Growth and Mortality of Captive Caribbean Spiny Lobsters, *Panulirus argus,* in Florida, USA

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ABSTRACT

A series of experiments rearing the Caribbean spiny lobster (*Panulirus argus*) was conducted to improve the growth and survival rates of laboratory-reared lobsters for subsequent experimentation. Seventeen groups of animals consisting of 25 to 63 pueruli were collected with modified Ross Witham collectors over five years in the Florida Keys. Groups of lobsters were raised communally for up to four years in 4000-liter aquaria and maintained at temperatures equivalent to local natural conditions. On average, both male and female lobsters grew to 76.2 mm CL, the minimum harvest size in Florida, in 1.2 years. The maximum size obtained in the laboratory after four years was 165 mm CL for males and 143 mm CL for females. Growth was best described by a seasonalized von Bertalanffy growth equation. Mortality in the laboratory was principally attributable to three factors: the pathogenic virus PaV1, poor nutrition, and overcrowding. During initial growth trials, viral infections were highly contagious and resulted in 98% mortality of juvenile lobsters. In subsequent growth trials, viral transmission and mortality from viral infection was nearly eliminated by recirculating aquaria water through an 18-W ultraviolet light sterilizer. Death associated with poor nutrition and overcrowding usually occurred during ecdysis and often resulted in cannibalism of postmolt individuals by conspecifics. These sources of mortality were reduced by supplementing the diet with live mollusks and crustaceans once per week and by reducing lobster density as size increased. These experiments identified several sources of mortality in the laboratory and improved protocols for rearing lobsters for subsequent experimentation and research.

KEY WORDS: *Panulirus argus*, growth, mortality, reproduction, von Bertalanffy

Crecimiento y Mortalidad de la Langosta Espinosa, *Panulirus argus,* en la Florida, USA

Se realizaron una serie de experimentos de crianza con la langosta espinosa del Caribe (*Panulirus argus*) para mejorar el crecimiento y la sobrevivencia de langostas criadas en laboratorio disponibles para experimentación subsecuente. En los Cayos de la Florida se colectaron 17 grupos de animales consistiendo de 25 a 63 puérulos durante cinco años, usando colectores de Witham. Las langostas recogidas mensualmente fueron criadas comunalmente por hasta 4 años en acuarios de 4000-liter y mantenidas a temperaturas equivalentes a las condiciones locales. En promedio, tanto hembras como machos crecieron hasta 76.2 mm CL, la talla mínima de captura en la Florida, en 1.2 años. La talla máxima obtenida en laboratorio después de 4 años fue de 165 mm CL para machos y 143 mm CL para hembras. El crecimiento fue descrito de mejor manera a través de una equación estacional de crecimento de von Betalanffy. La mortalidad en el laboratorio fue atribuida principalmente por tres factores, el virus patogénico PaV1, nutrición pobre, y densidades altas. Durante los experimentos de crecimiento iniciales, las infecciones virales fueron altamente contagiosas y resultaron en la mortalidad de 98% de las langostas juveniles. En experimentos de crecimiento subsecuentes, la transmisión viral y la mortalidad dada por infección viral fue eliminada casi totalmente al recircular el agua del acuario y pasarla a través de un esterilizador ultravioleta de 18-W. La muerte asociada a nutrición pobre y densidades altas usualmente ocurrió durante ecdisis y con frecuencia, generó canibalismo de individuos en post muda. Estas fuentes de mortalidad fueron reducidas al suplementar la dieta con moluscos y crustaceos vivos una vez por semana y al reducir la densidad de langostas a medida que estas aumentaron de talla. Estos experimentos permitieron identificar varias fuentes de mortalidad en el laboratorio y mejorar los protocolos para criar langostas para experientación subsecuente e investigación.

PALABRAS CLAVES: *Panulirus argus*, crecimiento, mortalidad, reproducción, von Bertalanffy

INTRODUCTION

As part of a larger research program investigating the age and growth of the Caribbean spiny lobster, *Panulirus argus*, pueruli were captured and subsequently reared and maintained in the laboratory for up to four years. Lobsters are commonly required for laboratory experiments, and we attempted to develop rearing techniques that would result in mortality rates near zero to reduce any artificial selection caused by conditions in the laboratory. The rearing techniques we developed in the laboratory may also be applicable to reducing lobster mortality in commercial aquaculture.

There is intense interest in the development of aquaculture techniques for the Caribbean spiny lobster. The high commercial value of this species and the limited extent of their wild fisheries make them an ideal candidate for commercial culture (Kittaka and Booth 2000).

Research has suggested that *Panulirus argus* could be a suitable candidate for grow-out aquaculture because of the apparent general availability of wild-captured pueruli and their rapid growth rate (Jeffs and Davis 2003). However, knowledge of optimal conditions for grow-out aquaculture is still fragmentary (Kittaka and Booth 2000). Large-scale commercial lobster aquaculture remains experimental (Staine and Dahlgren 2005) because of insufficient technological advances in the areas of nutrition, disease control, and grow-out systems (Phillips and Evans 1997). High mortality rates remain a major impediment in lobster aquaculture.

Estimated growth rates for *P. argus* are highly variable. This variability probably reflects both the natural variation in growth caused by differences in temperature, food availability, and injuries, as well as by differences in the methods used in the various studies. Growth estimates of wild lobster in South Florida range from 40 to 60 mm carapace length (CL) per year (Eldred 1972, Little 1972, Davis and Dodrill 1989, Davis 1981, Lyons *et al*. 1981, Hunt and Lyons, 1986, Forcucci *et al.* 1994, Sharp *et al*. 2000). Lellis (1991), after eliminating most of the mortality during culture, reared lobsters to 81 and 122 mm CL in one and two years, respectively. Higher than natural growth rates during culture of lobsters appears consistent for several species of lobster (Phillips and Evans 1997), but it has yet to be determined if the growth rates in culture reflect the maximum growth rate possible in the wild. The largest size reported for both male and female *P. argus* in the wild at one year is 70 mm CL and at two years is 92.3 or 102.7 mm CL for males and females, respectively, in Cuba (Phillips *et al*. 1992). Measuring the growth of lobster in the wild remains difficult and is a significant impediment to fisheries management.

There are multiple sources of mortality associated with laboratory and commercial culture of lobster (for review see Booth and Kittaka 2000). Poor water quality is a major, but often easily controllable, cause of mortality in the culture of *P. argus* (Lellis 1991). Molt death syndrome (MDS) is widely reported among captive spiny lobsters and has symptoms consistent with MDS in homarid lobsters (Bowser and Rosemark 1981, Conklin *et al*. 1991). Causes of MDS among other lobster species may include stress and poor nutrition but could also be related to the protein source or a lack of vitamins and/or minerals (Castell *et al.* 1991, Kanazawa 2000, Kittaka and Booth 2000). Cannibalism is widely reported in the group culture of *P. argus*, but it usually occurs after an extended period of confinement and is probably related to poor nutrition or overcrowding (Witham 1973, Briones-Fourzán and Lozano-Álvarez 1994, Assad *et al.* 1996, Lozano-Álvarez 1996). In general, spiny lobsters are considered physically robust, have few diseases (Evans *et al*. 2000), and have many behavioral features that make them amenable to captivity (MacDairmid and Kittaka 2000). A recently identified source of mortality is the naturally occurring lethal-pathogenic virus, PaV1 (Shields and Behringer 2004). The virus is highly contagious and may result in near total mortality of lobsters in high-density culture, as was seen in this study and in commercial facilities (Staine and Dahlgren 2005).

The aim of this study was to provide additional information on the potential growth rate of cultured *P. argus* and to identify methods to limit the mortality of lobsters associated with MDS, overcrowding, and the virus PaV1.

METHODS

Lobsters were raised in the laboratory at temperatures that were controlled to simulate those naturally occurring in the Florida Keys. Groups of recently settled pueruli and first-stage juveniles were collected periodically from modified Witham collectors located 100 m offshore of Big Munson Island (N 24° 37', W 81° 23') in the Florida Keys (Acosta *et al*. 1997). For the purposes of this study we consider the pueruli to be age 0; however, *P. argus* has an extended planktonic period with phyllosoma stages lasting many months (Lewis 1951, Lyons 1980). Each group of 25 to 64 pueruli was communally raised in a 1.6 m diameter by 0.8 m deep, 1,500 L aquarium at the Florida Fish and Wildlife Research Institute's South Florida Regional Laboratory in Marathon, Florida (Figure 1). The September 2001 group of lobsters was raised in a 3.6 m diameter by 1.0 m deep, 9,500 L aquarium. Each tank contained 4 to 6 concrete partition blocks for shelter. Water supply to the aquaria was pumped from nearby Florida Bay through a sand filter at approximately 10 liter/min. Water temperature in the aquaria was maintained within 1°C of the water temperature as measured by the C-MAN weather station near Long Key, Florida (National Data Buoy Center http://www.ndbc.noaa.gov/Maps/Florida.shtml) during the first year; subsequently, aquarium water temperatures were maintained within 1°C of water temperatures recorded in adult lobster habitat by the Sombrero Key C-MAN station. These temperatures reflect the conditions typical for juvenile and adult lobsters in the Florida Keys. Mean monthly temperatures ranged from 21 to 31°C in Florida Bay, a typical juvenile lobster nursery habitat, and from 23 to 30°C at the reef near Sombrero Key, a typical adult habitat. Large amounts of *Laurencia* spp. with attached epiphytes and other infaunal organisms including large numbers of the marine snail *Batillaria* sp. were collected from Florida Bay and placed in each aquarium for lobsters smaller than 25 mm CL. Frozen fish, shrimp, or squid was chopped into appropriate-sized pieces and provided daily *ad libitium*. We made an effort to drop a piece of food in front of each animal so that all animals had equal access to food. Fresh fish was provided occasionally when available. Live *Astraea americana* or other types of freshly killed mollusks and crustaceans were provided at least once per week. The volume of food was increased or decreased each day by approximately 10%, depending on the

presence or absence of leftover food in each tank. Uneaten food was removed daily.

Figure 1. 1500-liter aquarium at the South Florida Regional Laboratory equipped with heaters and an 18 watt ultraviolet sterilizer.

Control of the pathogenic virus PaV1 was initiated in September 2001. Seawater in each 1,500 L aquarium was partially recirculated through an 18-watt ultraviolet (UV) sterilizer at 25 L/min, which provides between 30,000 and 60,000 μWs/cm^2. Larger aquaria utilized a 25-watt ultraviolet sterilizer with seawater recirculating at 25 L/ min. Additional experiments to test the transmission of the virus between infected lobsters and uninfected lobsters were undertaken with and without recirculating aquaria water through UV sterilizers.

Seasonalized von Bertalanffy growth equations for male and female lobsters were determined following Sparre and Venema (1992) using TableCurve 2D©. This analysis included only lobsters collected in September 2001, because this group had very little mortality. L_{max} values were constrained to account for the limited size range of lobsters available in the laboratory by using the 99th percentile of the CL distribution of 3,600 spiny lobsters captured from Dry Tortugas National Park by divers between 1996 and 1998 (Bertelsen and Matthews 2001). The Dry Tortugas National Park was closed to lobster fishing in 1973, and likely represents the most undisturbed lobster population in Florida.

RESULTS

Mortality

The amount and timing of lobster mortality changed as the laboratory-rearing methods were improved. At one year, the mortality rate of the initial 14 groups of lobsters reared in the laboratory averaged 99%. Lobster mortality was 3% for the group of lobsters collected in September 2001. Mortality rates were 34% and 38% for lobsters collected in December 2001 and April 2002, respectively (Figure 2). The majority of the lobsters in the first 14 groups collected from December 1997 to May 2001 died one by one over time, beginning as early as 19 days after collection, but most of the deaths occurred between three and nine months. The few lobsters from these early groups that survived for one year tended to survive through the four year duration of the project. The lobsters collected in February 1999 were the only group of lobsters to die *en masse*. This event occurred over eight days at between 25 and 32 days after collection and resulted in 74% mortality of the 65 lobsters in the experiment. Few of the lobsters in the December 2001 and April 2002 experimental groups died within the first 60 days, but there was a relatively continuous loss of lobsters as the mean size of lobsters in each aquarium increased.

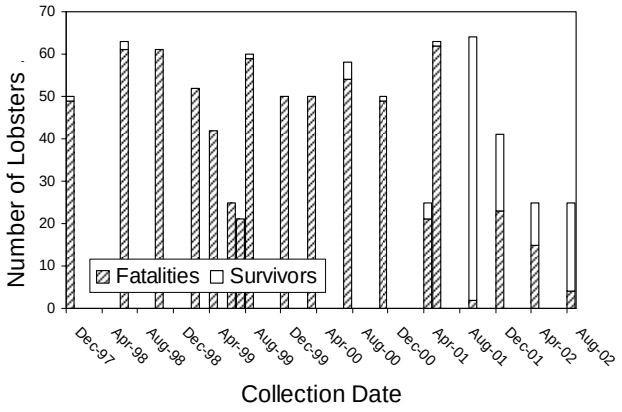

Figure 2. Number of lobster fatalities and survivors at one year in each group raised in the laboratory.

There were several causes of lobster mortality observed during the lobster-rearing experiments. The primary source of mortality in the first 14 experiments appeared to have been the lethal virus PaV1 which was subsequently described by Shields and Behringer (2004). The presence of the virus was not verified histologically, but the external appearance of the lobsters was consistent with the symptoms of infected lobsters (Figure 3). Mortality from the virus was eliminated after the installation of ultraviolet sterilizers. The cause of the mass-mortality event associated with the February 1999 group of lobsters was not identified but did not appear to be caused by the virus. The two lobsters that died in the September 2001 group had molted in the previous 12 hours and were partially cannibalized; we were unable to determine if cannibalization was the cause of or subsequent to death. Deaths of the lobsters in the December 2001 and April 2002 groups also usually occurred following molting; although the exuvia were often partially eaten by other lobsters in the aquaria, there were seldom indications of cannibalism or injury to the freshly dead lobsters.

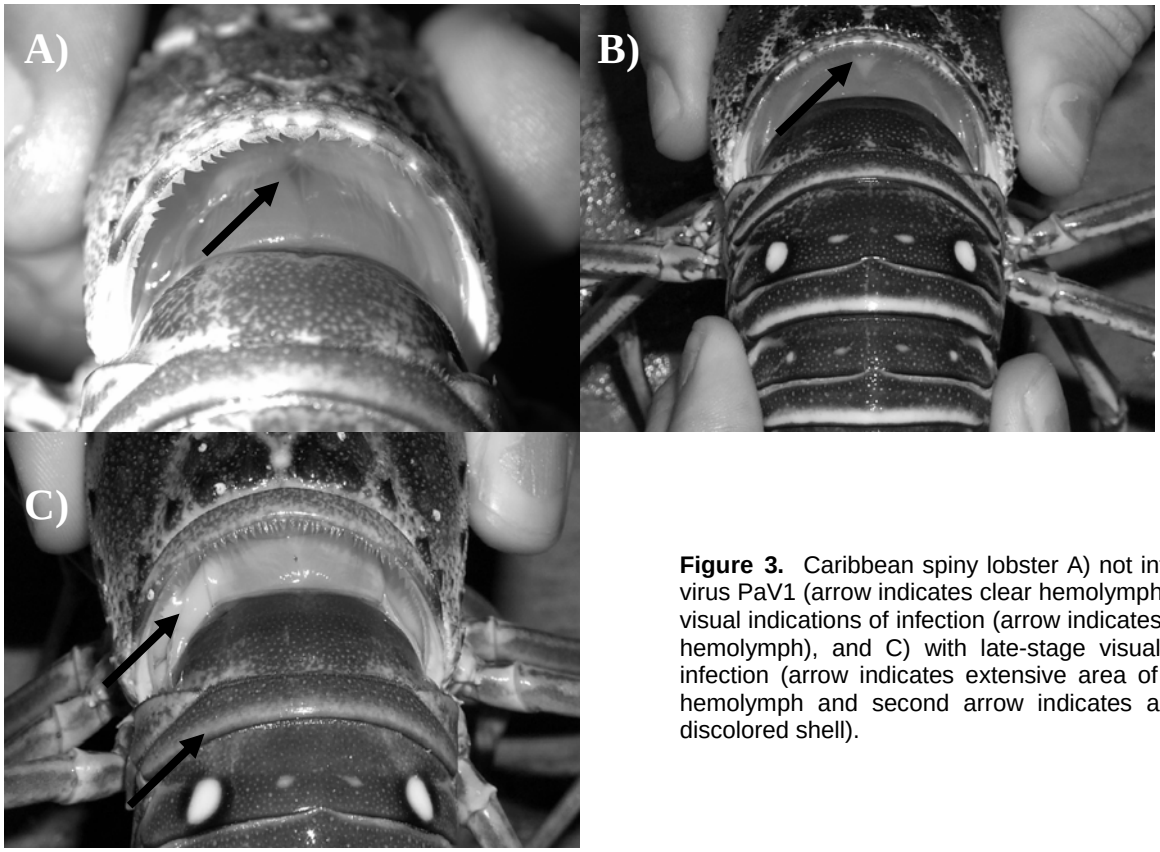

Figure 3. Caribbean spiny lobster A) not infected with the virus PaV1 (arrow indicates clear hemolymph), B) with early visual indications of infection (arrow indicates white-infected hemolymph), and C) with late-stage visual symptoms of infection (arrow indicates extensive area of white-infected hemolymph and second arrow indicates area with pink-discolored shell).

The onset of the visible symptoms of viral infection and the infection rate of the lobsters in different groups varied. Visible symptoms include milky-colored hemolymph and intestine and, in late-stage infections, a pink- or red-tinted exoskeleton, which was especially visible on the white portions of the shell (Figure 3). The appearance of symptoms in each group of lobsters occurred at between 20 days and 270 days, but usually occurred within 90 days after the collection of wild pueruli. There did not appear to be a seasonal component associated with infection rates. Near total mortality of lobsters in each group of lobsters exposed to the virus usually occurred between six to twelve months. Lobsters with visible symptoms of the virus generally died within 90 days. No lobsters with visible symptoms of the virus recovered; however, several lobsters that were confined with infected lobsters for more than one year never contracted visible symptoms of the virus and survived through the four year duration of the project.

Two experiments confining uninfected pueruli with infected juvenile lobsters verified the UV sterilizers prevent viral transmission. Pueruli captured from the wild and placed among infected lobsters in aquaria with UV sterilizers did not show symptoms of the virus after six months. Control experiments without UV sterilizers resulted in infections in most lobsters by six months. All infected lobsters in these experiments died within 90 days. One experimental trial was discontinued when the 1-year life expectancy of the UV bulb was exceeded and the treatment did not receive the level of UV treatment anticipated.

Food quality appears to be the causative factor in incidents both cannibalism and MDS in our laboratory-rearing experiments. In the August 2000 group, fresh food was not readily available in the spring and early summer of 2001. After approximately three months on a diet of frozen squid and shrimp, several animals died during the molting process and were subsequently eaten by other lobsters in the aquaria. No further incidents of MDS occurred after the addition of freshly killed shrimp to their diet. In a second experiment, 20 lobsters between 67 and 82 mm CL were collected in May 2005 and raised communally in an aquarium on a diet of frozen shrimp and squid. The first incident of MDS occurred in August, 91 days later. Again, after the addition of fresh food (live snails and fresh shrimp or crab) to the diet, no further incidents of MDS occurred.

Overcrowding appeared to be the primary source of mortality in the rearing experiments that began in December 2001 and April 2002. The experiments were conducted in 1500-liter aquaria (Figure 1) with 40 or 25 pueruli. As the lobsters grew, the number of deaths of postmolt lobsters increased (Figure 4). On several occasions, the

largest lobster in the aquarium died. The dead lobsters were not cannibalized and there were no obvious signs of injury. Although there were numerous artificial dens provided in each aquarium, as lobsters exceeded approximately 40 mm CL, they began to frequently move between dens and make frequent physical contact with other lobsters. The amount of physical contact increased as the lobsters grew larger. This increased level of activity caused near-constant disturbance of post-molt lobsters and may have interfered with the molting process and ultimately led to the death of these individuals.

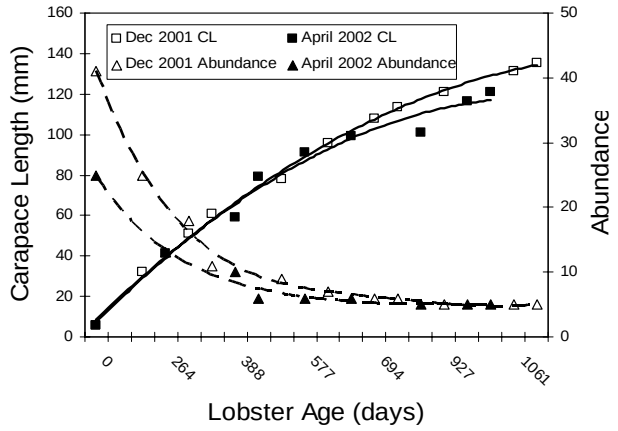

Figure 4. Carapace length (squares) and number of lobsters (triangles) surviving in 1500-liter aquaria from groups of pueruli captured in December 2001 (open) and April 2002 (filled).

The relationship between the number of lobsters that can be maintained in aquaria appears related to the length and number of the lobsters and not to their total biomass (Figure 5). The biomass (sum of the weight of all lobsters) in each tank continued to increase linearly over time (Figure 5a); where as, an index, based on lobster abundance * CL, remained at approximately 600 for lobsters ranging from 60 mm to 120 mm CL. The index illustrates that as lobsters grew, increased in CL, additional lobster mortality occurred and the abundance of lobsters in each tank declined. This index appears to reflect the maximum amount of lobsters that can be maintained in a 1,500 liter aquarium (Figure 5b). No such relationship was apparent in the 9500-liter aquaria, when up to 100 50-mm to 75-mm CL lobsters were maintained during other projects.

The single incident of intraspecific aggression resulting in death or injury occurred between two mature male lobsters (larger than 100 mm CL). Although male to male aggression during the reproductive season in the form of grappling, pulling, and pushing using both the antennae and the enlarged second pair of pereopods was common, the smaller lobster or the lobster located on a lower portion of the artificial structures usually retreated from the encounter. The dead lobster had a puncture wound, consistent with the size of a lobster dactyl, between the abdomen and the carapace. The injured lobster apparently bled to death, but there were no indications of cannibalism.

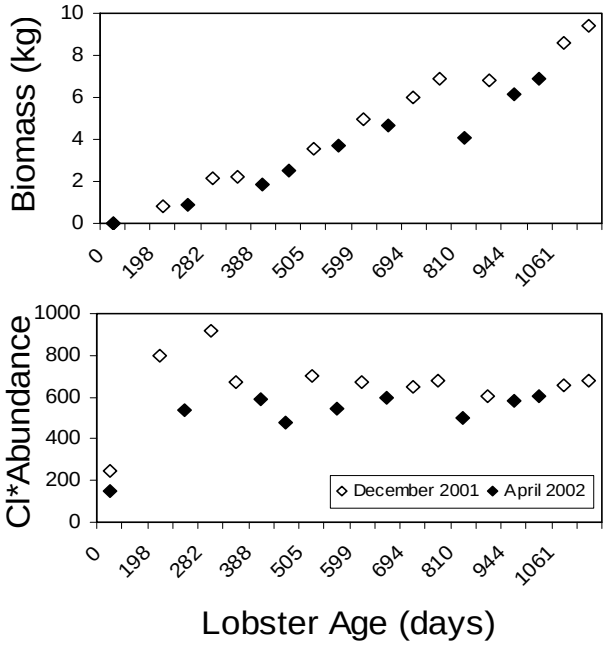

Figure 5. Relationship between a) weight of all lobsters (biomass) and b) an index representing average carapace length * abundance for two groups of lobsters collected in December 2001 and April 2002 and raised in 1,500 liter aquaria.

Growth

Spiny lobsters in our study grew rapidly and averaged 63 mm CL at one year. By year two, male and female growth rates differed, and their average size was 109 and 100 mm CL, respectively. For lobsters larger than 100 mm CL, the average growth increment was 7.8 mm and the molt interval was 118 days, suggesting that large lobsters are capable of molting three times per year. Growth for both males and females appears to begin to asymptote (Figure 6), but the limited age range of the lobsters examined herein probably does not fully reflect the decrease in growth rate for either males or females. The growth curve obtained by age-at-length data was well described by a seasonalized von Bertalanffy growth model, where L_{max} (maximum length) = 180 mm CL for males and 145 mm CL for females, t = age in years, t_S (parameter of seasonalized VBGF) = 0.941 for males and 0.923 for females, C (parameter of seasonalized VBGF) = 0.033 for males and 0.038 for females, t_0 (age at length 0) = 0.132 for males and 0.123 [for] females, and K (stress factor,

parameter of seasonalized VBGF) = 0.492 for males and 0.615 for females. The seasonalized VBGF resulted in an R^2 of 0.971 for males and 0.974 for females as follows:

$$L(t) = L_{max}*(1-\exp(-K*(t- t_0) – (CK/2\pi)*\sin(2\pi*(t- t_S)))).$$

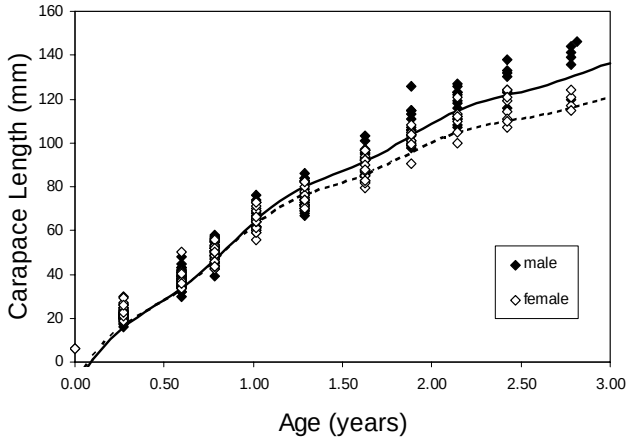

Figure 6. Seasonalized von Bertalanffy growth model for males (black diamonds and solid line) and females (white diamonds and dotted line) showing the effects of season on growth in *P. argus.*

DISCUSSION

The goal of this project was to develop methodologies for raising lobsters in the laboratory from pueruli with near zero mortality. The rearing techniques we developed in the laboratory may also be applicable to reducing lobster mortality in commercial aquaculture. The identification and alleviation of the sources of mortality in aquaculture is a major impediment to the development of a cost-effective, commercial-scale aquaculture program (Kittaka and Booth 2000). Research has suggested that in Florida and the Caribbean, the tropical lobster *Panulirus argus* could be a suitable candidate for land-based culture (Lellis 1991, Davis *et al*. 2007), and there is currently at least one program attempting to develop production on a cost-effective, commercial scale (Staine and Dahlgren 2005).

There were multiple sources of lobster mortality during this study. The source of the most catastrophic loss of lobsters, when 74% of lobsters collected in February 1999 died 25 to 32 days after collection, remains unidentified. Water quality was often a major cause of mortality in early aquaculture systems for lobsters (Kensler 1967, Lellis 1991), but these problems were generally resolvable with improved technology. For most of the duration of this experiment, the principal source of mortality was the lethal virus PaV1. The 98% mortality rate caused by the virus in our aquaria masked the other two, more chronic, sources of mortality: poor nutrition and overcrowding.

The PaV1 virus was first recognized in the Florida Keys in 1999 (Shields and Behringer 2004). It has subsequently been observed in Fort Pierce, Florida (Serena Cox and Meagen Davis Pers. comm.), St. Croix (Lyn Cox Pers. comm.), and Belize (Craig Dahlgren and Robert Usher Pers. comm.). The virus predominately affects small juvenile lobsters and is rarely observed in adult lobsters. In the Florida Keys the virus seems to be present in from 6 to 8% of the lobster population, but it is more abundant in specific locations (Shields and Behringer 2004). The virus may have a substantial effect on the lobster population in Florida. If infected lobsters survive for 90 days or less and the infection rate is 6-8%, between 24 and 32% of each year-class may be affected by the virus. Prior to 1998, there appear to be no reports of mass mortality with the obvious external symptoms associated with this viral infection, and many researchers have collected pueruli and maintained lobsters in the laboratory over the past 30 years (Ting 1973, Lellis 1991, FWC unpublished data). We are left to hypothesize that this is a newly evolved viral strain or that environmental conditions have changed so that lobsters are more susceptible to infection.

There was no relationship between the first appearance of the virus in each experimental group and the time of the year or the number of lobsters in each experimental group. The lack of any obvious elements that contribute to the occurrence of the virus in the laboratory is probably not indicative of the epidemiology of the virus in the wild. As yet unknown conditions probably affect infection rates in the wild (Behringer *et al*. 2006). The slow progression of infection and death of all but 2% of the lobsters in each of the early experimental groups suggests that there may be other factors that permit or prevent infections. Behringer *et al*. (2006) reported that healthy lobsters avoid infected lobsters and hypothesized that this behavior might reduce viral transmission rates. Additional work is required to explore the possibility that a small number of lobsters may be resistant to infection or may survive and be carriers. Although there is no treatment for lobsters infected with the virus, transmission of the virus seems to be controlled by recirculating seawater through a UV sterilizer.

Cannibalism has been reported to be a persistent problem in the culture of *P. argus* (Ting 1973, Witham 1973, Díaz-Iglesia *et al*. 1991, Baez Hidalgo *et al*. 1996), although it is unreported in the wild. In this study, cannibalism appeared to be a symptom of poor nutrition, specifically poor food quality not quantity. Incidents of cannibalism in this study occurred after to extended periods (90 days) when fresh mollusks or crustaceans were not supplied as a once weekly supplement to the normal regime of an abundant supply of frozen shrimp and squid and the occasional fresh fish. Our explanation for the cause of cannibalism appears consistent with the 45-day delay in the onset of cannibalism and the increased aggression for food in shore-cultured lobsters in Mexico (Briones-Fourzán and Lozano-Álvarez 1994). In general, cannibalism appears to be an uncharacteristic activity and

may only be a symptom of poor food quality. Additional research is required to ascertain which dietary components are absent in frozen as opposed to fresh food.

Molt death syndrome (MDS) is also recognized as a symptom of poor nutrition in crustaceans (Castell *et al*. 1991, Conklin *et al*. 1991, Davis and Gatlin 1996, Kanazawa 2000, Kittaka and Booth 2000). MDS is relatively easily prevented in experimental-scale culture. In this study, we provided natural foods once per week, but it appears likely that less frequent addition of natural food to the diet may prevent MDS (Pardee and Foster 1999). However, the sourcing of appropriate feeds and the lack of a suitable artificial feed remains a major impediment to commercial-scale aquaculture (Kittaka and Booth 2000).

Caribbean spiny lobsters are naturally gregarious (Berrill 1975, Herrnkind *et al*. 1975, Childress and Herrnkind 1996) and, given appropriate refuge and space, should be resistant to problems associated with overcrowding during culture. Our small aquaria (1,500 L) appear to be suitable for culturing early post-pueruli up to approximately 25 mm CL. For *Jasus edwardsii*, stocking density also did not appear to affect the rate of cannibalism or mortality of animals below 25 mm CL (James *et al*. 2001). In our study, the use of relatively small aquaria may not have provided adequate isolated refuges for post-molt lobsters despite the availability of numerous shelters. Increased mortality has also been associated with increased stocking density in other studies (Díaz-Iglesia *et al*. 1991). In our study, stocking density did not appear to affect mortality of lobsters below 25 mm CL, but as lobsters grew and became more active, stocking density appears to have become the primary cause of mortality. Larger aquaria may be more suitable for rearing lobsters. The 9,500 L aquarium successfully maintained 12 times more lobster than the 1,500 L aquaria despite having only five times the surface area. The primary difference between the behavior of lobsters in the small and large aquaria appeared to be the use of specific artificial shelters as refuges after molting. Postmolt lobsters were often isolated or cohabitating with other recent postmolt lobsters in specific shelters. The distance between shelters in the 9,500 L aquarium may have reduced the frequency of intrusions from other lobsters.

Growth

Growth rates in our study were among the highest recorded for the species. Lobsters in previous laboratory growth experiments by Lellis and Russell (1990) had a growth rate of 450 g/year, the highest observed for this species, principally because the optimal temperature for growth was maintained. Our lobsters were maintained at ambient temperatures for the Florida Keys, and the variable seasonal growth rates for both male and female lobsters (Figure 6) reflected the characteristic winter decline in growth rate in Florida (Hunt and Lyons 1986, Forcucci *et al.* 1994, Sharp *et al*. 2000). The seasonal component to growth diminishes, but is still present, for large lobsters (> 100 mm CL). There was no abrupt change in growth rate for large lobsters, only the gradual decrease in growth rate revealed by the von Bertalanffy growth equation. Our estimation of L_{max} for male lobsters is consistent with other values in the literature, but our estimate for females is lower than has been reported (for review see FAO 2001). For both male and female lobsters, our estimates of K are higher than previously reported in Florida (FAO 2001) and would represent an estimated age at legal size (3 inch CL in Florida) of 15 months for both male and female lobsters. Previous von Bertalanffy growth estimates in Florida suggested legal size would be reached in 19 months (FAO 2001). We therefore consider our estimates of growth to be near the maximum potential growth of *P. argus* and stress the importance of considering the potential range of growth variability when conducting analyses that include estimating age (Lellis 1991, Phillips *et al*. 1992, Sharp *et al*. 2000).

Determining the growth rates of lobsters is highly problematic. In laboratory studies, too many variables may be controlled and in field studies, insurmountable sampling biases are often encountered. In several groups of lobsters in this study, overcrowding caused differential mortality of lobsters that molted most frequently and growth would have been underreported. These groups of lobster were not used in our growth calculations, but differential mortality or recapture of lobsters is an issue in many growth studies. In tagging studies in Florida, few lobsters were usually recaptured after one year (Lyons *et al*. 1981, Hunt and Lyons 1986, Davis and Dodrill 1989, Forcucci *et al*. 1994). Likely explanations for the low recapture rates include the mobility of the species and the high fishing pressure; however, tag-induced mortality and tag loss may also have differential effects on the recapture rates of lobsters that molt more frequently (Davis 1978). Even studies with relatively noninvasive microwire tags may have differential recapture rates that cause growth to be underestimated (Sharp *et al*. 2000).

CONCLUSIONS

Caribbean spiny lobsters can be maintained in the laboratory for many years with near-zero mortality. Historically common sources of mortality related to water quality, molt death syndrome (MDS), and cannibalism are controllable. Poor nutrition is likely the cause of MDS and we suspect cannibalism is also an artifact of poor nutrition. The lethal virus PaV1 appears to be a new cause of mortality that affects both lobsters in the wild and in culture, where it can be pervasive. Fortunately, transmission of the virus in the laboratory appears to be preventable via the use of relatively low-intensity ultraviolet sterilizers. Growth rates of lobsters in the laboratory are high, and typical market-size tails (5 oz or 142 g) can be produced in 15 months. Less time might be required if lobsters were held near optimum temperatures. However, feeding costs

in this study were high. Additional survival and growth trials are needed to develop and assess artificial feeds for use in commercial-scale culture (Kittaka and Booth 2000). Current impediments to the commercial culture of Caribbean spiny lobsters appear to be associated with the economies of scale and the sourcing of appropriate feeds.

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