

Growth and Survival of Caribbean spiny lobster, *Panulirus argus*, raised from puerulus to adult Size in Captivity

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ABSTRACT

Aquaculture of the Caribbean spiny lobster, *Panulirus argus*, may be a means of increasing production of this valuable species without depleting wild stocks. At present, however, full life cycle aquaculture has not been successful, so efforts have focused on the grow-out of lobsters from puerulus post-larval stages legally harvestable size. In this study, growth and survival of lobsters grown in captivity from puerulus stage was examined in the Bahamas and Belize using low cost natural food sources and simple flow-through seawater systems. Growth rates of lobsters fed a diet of cerithid gastropods produced the greatest growth rates, at a ration of 0.1 g of snails per gram of lobster biomass fed twice daily. Growth rates using a variety of feeds, however, produced legally harvestable lobsters in a period of less than two years. Lobster survival ranged greatly, from as little as 3% mortality per month to >30% mortality per month during incidents of disease. Regular sources of mortality included death during molting and cannibalism of newly molted lobsters. Periodic disease outbreaks, however were the greatest source of lobster deaths, but the effect of disease was reduced by the addition of improved filtration and ultraviolet sterilization of seawater. Based on the results of these experiments, the grow-out of juvenile lobsters to legally harvestable size may be achieved at a low cost, however, further investigations into disease prevention, and ensuring an adequate supply of puerulus and high quality feed for juveniles is essential.

KEYWORDS: *Panulirus argus*, aquaculture, grow-out

Crecimiento y supervivencia de la langosta espinosa del Caribe, *Panulirus argus*, levantado de Puerulus al tamaño del adulto en cautiverio

La acuicultura de la langosta espinosa del Caribe, *Panulirus argus*, puede ser el medio de aumentar la producción de esta valiosa especie sin agotar la recursos silvestres. En este momento, sin embargo, la acuicultura completa del ciclo de vida no ha tenido éxito, así que los esfuerzos se han centrado en el crecimiento de langostas de las etapas post larvales del puerulus post-larval hasta las tallas legales de captura. En este estudio, el crecimiento y la supervivencia de las langostas crecidas en cautiverio de la etapa del puerulus fueron examinados en las Bahamas y Belice usando fuentes naturales de alimento de bajo costo y simple sistemas de circulación de agua de mar. Los índices de crecimiento de langostas que se alimentaron con una dieta de los gasterópodos del género cerithid produjeron las mayores tasas de crecimiento, en una relación de 0.1 g de caracoles por el gramo de la biomasa de la langosta alimentado dos veces al día. Las tasas de crecimiento que usaban una variedad de alimentos, sin embargo, produjeron langostas a la talla legal de captura en un período de menos de dos años. La supervivencia de la langosta se extendió grandemente, de tan poco como la mortalidad del 3% por mes a mortalidades de 30% por mes durante incidentes de la enfermedad. Fuentes regulares de mortalidad incluyen la muerte durante las mudas y canibalismo de langostas con nuevas mudadas. Los brotes periódicos de la enfermedad, fueron la mayor fuente de muertes para la langosta, sin embargo el efecto de las enfermedades fueron reducidos al mejorar filtración y la esterilización ultravioleta del agua de mar. De acuerdo con los resultados de estos experimentos, el crecimiento de las langostas de juveniles al tamaño de captura legal se puede alcanzar a un bajo costo, sin embargo, otras investigaciones relacionadas con la prevención de las enfermedades, asegurarse de una fuente adecuada de puerulus y de una alta calidad de alimentos para los juveniles son esenciales.

PALABRAS CLAVES: *Panulirus argus*, acuicultura

INTRODUCTION

The Caribbean spiny lobster, *Panulirus argus*, is the most valuable fishery species in the wider Caribbean region. Around the Caribbean, the spiny lobster fishery has seen rapid expansion in the past three decades; however, there is growing concern that, throughout much of the Caribbean, *P. argus* harvests may be at or above sustainable levels (FAO 2003). While the threat of overfishing

necessitates fishery management plans that restrict growth of the fishery or even implement measures to decrease production in some places (Siejo 2003), the global demand for lobster is likely to still be increasing. Thus, investigations have begun into the culture of *P. argus* as a means of meeting the growing demand for lobster without increasing fishing pressure on wild stocks (e.g., Lellis 1991, Alvarez 1996, reviewed by Kittaka and Booth 2000).

To date, attempts at *P. argus* aquaculture have been limited by its complex life cycle, which includes a prolonged planktonic larval duration, during which lobsters go through several different stages (Kittaka and Booth 2000). These larval stages have proven difficult to maintain in an aquaculture setting and have led to the failure of raising lobsters through their full life cycle (reviewed in Kittaka and Booth 2000, Kittaka 2000). Several studies, however, have captured lobster puerulus (post-larvae or PL) from the wild to grow-out to legally harvestable sizes (reviewed by Booth and Kittaka 2000). This form of grow-out aquaculture could directly lead to the development of lobster aquaculture if the grow-out of post-larvae is a cost-effective means to produce lobsters. Information gained from successfully growing-out lobsters from post-larvae through juvenile stages will also contribute to the development of techniques for culturing lobsters in captivity, and will provide an important step in the development of whole life cycle culture and production-scale aquaculture.

In this study we build on past grow-out aquaculture techniques to develop a low cost means of effectively culturing *P. argus* from the post-larval stage to adult (and/or market) size. Specifically, we attempt to improve upon past studies by (1) increasing growth rates achieved in captivity using low cost natural food items, (2) providing high survival rates in captivity; and (3) determining the scale at which lobster production may be achieved through grow-out aquaculture in the Bahamas and Belize.

METHODS

This project was conducted in two stages. The first stage was conducted in the Bahamas at the Perry Institute for Marine Science's field station on Lee Stocking Island and the second stage was conducted in Caye Caulker, Be-

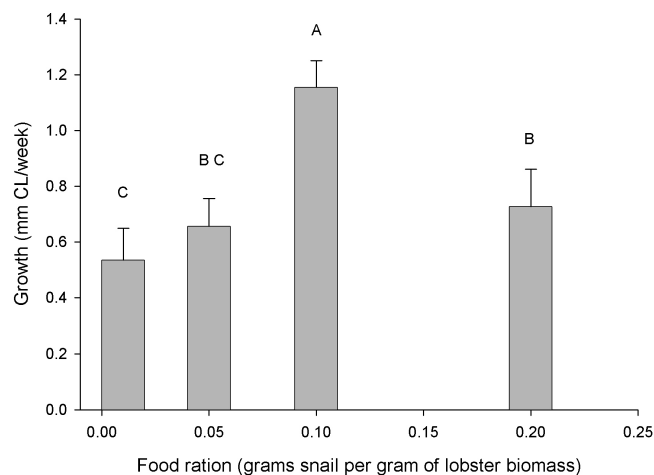


Figure 1. Growth of lobsters fed different rations of *Cerithium* spp. snails. Letters above bars indicate groupings of treatments that did not differ significantly. Error bars represent 1 SE.

elize at the Northern Fishermen Co-operative Society's Lobster Aquaculture Buildings (LABs). During the first stage conducted in the Bahamas, the primary focus was on small-scale aquaculture experiments in a laboratory setting to examine growth and survival of lobsters in captivity, as well as factors influencing growth and survival. During the second stage conducted in Belize, the focus was on scaling-up aquaculture to see if production-scale aquaculture was feasible.

Stage One – Bahamas:

Research in the Bahamas began in June 2003 and continued through 2004. Puerulus (post-larval or PL) stage *P. argus* were collected from the southern Exuma Cays around Lee Stocking Island and Great Exuma Island using modified witham collectors (i.e., identical to those used by Lipcius *et al.* 1997 in the Bahamas). Following their capture, PLs were brought to laboratory facilities on Lee Stocking Island (LSI) for grow-out aquaculture experiments. On LSI, lobsters were initially held in an air conditioned wet lab facility with a flow through seawater system. Water was drawn from within 20m of the western shoreline of LSI and was run through a sand filter prior to entering the wet lab facility. Within the lab, lobsters were held in 190 liter aquaria in this facility from the time of their capture and measured weekly until they reached a size of 15 mm carapace length (CL), at which time they were moved to large outdoor raceways and eventually into large holding ponds when they reached a size of 50 mm CL. All experiments reported here were conducted on lobsters prior to their movement into raceways and holding ponds. Small lobsters in aquaria were provided sheets of natural fiber (i.e., hog's hair) air conditioner filter material, which provided structure similar to their natural macroalgal habitat

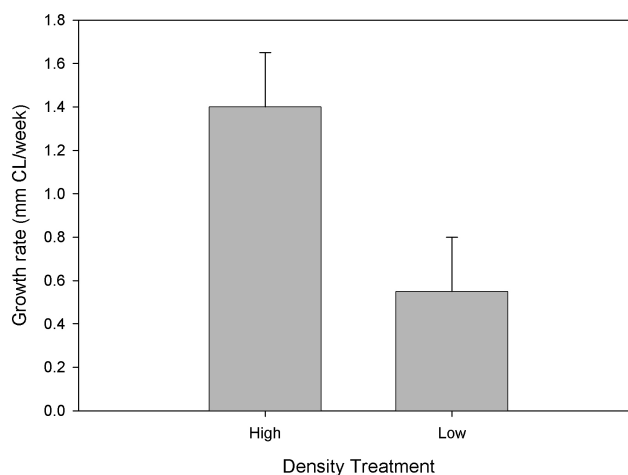


Figure 2. Growth rates of lobsters grown under high and low density conditions. Error bars represent 1 SE.

Table 1. Comparison of lobster growth with different water temperatures and diets from several published studies

Starting size (mm)	Diet	Temperature (°C)	Duration (weeks)	Mean growth rate (mm CL/Duration)	Reference
6.4	Live Artemia (to excess)	24	10	1.9/10 weeks	Lellis & Russel 1990
6.4	Live Artemia (to excess)	27	10	3.8/10 weeks	Lellis & Russel 1990
6.4	Live Artemia (to excess)	30	10	4.6/10 weeks	Lellis & Russel 1990
6.3	Live Artemia (to excess)	33	10	2.9/10 weeks	Lellis & Russel 1990
5.0	Live Artemia (to excess)	N/A	9	2.5/9 weeks	Pardee 1992
5.8	Live Artemia	28	12	3.4/12 weeks	Ryther <i>et al.</i> 1988
5.9	Frozen Artemia	28	12	1.2/12 weeks	Ryther <i>et al.</i> 1988
6.0	Kyowa-C	28	12	2.3/12 weeks	Ryther <i>et al.</i> 1988
5.9	Kyowa-C + Artemia	28	12	2.5/12 weeks	Ryther <i>et al.</i> 1988
6.1	Dupont Feed	28	12	0.8/12 weeks	Ryther <i>et al.</i> 1988
6.0	Dupont + Artemia	28	12	1.4/12 weeks	Ryther <i>et al.</i> 1988
5.9	Alma Feed + Artemia	28	12	1.3/12 weeks	Ryther <i>et al.</i> 1988
6.1	Cerithium spp.	Variable (23-32)	5	2.7-5.8/5 weeks	Current study - Bahamas
6.0	Shrimp/fish	Variable ()	10	1.6-1.7/10 weeks	Current Study - Belize

(Marx and Herrnkind 1985), and small concrete blocks for shelter. Larger blocks and natural holes and ledges in the ponds and raceways provided shelter for lobsters outside. Water temperatures were allowed to fluctuate based on ambient seawater temperature at the intake, which ranged from 23° C in the winter to 32° C in the summer.

Because PL recruitment to the area near Lee Stocking Island and Great Exuma Island was too low to test the feasibility of large-scale grow-out aquaculture (Lipcius *et al.* 1997), PLs collected in the Bahamas were used in small scale experiments to examine growth and survival in captivity. Prior to experiments, lobsters were held in captivity to determine what foods they would eat and to establish the relationship between carapace length and total weight for comparisons with other studies. Results of these experiments may be used to determine the time necessary to raise lobsters to legally harvestable sizes, which can be length or weight-based depending on the country.

After these initial pilot studies, a suite of experiments were conducted to examine growth and survival under different grow-out conditions. The first experiment examined growth rates of lobsters fed different amounts to approximate optimal feeding rates for further experiments. The foods source used in this experiment consisted of small snails (*Cerithium* spp. and *Batillaria* sp.) commonly found on the rocky and muddy shoreline of LSI's lagoon. These snails were available in abundance and were readily eaten by lobsters during pilot studies; however, lobsters less than 10 mm CL required the shells to be cracked manually to

feed on snails. This was done with a mortar and pestle immediately prior to feeding.

During experiments, lobsters were fed twice daily (morning and evening) according to one of four different feeding treatments (grams of snail, including shell) that were scaled according to the total lobster biomass for each aquarium: (1) 0.01g snail per gram of lobster biomass; (2) 0.05g snail per gram of lobster biomass; (3) 0.1g snail per gram of lobster biomass; and (4) 0.2g snail per gram of lobster biomass. Lobsters used in this experiment averaged 6.1mm CL (± 1.2 mm) at the start of the experiment, with a minimum of 5 lobsters per aquarium. Water temperature did not differ between aquaria, and ranged seasonally from 28-32° C. Size of lobsters in aquaria assigned to each treatment ($n = 3$ per treatment) were measured weekly for 6 weeks to calculate average growth rates for each aquarium. Growth rates from this experiment were also used to calculate feed conversion ratios based on snail whole weight and snail meat weight (factoring out shell weight) and lobster growth rate in grams.

The second set of experiments examined the effect of lobster density and size distribution on growth. In this experiment, lobsters were held in aquaria at two different density treatments, and three different size treatments. Density treatments were low (4 lobsters per 0.45m²) and high (8 per 0.45m²). Size treatments included large (9.8 ± 0.4 mm CL), small (6.1 ± 0.7 mm CL) and mixed, which included half of the lobsters from the large size class and

half from the small size class. Lobsters were kept under experimental conditions for four weeks and fed at identical rates (grams of snails per total grams of lobster biomass) that produced the greatest growth rates in the previous experiment.

Stage 2 – Belize:

The Belize component of this project began in August 2003. Lobster puerulus and were collected using modified witham collectors from an area around Caye Caulker, Belize during monthly collection periods. Starting in June 2004 lobsters were kept in glass aquaria (568 l) with flow through seawater drawn from 1.5 m of water approximately 20 m offshore. Water temperatures at this site ranged from 25°C to 34°C. Water flow rates to aquaria were approximately 8 liters per minute. From June 2004 to July 2005, seawater was unfiltered. In July 2005, a sand filter and ultraviolet sterilizer were installed to filter seawater before entering aquaria. In November 2005, the largest lobsters were moved from aquaria to large tanks (2.5 m x 4 m x 1 m). In all aquaria and holding tanks, lobsters were provided some shelter (e.g. bricks with small holes or larger concrete blocks) scaled to their body size.

After an initial trial period in which a variety of potential lobster feeds were used, all lobsters were fed either fish (primarily Clupeidae) or shrimp that were bycatch from shrimp trawls operated by the Northern Fishermen Cooperative Society. These feeds were used based on their low cost and availability, as well as observations that lobsters readily ate both sources of food. Other sources of lobster feed were attempted, including snails, pieces of conch discarded during the cleaning process, and farm raised shrimp, but lobsters did not eat the conch or farm raised shrimp, and snails were too scarce to use as a major food item (F.S. unpublished data). Lobster feed prepara-

tion included scaling fish and removing the head and guts before chopping the whole fish into pieces scaled to lobster size. Similarly, shrimp (stored frozen and not treated with preservatives) had their heads removed before being chopped into small pieces scaled to lobster body size. Lobsters were fed to excess each evening and the uneaten food remaining the following day was removed.

Lobsters were assigned aquaria based on size so that all lobsters kept together were of a similar size. On a periodic basis, lobsters from each aquarium were counted and measured (Carapace Length; CL) to determine average growth rates and maintain size segregation. Although attempts were made to measure lobsters weekly, limited availability of personnel frequently interrupted this schedule.

All aquaria were checked on a daily basis for dead and molted lobsters. Dead lobsters were removed and both their size and potential factors contributing to their deaths (e.g., cannibalism, obvious signs of disease, death while molting or recently molted) recorded whenever possible. All molts were removed on a daily basis and those that were intact were measured (CL). Frequently, molts were partially eaten preventing their measurement. When possible, the newly molted lobster was also captured, measured, and isolated from other lobsters in the aquarium for up to 24 hours by placing it within a basket enclosure suspended at the surface of the aquarium.

Analyses

In the Bahamas, weekly measurements and counts of lobsters in captivity were used to calculate growth and survival rates covering the period from their collection until they reached a size of 15 mm CL. Experiments comparing growth when fed different rations were analyzed using a one-factor ANOVA model to determine whether different food rations produced different growth rates, followed by a

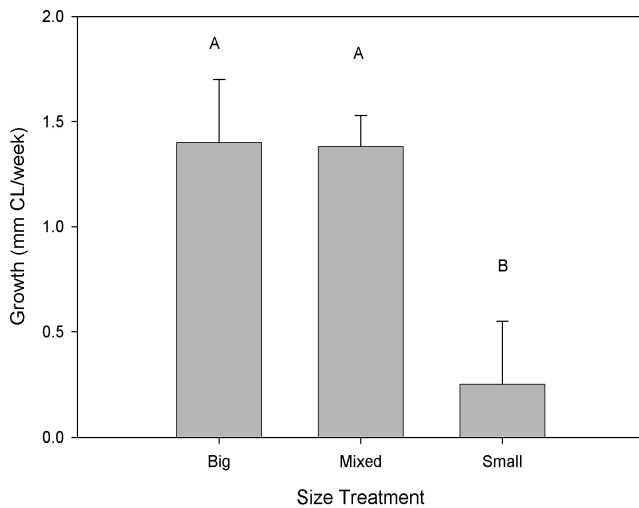


Figure 3. Growth rates of lobsters based on size distribution. Letters above bars indicate groupings of treatments that did not differ significantly. Error bars represent 1 SE.

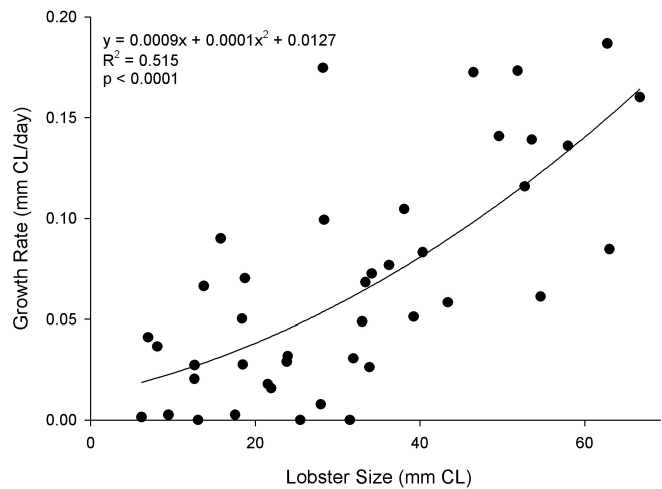


Figure 4. Size-specific Growth curve derived from lobsters grown in captivity in Belize.

Tukey's post-hoc comparison to examine differences between specific treatment effects. Based on snail total weight and wet meat weight (i.e., the total weight of the snail minus the shell weight, since lobsters ate little if any of the shell) and lobster biomass, a feed conversion ratio was calculated for this experiment for comparisons with other studies. Experiments examining the joint effects of density and size structure were analyzed using a two-factor ANOVA model, and included the interaction between size and density effects.

For lobsters raised in Belize, an average growth curve was calculated using a non-linear regression model to determine size-specific growth rates and determine the time it would take to raise lobsters from post-larvae to legally harvestable size. Because size data was not collected on a consistent schedule, data used in analyses were limited to periods during which size was measured over a minimum

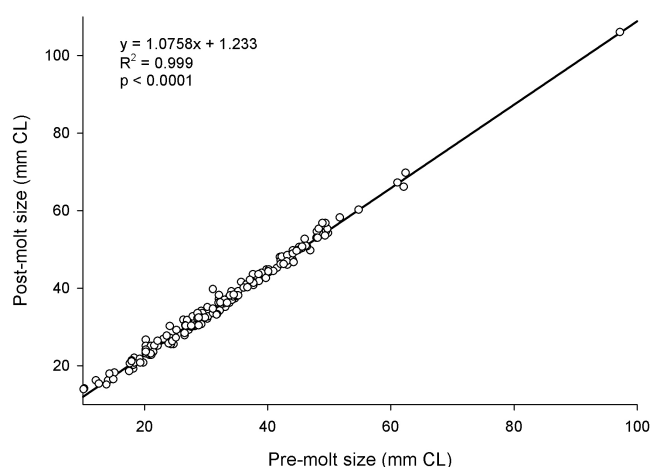


Figure 5. Size increase per molting as a function of body size from lobsters grown in captivity in Belize

period of three weeks. Because lobster grow in spurts associated with molting and the interval between molts frequently extend for more than a week, a three week period was the minimal period to ensure that growth was observed by at least a few individuals in an aquarium. Additional growth information was obtained by examining the timing of molting lobsters and growth per molting period. To determine if the timing of molting was related to lunar phase, cross-correlation analyses were performed for lobster molting and lunar phase time series. To remove the effects of autocorrelations in time series datasets, Auto Regressive Integrated Moving Average (ARIMA) models were fit to the data and residuals from these models were used in cross-correlation analyses. Lobster survival rates were calculated based on weekly count and recorded deaths and the relative frequency of various causes of death was assessed.

RESULTS

Stage 1 – Bahamas:

Between June 2003 and November 2004 (18 months), lobsters were grown in captivity from early juvenile stages (5-6 mm CL) to maximum sizes of > 60 cm CL. A length-weight conversion equation based carapace length and total weight of lobsters collected from the wild and raised in captivity was calculated to be:

$$\text{Total Weight (g)} = 0.0416\text{CL}^2 - .4711\text{CL} + 1.518,$$

where CL is the carapace length in mm. Survival of lobsters from PL stages to sizes greater than 15 mm CL was 80% and took as little as 9 weeks, with the average time taken to reach this size being 14 weeks.

Lobster growth varied significantly based on the amount of snails fed to lobsters ($F_{3,12} = 19.776$, $p < 0.001$).

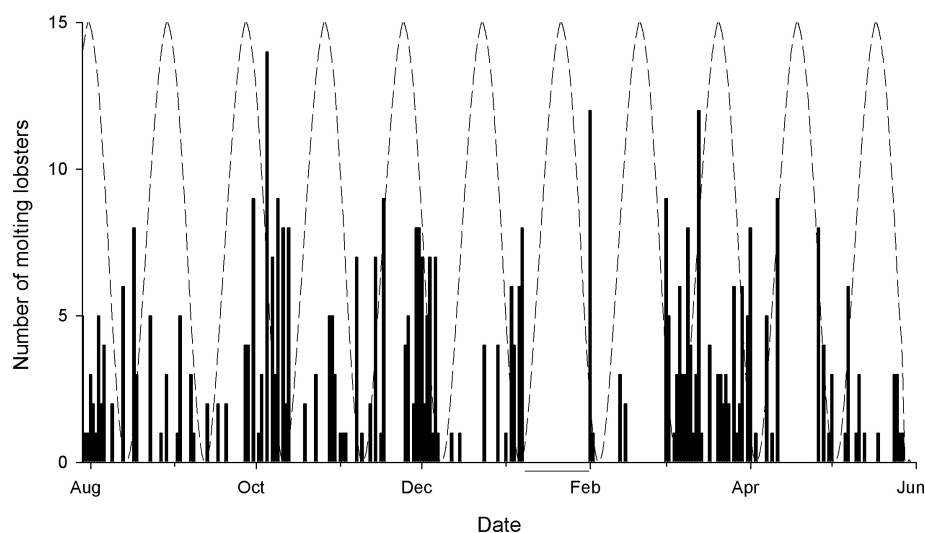


Figure 6. Frequency of molting of lobsters grown in captivity in Belize over time. Bars indicate the number of molting lobsters. The dashed line indicates lunar phase (percent illumination), with peaks corresponding to full moon periods and valleys corresponding to new moon periods. No data was available for the period underlined on the graph..

Lobsters fed 0.1 g snail per gram of lobster biomass had the highest growth rates, followed by those fed 0.2 g snail per gram of lobster biomass (Fig. 1). The feed conversion ratio for lobsters fed 0.1g snail per gram of lobster was

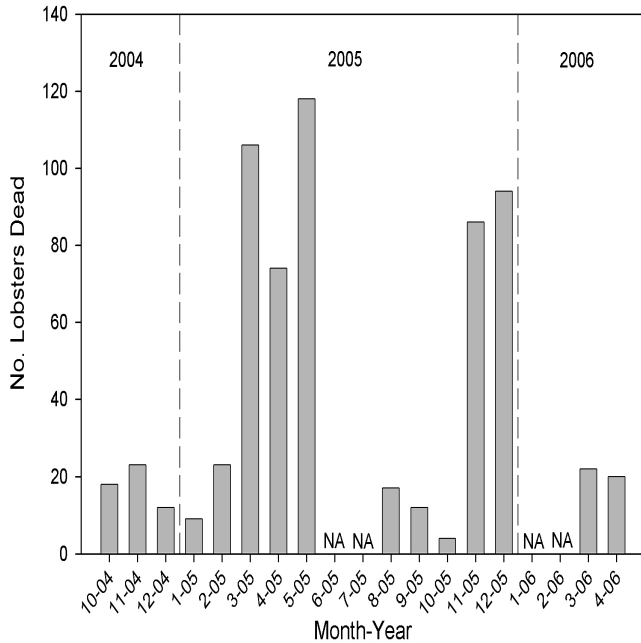


Figure 7. Monthly lobster deaths for lobsters grown in captivity in Belize. During months for which no data was available, there were interruptions in the daily accounting of dead lobsters. In June and July 2005, high death rates and a need to rapidly remove and dispose of dead lobsters interrupted accounting of dead lobsters.

calculated to be 3.39:1 based on whole snail weight. Based on measured comparisons of the ratio of snail wet meat weight to total snail biomass (snail wet meat weight averaged 42% of snail total biomass; C.D., unpublished data), the feed conversion ratio was calculated to be as low as 1.42:1 (g snail wet meat weight per g of lobster production) when lobsters were fed at the rate that produced the greatest growth rates.

Lobster growth also varied significantly due to density and size when feeding rates were held at a constant amount of food per gram of lobster biomass. In the second experiment an increase in lobster density resulted in greater measured growth rates ($F_{1,16} = 5.158, p = 0.037$; Fig. 2), and both large and mixed lobster treatments had higher growth rates than small lobsters ($F_{2,16} = 3.62, p = 0.05$, Fig. 3), but there was no significant interaction between density and size ($F_{1,16} = 2.103, p > 0.1$). When small and large lobsters were kept together, the majority of the growth observed could be attributed to growth by the larger lobsters, which molted more frequently and grew at a greater rate than the small lobsters. In the mixed treatment three small lobsters died but no large lobsters died.

Stage 2 – Belize:

By April 2006, over 20 lobsters that were collected in the summer of 2004 were greater than 75 mm CL and had a tail weight exceeding 113.4g, the legally harvestable size in Belize. Lobster growth rates were tracked regularly over a range of sizes from 6 mm CL to more than 60 mm CL (Fig. 4). Based on the length-weight relationship established with lobsters in the Bahamas, this represented whole body weight range from less than 0.2 g to greater than 118 g. The statistical model that provided the best fit to the size-

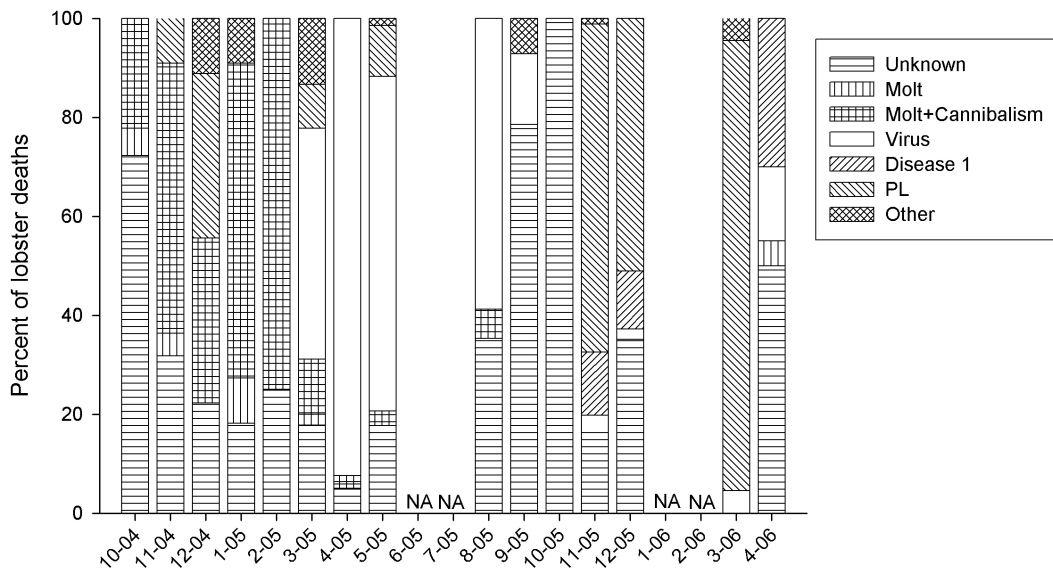


Figure 8. Cause of lobster deaths expressed as a percentage of the total monthly deaths observed for lobsters grown in captivity in Belize.

specific growth per day was a quadratic function ($p < 0.0001$, Fig. 5). Based on the growth curve, it is estimated that the time necessary to bring a lobster from the PL stage to legally harvestable size is on the order of 18 months; however, our measured data only extended to a size of 60 mm CL, so growth rates for sizes above 60 mm CL is extrapolated.

Lobsters were initially observed to molt in aquaria from 1-7 days after capture as PLs. Due to their small size and delicate nature, however, we did not measure lobster growth per molt of lobsters at this stage. The smallest lobster molts that we measured were 10 mm CL and the largest was 97.2 mm CL. Lobster growth increased linearly with body size ($p < 0.001$) and without much deviation from this relationship ($R^2 = 0.99$, Fig. 5). The frequency of molting was related to its size, with smaller lobsters molting more frequently than larger lobsters (F.S. personal observation). Although the timing of lobster molting was not significantly correlated with lunar phase, there was a trend for molting to occur less frequently during full moon periods than during quarter and new moon periods (Fig. 6).

Lobster survival varied considerably over the course of the study period from October 2004 through April 2006. From October 2004 through February 2005 the death rate of lobsters ranged from 9-23 lobsters per month or an average rate of 2.5-8% mortality per month (Fig. 7). During this time, the most common identifiable cause of death was lobsters dying during molting or being consumed by others in the tank immediately following molting (Fig. 8). In March 2005, death rates increased dramatically (Fig. 8) and remained high for several months, exceeded lobster post-larval collections at this time and killing a significant portion of lobsters in captivity, particularly those in the smaller size ranges. Most lobsters dying at this time had a pink coloration to their carapace, had milky fluid under their carapace (as opposed to clear fluid in healthy lobsters), were sluggish, and went through rapid tissue decomposition upon their death. These signs are consistent with those of a virus described by Shields and Behringer (2004). By July 2005, lobster deaths decreased following the installation of a new filtration and UV sterilizer system, which is expected to reduce the spread viral infections. While several lobsters continued showing signs of viral infection for the remainder of the study period, often dying up to 3 months after first showing signs of infection, these lobsters were only a small percentage of the total that died after July 2005. Subsequent increases in lobster deaths later in 2005 and 2006 reflected an increase in the number of post larvae dying within their first week after capture and an increase in lobsters showing signs of loss of equilibrium followed by movement of legs (usually with the lobster on their side), then the rapid onset of paralysis.

DISCUSSION

It is possible to raise *Panulirus argus* in captivity from PL to legally harvestable sizes within 18 months, using

natural sources of food and without controlling for temperature and other environmental parameters. Nevertheless, a number of factors may influence the successful grow-out of *P. argus* and the development of production scale aquaculture for this species. Experiments in the Bahamas highlighted the effect of food ration, density, and size on growth rates. In Belize, several different causes of lobster death were identified.

Lobster growth rates in this study were equal to or greater than that of the majority of published studies on the grow out of juvenile *P. argus* (Table 1). In the Bahamas, a diet of snails at a rate of 0.1 g of snail per gram of lobster biomass (2x per day) produced growth rates that more than doubled growth rates for most other studies. Even the snail diet that produced the lowest growth rate in this study produced greater growth rates that all studies using other sources of food (Table 1). The feed conversion ratio of 3.39:1 (1.42:1 for snail meat weight: lobster biomass increase) resulting from this diet is among the highest reported for lobster. A review of spiny lobster (all species) aquaculture studies by Booth and Kittaka (2000) found a range of feed conversions from 3.6:1 to 9.1:1 (wet weight, with dry weight conversion ratios reaching as low as 1.46:1), with diets of mollusks producing some of the most efficient conversion of biomass. The diet of gastropods as we used in our study is likely to be a close approximation of the natural diet of lobsters in this size range (e.g., Marx and Herrnkind 1985, Briones-Fourzán *et al.* 2003) and may explain why growth rates in this study were greater than those of other studies.

Growth rates of lobsters in Belize using fish and shrimp appeared to be comparable to those experienced in other studies. The diet of fish and shrimp from Belize was chosen primarily based on their availability. Other studies have indicated that fish and fish meal are not optimal feed items for lobsters and may result in an increase in incidence of death during molting (Lellis 1990, 1992). Although crustaceans make up a significant portion of the diet of juvenile lobsters in the wild (e.g., Marx and Herrnkind 1985, Briones-Fourzán *et al.* 2003), penaeid shrimp used in these experiments are not common prey items and may provide lobsters with less nutritional value than crustaceans naturally consumed in the wild.

A range of other physical factors can also influence growth rate. Several studies have indicated that water temperature can influence growth rates, with temperatures of 27-30°C producing the greatest growth rates (Lellis and Russel 1990). While our studies allowed water temperature to fluctuate, and we did not statistically test the affect of water temperature, growth rates did appear to be greater in the spring and summer than in the winter. Other factors that may influence growth rate include photoperiod and salinity (reviewed in Booth and Kittaka 2000).

Lobster density also affected growth rate in this study. Surprisingly, greater growth rates for the higher density treatment. This finding contradicts the hypothesis that

higher densities may lead to crowding that suppresses growth rates, as has been demonstrated in other spiny lobster species (e.g., *Jasus edwardsii*; Rayns 1991). Other studies with *P. argus*, grown out at densities approximately doubled that of our study found no affect of density on growth and survival rates (Pardee 1992), however, lobsters grown communally to have greater growth rates than those in isolation (Ryther *et al.* 1988). In the current study densities were relatively low and crowding effects may still occur at densities greater than those tested in this experiment and those of other experiments (e.g., greater than 34.8 lobsters/m², Pardee 1992).

Greater growth rates in the higher density treatment may be the result of an experimental bias whereby having more lobsters in the experimental treatment increased the frequency at which molting (i.e., growth) was observed and artificially inflating overall growth rates during our limited study period. Alternatively, higher growth rates in higher density treatments may have a biological underpinning, due to pheromones or other chemicals released by molting lobsters that induce molting in other lobsters. While chemical communication in *P. argus* is a primary means of social behavior (e.g., Ratchford and Eggleston 1998, 2000), whether such a molting pheromone is produced is unknown. In Atlantic lobster, *Homarus americanus*, for example, pheromones released by females at the time of molting trigger reproductive behaviors (Bushman and Atema 1997). Our observation of a concentration in molting around quarter moons and into new moon periods may result from an endogenous cycle exogenous environmental cues (e.g., nighttime light levels) or a combination of environmental cues and chemicals released by molting lobsters. Further investigation into lobster chemical communication during molting may be a fruitful area for ecological research.

In the current study, death rates in the Bahamas of 20% during the time it took lobsters to grow from PL (5-6 mm CL) to 15mm CL (an average of 14 weeks) translates to monthly death rates on the order of 6-7%. When size groups were manipulated, smaller individuals died more frequently than larger ones in mixed groups, and more frequently than when small lobsters were held together. This is probably the result of competition for food, in which the larger lobsters out-compete the smaller ones, suppressing their growth and possibly leading to starvation in smaller lobsters. Such competition may be reduced significantly by segregating lobsters by size, particularly during the early juvenile stages.

Death rates in Belize were similar to the Bahamas prior to March 2005. During this time, one of the greatest identifiable causes of death was complications during molting. In many instances, lobsters died during the process of molting (molt death syndrome) or immediately afterwards without a readily identifiable cause. In other cases, lobsters molted successfully, but were then cannibalized by other lobsters in their holding tank. While such cannibal-

ism was observed occasionally during molting in the Bahamas study, its occurrence was rare. This may be due to the difference in diet between the Bahamas and Belize, whereby lobsters in captivity in Belize suffered from poorer nutrition and resorted to cannibalism to compensate for a deficiency within their diet. Other studies have suggested a link between low nutrition diets of fish or fish meal can contribute to death during molting (Lellis 1990, 1992). Cannibalism of lobsters at this vulnerable time, however, may be mitigated by the addition of adequate shelters for molting lobsters, or by isolating lobsters when they are ready to molt.

Other unidentified sources of death reported in Belize may have been the result of nutritional problems, poor water quality, pathogens or a combination of these factors. Although lobsters of the genus *Panulirus* have few reported diseases (Evans and Brock 1994, Evans *et al.* 2000), two distinct diseases that each showed unique signs could be identified as a cause of death of a large number of lobsters in Belize. This first was a viral infection, first described by Shields and Behringer (2004). This virus infects the hemocytes and connective tissue of lobsters and may kill lobsters by compromising their energy stores and cause metabolic exhaustion and ischemia from anaerobic metabolism (Shields and Behringer 2004). The occurrence of lobsters showing signs consistent with this viral infection is rare and our study is the first to report this outside Florida. Although the first lobsters that we observed to die showing signs of this infection occurred in March 2005, they may have been infected for several months prior to this. We cannot identify how this virus was introduced into the lab facility; however, the rapid spread of the disease to lobsters in aquaria with no exchange of water, feed or animals suggests that the virus was introduced to multiple aquaria via a common source of water or food. Although there may be multiple routes of transmission of the virus, the most likely scenario for introduction was via the seawater system. In response to this, the inclusion of a sand filter and ultraviolet sterilizer on the previously unfiltered seawater intake line appeared to at least reduce the occurrence of the disease, further supporting the hypothesis that the virus was water-borne. Lobster deaths following the implementation of biosecurity measures may have been infected earlier, but the disease was observed to take up to three months following onset of signs of infection to kill lobsters. Regardless of its method of introduction, between March 2005 and July 2005, the majority of the lobsters in captivity that were less than 50 mm CL died. Lobsters greater than 40 mm CL rarely showed signs of infection and those above 50 mm CL were not affected by this viral outbreak.

The second observed disease was initially noticed in 2006, when lobsters were observed to have lost their equilibrium but continued to move their legs while on their side prior to partial, and eventually total, paralysis and death. The onset of this disease was rapid and lobsters frequently went from showing no outward signs to being dead in a

matter of an hour or two. While the cause of this disease remains unknown, the occasional observance of lobsters showing signs of this disease in aquaria also holding fish showing cases of exophthalmia suggests that the lobster's infection may have a common cause. While several bacterial or fungal infections can cause exophthalmia, *Vibrio* is a potential candidate.

One last major source of lobster deaths was the occasional mass die-off of PLs prior to their molting into juveniles. The cause of death in these cases remains unknown, but may be the result of holding conditions in the lab (Jeffs 1999), such as exposure to disease upon introduction into the LAB facility, a change in water quality or environmental conditions, or a combination of multiple sources of stress. Many of these instances occurred when large numbers of PLs were held together, suggesting that density may contribute to this source of mortality.

The occurrence of observed diseases and subsequent high mortality rates in Belize may have been exacerbated by poor water quality. Adjacent to the seawater intake was a fish processing station, fuel dock, municipal dock used by barges and cargo vessels, and numerous homes. Wastewater runoff around the fuel dock, domestic wastewater leached into the sea, and waste runoff from the co-op's receiving station may have all caused periods of decreased water quality. In addition to these sources, barges coming in to the shallow municipal dock stirred up sediments to noticeably reduce water clarity around the intake pipe and in aquaria in the LAB facility. Sediment resuspension by barges may have also resuspended chemicals or pathogens that then entered aquaria in the LAB via the seawater system.

While this study advanced grow-out aquaculture of *P. argus*, we have still not reached the point where production-scale grow out aquaculture is feasible. Part of the problem lies in the lack of adequate puerulus for large-scale grow out. Lobster growth and survival rates from the Bahamas, however, suggest that if an adequate supply of PLs, large scale grow-out may be possible. Our ability to rapidly grow-out juvenile stages to legally harvestable size (<18 mos.) also suggests that further research into larval culture and a shift to full life-cycle aquaculture is warranted and may provide the greatest opportunities for lobster aquaculture in the future. Our experience in Belize indicates that controlling for water quality, disease control, and nutrition are key elements in determining the success of grow-out aquaculture for *P. argus*.

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