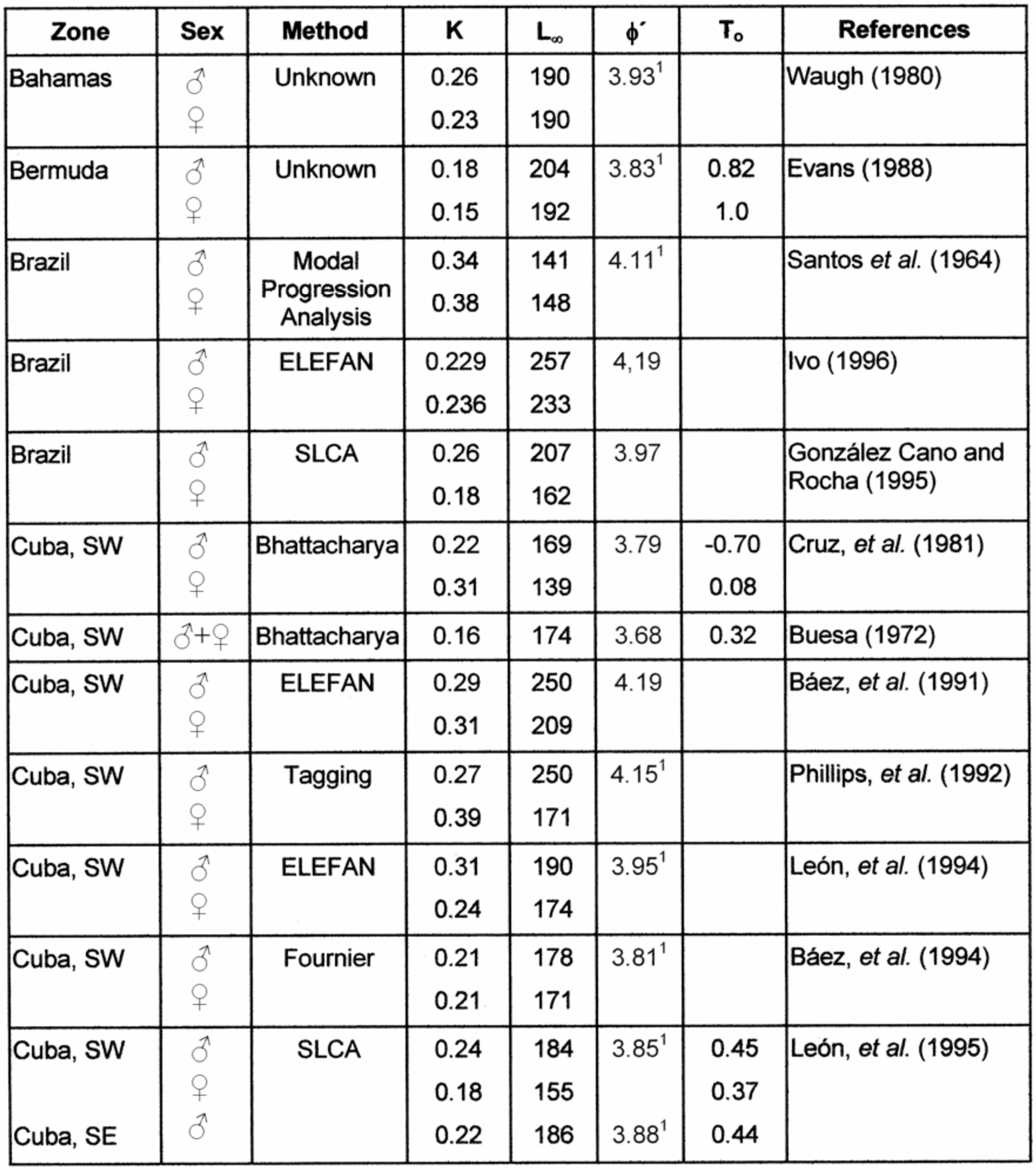
5. Growth

Temperature, maturation state, season, and sex have all been shown to affect the growth of the spiny lobster, *P. argus* (Arce & de León, 2001). Adult females have been shown to grow at 2/3 the rate of adult males (Hunt and Lyons, 1986). Physical growth of lobsters occurs through molting. The molt cycle begins with the intermolt period, the time when a new cuticle is formed, tissue growth is rapid, and the lobster actively forages. This period culminates in ecdysis, the shedding of the old cuticle (Lipcius and Herrnkind, 1982). Molting occurs primarily at night as a means of decreasing the risk of cannibalism and predation during day light. For adult lobsters, molts occur at an average rate of 2.5 year^{-1}, with each molting event requiring about 12 days for the new exoskeleton to harden and a full 28 days to completely form (Lipcius and Herrnkind, 1982; Williams, 1984).

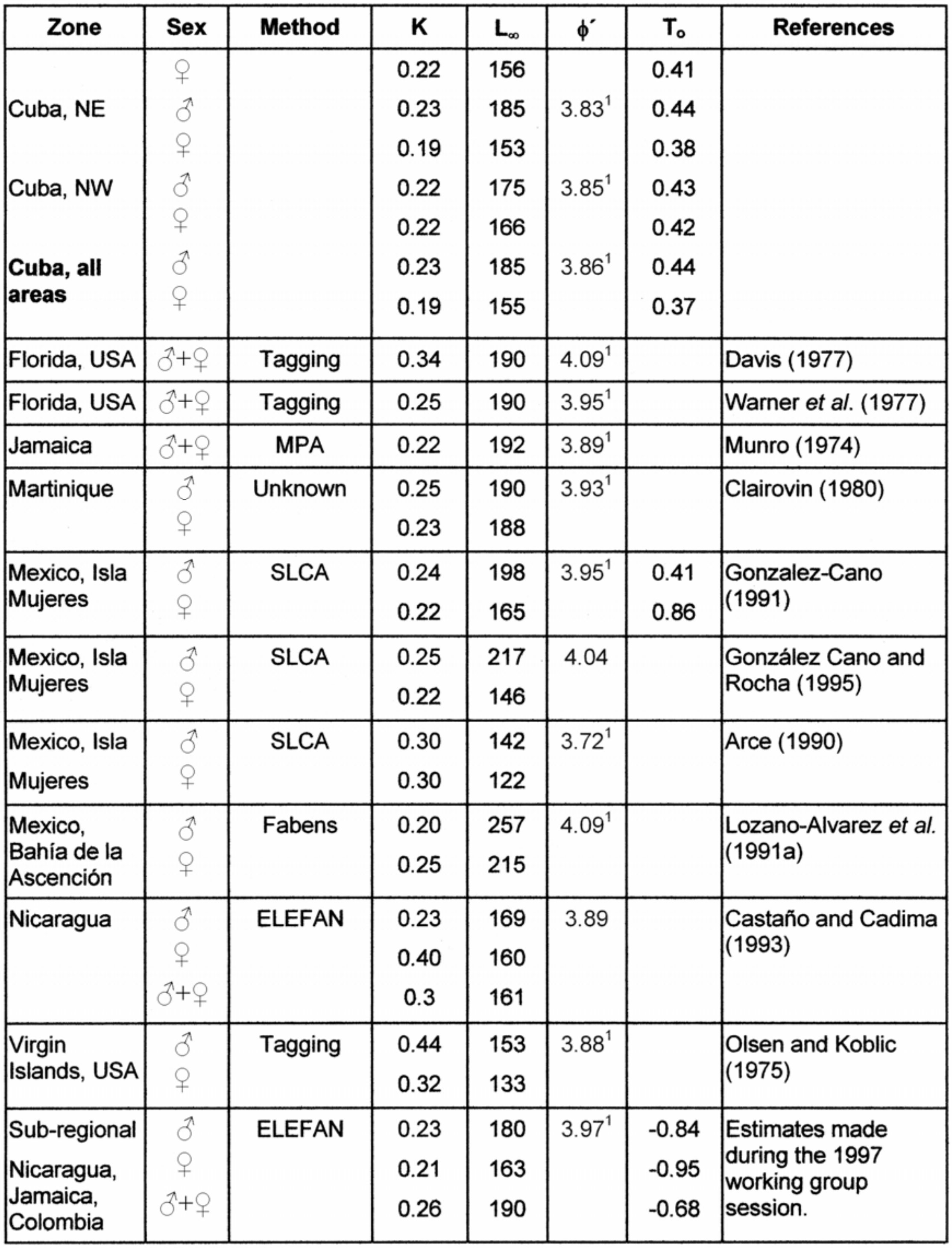
5.1 von Bertalanffy Growth Model

Despite the wide body of literature on this species, limited information is available on the growth and aging of the Caribbean spiny lobster due, in part, to the interference of molting habits with tagging efforts. Consequently, length data, which is substantially easier and less costly to attain, has been the dominant source of information used to estimate growth in *P. argus*. Gonzalez-Cano (1991) and Arce & de León (2001) have compiled some of this growth data from the Caribbean (Table 5.1, Figure 5.1). According to Arce & de León (2001), the de León et al. (1995) estimates for Cuba, which used large sample sizes and were obtained using the SLCA method, were considered the most reliable.

TABLE 5.1 – Von Bertalanffy growth parameter estimates
(Arce & de León, 2001)



Zone	Sex	Method	K	L_∞	ϕ'	T_o	References
Bahamas	♂	Unknown	0.26	190	3.93[1]		Waugh (1980)
	♀		0.23	190			
Bermuda	♂	Unknown	0.18	204	3.83[1]	0.82	Evans (1988)
	♀		0.15	192		1.0	
Brazil	♂	Modal Progression Analysis	0.34	141	4.11[1]		Santos *et al.* (1964)
	♀		0.38	148			
Brazil	♂	ELEFAN	0.229	257	4,19		Ivo (1996)
	♀		0.236	233			
Brazil	♂	SLCA	0.26	207	3.97		González Cano and Rocha (1995)
	♀		0.18	162			
Cuba, SW	♂	Bhattacharya	0.22	169	3.79	-0.70	Cruz, *et al.* (1981)
	♀		0.31	139		0.08	
Cuba, SW	♂+♀	Bhattacharya	0.16	174	3.68	0.32	Buesa (1972)
Cuba, SW	♂	ELEFAN	0.29	250	4.19		Báez, *et al.* (1991)
	♀		0.31	209			
Cuba, SW	♂	Tagging	0.27	250	4.15[1]		Phillips, *et al.* (1992)
	♀		0.39	171			
Cuba, SW	♂	ELEFAN	0.31	190	3.95[1]		León, *et al.* (1994)
	♀		0.24	174			
Cuba, SW	♂	Fournier	0.21	178	3.81[1]		Báez, *et al.* (1994)
	♀		0.21	171			
Cuba, SW	♂	SLCA	0.24	184	3.85[1]	0.45	León, *et al.* (1995)
	♀		0.18	155		0.37	
Cuba, SE	♂		0.22	186	3.88[1]	0.44	



Zone	Sex	Method	K	L_∞	ϕ'	T_o	References
	♀		0.22	156		0.41	
Cuba, NE	♂		0.23	185	3.83[1]	0.44	
	♀		0.19	153		0.38	
Cuba, NW	♂		0.22	175	3.85[1]	0.43	
	♀		0.22	166		0.42	
Cuba, all areas	♂		0.23	185	3.86[1]	0.44	
	♀		0.19	155		0.37	
Florida, USA	♂+♀	Tagging	0.34	190	4.09[1]		Davis (1977)
Florida, USA	♂+♀	Tagging	0.25	190	3.95[1]		Warner *et al*. (1977)
Jamaica	♂+♀	MPA	0.22	192	3.89[1]		Munro (1974)
Martinique	♂	Unknown	0.25	190	3.93[1]		Clairovin (1980)
	♀		0.23	188			
Mexico, Isla Mujeres	♂	SLCA	0.24	198	3.95[1]	0.41	Gonzalez-Cano (1991)
	♀		0.22	165		0.86	
Mexico, Isla Mujeres	♂	SLCA	0.25	217	4.04		González Cano and Rocha (1995)
	♀		0.22	146			
Mexico, Isla Mujeres	♂	SLCA	0.30	142	3.72[1]		Arce (1990)
	♀		0.30	122			
Mexico, Bahía de la Ascención	♂	Fabens	0.20	257	4.09[1]		Lozano-Alvarez *et al.* (1991a)
	♀		0.25	215			
Nicaragua	♂	ELEFAN	0.23	169	3.89		Castaño and Cadima (1993)
	♀		0.40	160			
	♂+♀		0.3	161			
Virgin Islands, USA	♂	Tagging	0.44	153	3.88[1]		Olsen and Koblic (1975)
	♀		0.32	133			
Sub-regional	♂	ELEFAN	0.23	180	3.97[1]	-0.84	Estimates made during the 1997 working group session.
Nicaragua, Jamaica, Colombia	♀		0.21	163		-0.95	
	♂+♀		0.26	190		-0.68	

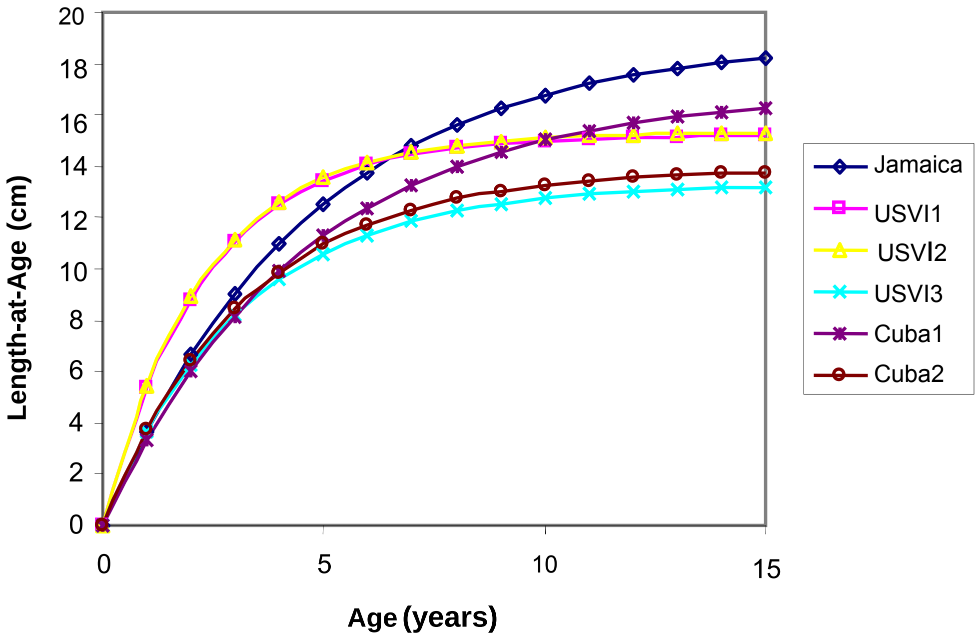


FIGURE 5.1 – von Bertalanffy Growth Curves for *P. argus* in the Caribbean. (Gonzalez-Cano, 1991; Munro, 1974; Olsen & Koblic, 1975; Cruz et al., 1981)

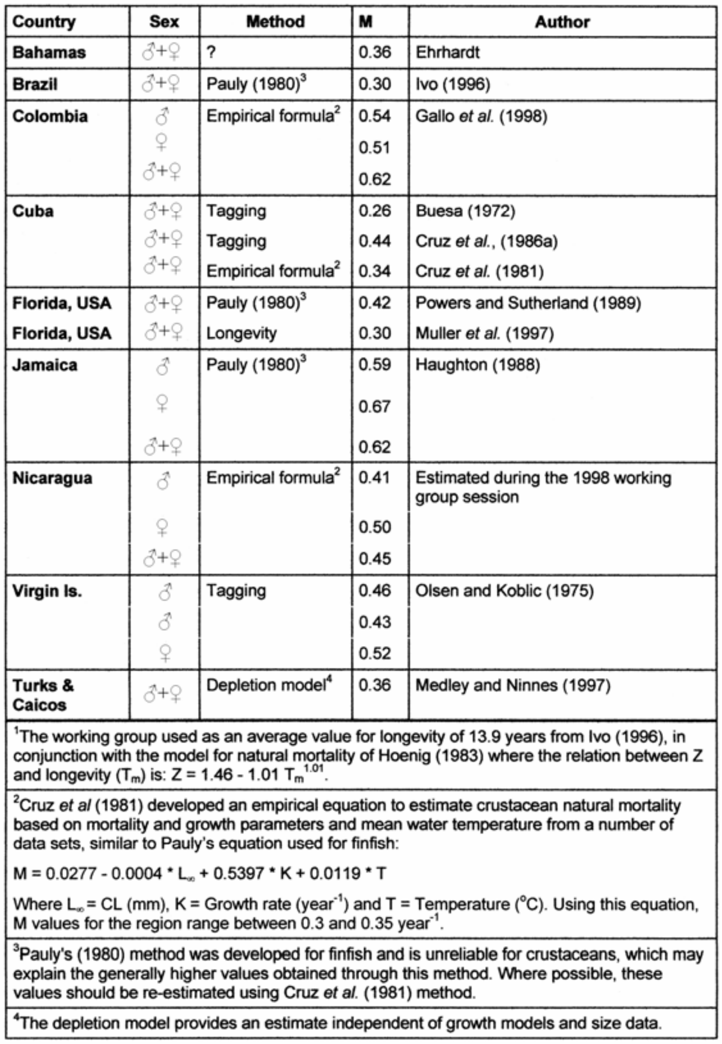
5.2 Molt increment models

Arce et al. (1991) used a model that utilizes the two components of lobster growth: molt increment and molt interval, to model growth in *P. argus*. Muller et al. (1997) modeled molt intervals by calculating the probability of molting with respect to carapace length, sex, season, and location. Both models have proven to provide a better fit to the data, due to their more realistic modeling of the lobsters' life-history, however, they are less widely applied, as they require more rigorous data (Arce & de León, 2001).

6. Mortality

Caribbean spiny lobster populations have been affected by such high fishing pressure for such a significant period of time that natural mortality rates have been difficult to isolate from fished mortality rates, however, larger animals such as sharks and finfish are known to prey on adult lobsters (Herrnkind, 1980) The most reliable estimates for natural mortality range between 0.3-0.4 year^{-1} (Table 6.1) (Arce & de León, 2001).

TABLE 6.1 – Estimates of natural mortality (year^{-1})
(Arce & de León, 2001)



Country	Sex	Method	M	Author
Bahamas	♂+♀	?	0.36	Ehrhardt
Brazil	♂+♀	Pauly (1980)[3]	0.30	Ivo (1996)
Colombia	♂	Empirical formula[2]	0.54	Gallo *et al.* (1998)
	♀		0.51	
	♂+♀		0.62	
Cuba	♂+♀	Tagging	0.26	Buesa (1972)
	♂+♀	Tagging	0.44	Cruz *et al.*, (1986a)
	♂+♀	Empirical formula[2]	0.34	Cruz *et al.* (1981)
Florida, USA	♂+♀	Pauly (1980)[3]	0.42	Powers and Sutherland (1989)
Florida, USA	♂+♀	Longevity	0.30	Muller *et al.* (1997)
Jamaica	♂	Pauly (1980)[3]	0.59	Haughton (1988)
	♀		0.67	
	♂+♀		0.62	
Nicaragua	♂	Empirical formula[2]	0.41	Estimated during the 1998 working group session
	♀		0.50	
	♂+♀		0.45	
Virgin Is.	♂	Tagging	0.46	Olsen and Koblic (1975)
	♂		0.43	
	♀		0.52	
Turks & Caicos	♂+♀	Depletion model[4]	0.36	Medley and Ninnes (1997)

[1] The working group used as an average value for longevity of 13.9 years from Ivo (1996), in conjunction with the model for natural mortality of Hoenig (1983) where the relation between Z and longevity (T_m) is: $Z = 1.46 - 1.01\ T_m^{1.01}$.

[2] Cruz *et al* (1981) developed an empirical equation to estimate crustacean natural mortality based on mortality and growth parameters and mean water temperature from a number of data sets, similar to Pauly's equation used for finfish:

$$M = 0.0277 - 0.0004 * L_\infty + 0.5397 * K + 0.0119 * T$$

Where L_∞ = CL (mm), K = Growth rate (year^{-1}) and T = Temperature (°C). Using this equation, M values for the region range between 0.3 and 0.35 year^{-1}.

[3] Pauly's (1980) method was developed for finfish and is unreliable for crustaceans, which may explain the generally higher values obtained through this method. Where possible, these values should be re-estimated using Cruz *et al.* (1981) method.

[4] The depletion model provides an estimate independent of growth models and size data.

7. Summary

This report has been prepared for the upcoming Southeast Data Assessment Review (SEDAR) workshop. Effective management of *P. argus* is not possible without a thorough understanding of its biology. Unfortunately, uncertainty is still present in both the growth models and the estimates of natural mortality for *P. argus*, and the estimated parameters vary across the range of the species. The growth models for this species are especially important to its stock assessment as *P. argus* cannot be directly aged.

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