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## Habitat Use and Population Biology of Bahamian Spiny Lobster

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### ABSTRACT

Describimos patrones anuales para distribución por tamaño, uso de habitáculo, reproducción y muda de la langosta *Panulirus argus*, en la vecindad de la isla Lee Stocking, Bahamas. Se llevaron a cabo inspecciones de reconocimientos submarinas en habitáculos oceánicos, bajos y canales que abarcaron arrecifes, afloramientos de corales, praderas de yerbas, lechos rocosos y bancos de arena, a profundidades entre uno y veinte pies. El largo promedio del carapacho de la langosta para el período de septiembre de 1979 a junio de 1980, fue de 113 a 121mm para los machos y de 98 a 106mm para las hembras. Las langostas se segregan de acuerdo al hábitat; los subadultos y adultos pequeños se encontraron en los bancos y canales, mientras que los adultos más grandes estaban en los "refugios" oceánicos. La reproducción y la muda son específicas en lo referente a tamaño, época, y habitáculo. Toda reproducción se observó en sitios hacia el océano; la muda ocurrió, predominantemente, en las áreas de bancos y canales. Los patrones temporeros en la reproducción, muda y uso de habitáculos variaron por tamaños, indicando esto un movimiento gradual de langostas pequeñas de rápido crecimiento, desde bancos en aguas llanas, a través de canales, y hacia los arrecifes en el océano, los cuales albergan agregaciones dispersas de adultos grandes en estado de reproducción.

### INTRODUCTION

The spiny lobster *Panulirus argus* is extremely important both for basic scientific research (Davis, 1980) and the seafood industry. Despite the economic significance of Bahamian lobsters, their ecology has been the subject of limited study. Investigators have recorded fishery information (Smith, 1948, 1951), mass migration (Herrnkind and Kanciruk, 1978; Kanciruk and Herrnkind, 1978; Herrnkind, 1980), autumnal reproduction (Kanciruk and Herrnkind, 1976), commercial size composition (Simpson, 1976), life history and ecology of juveniles, and experimental fishing techniques (Waugh and Waugh, 1977; Waugh, 1980).

Most of the above work was performed near Bimini and Grand Bahama Island; only Waugh's studies spanned a full year. Extensive studies of lobsters in Cuba (Buesa Mas, 1965), Florida (e.g., Dawson and Idyll, 1951; Davis, 1977; Warner *et al.*, 1977; Lyons *et al.*, 1981) and the Caribbean (e.g., Munro, 1974; Peacock, 1974; Herrnkind *et al.*, 1975; Olsen *et al.*, 1975; Aiken, 1977) demonstrate that spiny lobster population structure and dynamics differ seasonally and by ecological conditions in different regions. Therefore it is necessary to examine discrete populations for at least one year to characterize

them and to gain knowledge relevant to fishery management. We report here on a 10-month (Sept., 1979-June, 1980) study of *Panulirus argus* in the region of Lee Stocking Island, north of Great Exuma Island. Size distribution, habitat, reproduction, and molting cycles are emphasized.

#### ENVIRONMENTAL FEATURES

Lee Stocking Island lies on the southeastern edge of the Great Bank adjacent to Exuma Sound (Figure 1). We diver surveyed the area approximately 2 km around Lee Stocking Island, to a maximum depth of 20 m offshore, and along the shore and channels of the Brigantine Cays some 10 km westward on the Bank (Table 1). The seaward channels and offshore substrates show mixed open sand and hard outcroppings dominated by massive corals and alcyonarians; depths ranged from 2-10 m nearshore, dropping to 10-20 m within 1 km offshore. Toward the Bank, the channels spread into shallows of 1-3 m depth characterized variously by patches of coral heads, turtle grass beds (*Thalassia*) and calcareous sand. The Brigantine Cays nearshore comprised mainly rock ledges, turtle grass, and fine sediments. The waters were characteristically clear (underwater visibility 10-25 m), except after

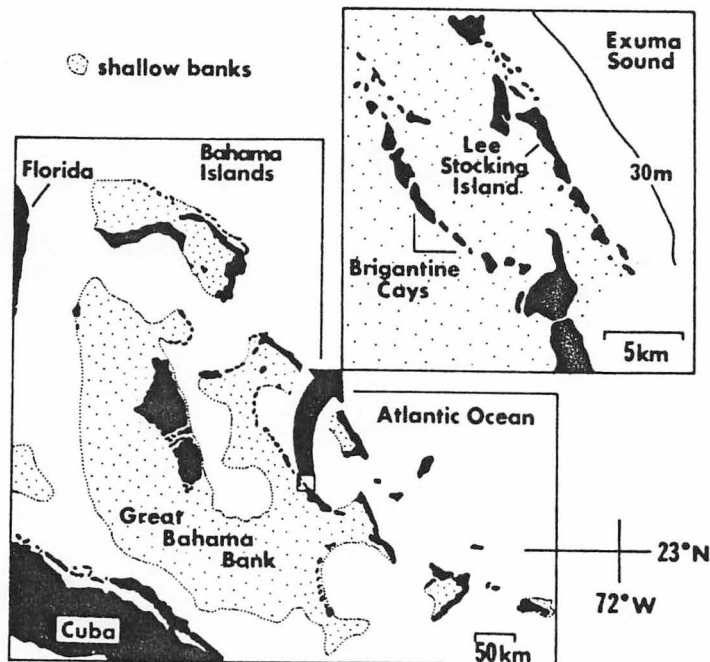


Figure 1.

**Table 1.** Habitat descriptions of sites sampled September 1979 through June 1980 in the vicinity of Lee Stocking Island and the Brigantine Cays, Bahama Islands (Figures 1 and 3).

Type	Reference	Depth Range (m)	Features
Offshore	Figure 3a	2—10	Massive and smaller coral ( <i>Acropora</i> , <i>Millepora</i> , and <i>Agaricia</i> spp.) reefs; patch coral heads, esp. <i>Montastrea</i> sp.; <i>Porites</i> outcrops; limestone undercuts and ledges; generally over sand-rock bottom on oceanside of Lee Stocking Island and in deeper channels leading to Exuma Sound.
Bank	Figure 3b	1—3	Patch coral heads; scattered crevices near <i>Thalassia</i> beds, sometimes over soft bottom; rock crevices and shoreline ledges; generally near the undercut shoreline ledges adjacent the Brigantine Cays and in shallow channels leading to the Great Bahama Bank.
Inshore	Figure 3c	1—3	Small <i>Acropora</i> coral reefs; shoreline ledges; patch coral heads; rock out-crops and limestone crevices, often adjacent <i>Thalassia</i> grass beds; generally over sandrock bottom on the inside of Lee Stocking Island near shoals and in shallow channels.

squalls, and probably have low phytoplankton productivity. Seawater temperatures were recorded irregularly, and follow the range and pattern for Nassau. Winds and tidal currents appear to dominate nearshore current flow; flumes of notably greenish bank water flush outward up to 1 km (est.) offshore on ebbing tides while clear, bluish oceanic water flushes well onto the Bank on flood tides. Based on diver observations, swift currents ( $\geq 2$  km/hr) in the tidal channels moderate over the bank shallows; currents offshore are light.

#### METHOD

Tow-boarding skin divers, pulled by a boat at approximately 5-6 km/hr, surveyed sites. SCUBA was used to search in typical lobster habitats and to collect all detected lobsters. Certain lobstering sites favored by local fishermen were also searched. We re-sampled sites at approximately bimonthly intervals. Offshore searches were limited to the 20 m depth contour, beyond which depth no lobsters were found at the limit of towboard range. We attempted to capture all lobsters by non-injurious tail snare (Kanciruk and Herrnkind, 1976). Carapace length (CL measured from between the rostral horns to the posterior carapacial margin), molt state (premolt or postmolt), sex, and female reproductive state (bearing eggs and/or spermatophore) were recorded, and the lobsters were released in the area of capture.

RESULTS AND DISCUSSION

Distribution

Seven collections yielded 479 *P. argus* (256 males; 223 females); size-frequency distributions for each collection appear in Figures 2 and 3 and Tables 2 and 3. Offshore collections were made during all sampling periods in areas located along inter-island channels and offshore reefs or rock ledges (Figure 3a), while June collections were made there, along the Brigantine Cays (Figure 3b), and just inshore of Lee Stocking Island (Figure 3c). Lobsters in all habitats were found only in crevices in hard substrate (Table 1); they occurred both singly and communally up to 20 + per den. While dens in inshore habitats contained approximately equal numbers of males and females, those in oceanic habitats were sometimes unequally distributed, with single, large males

Table 2. Analysis of variance results for spiny lobster size (untransformed carapace length) with sex and time (seven samples) as factors. Sampling times are given in Figure 2.<sup>a</sup>

Source of Variation	SS	df	MS	F
Sex	22229.1	1	22229.1	73.9****
Time	1595.8	6	266.0	0.9 ns
Sex by Time	1108.7	6	184.8	0.6 ns
Error	115180.8	383	300.7	

\*\*\*\*P<0.001; ns P>0.05

<sup>a</sup>All samples collected from offshore habitats.

Table 3. Spiny lobster size (untransformed carapace length) as a function of sampling time and habitat.

Date	Habitat	Carapace Length (mm)					
		Males			Females		
		N	Mean	SD	N	Mean	SD
1-9	Offshore	27	116.9	20.8	28	103.9	15.0
3-1	Offshore	36	114.4	19.6	31	102.7	16.5
3-25	Offshore	31	120.3	18.6	17	106.2	11.7
6-8	Offshore	27	120.1	21.9	26	98.8	13.0
	Inshore	26	80.8	12.7	21	78.3	11.1
	Bank	15	75.7	24.6	20	72.0	12.6
9-5	Offshore	24	112.1	18.5	27	101.3	15.0
10-22	Offshore	23	119.3	17.0	22	102.3	17.2
11-28	Offshore	47	115.2	19.6	31	98.5	10.2

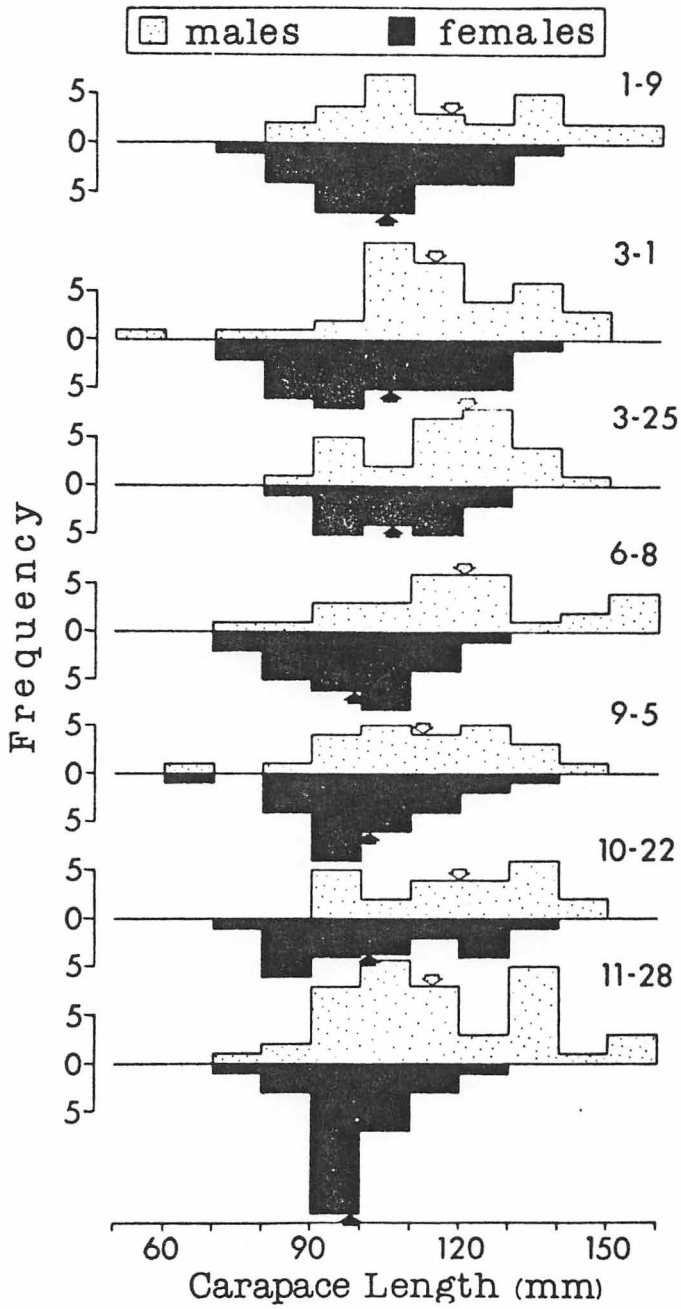


Figure 2.

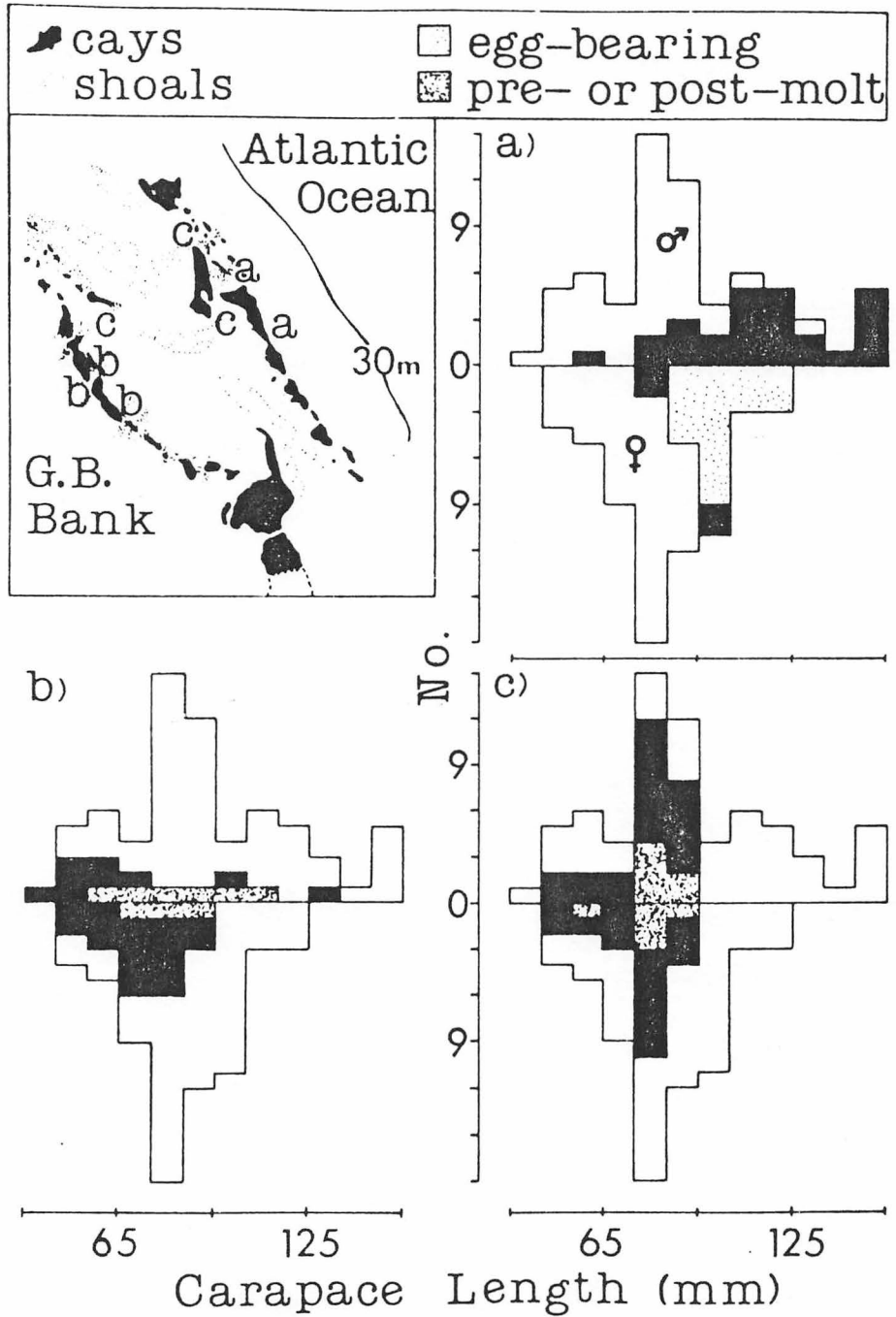


Figure 3.



found in residence with numerous egg-bearing females (Figure 4). These observations suggest that some large males may protect harems of reproductively-active females, in concordance with laboratory (Lipcius and Herrnkind, 1985) and field (Lipcius *et al.*, 1983) observations. The offshore habitats contained significantly more large lobsters than the inshore areas and Brigantine Cays (Table 4), while the Brigantine Cay lobsters were significantly smaller than lobsters taken immediately inshore of the seaward island chain. The Brigantine Cay lobsters (mean CL = 75.7 mm) were largely juveniles, based on the minimum size of female reproduction in our collections and those elsewhere (approximately 75–85 mm CL: Davis, 1975; Kanciruk and Herrnkind, 1976; Gregory and Labisky, 1981; Lyons *et al.*, 1981). The few female lobsters over 80 mm CL from the Brigantine Cays showed no signs of reproductive activity, while both sexes displayed incipient molting. The inshore collection, comprising lobsters mainly 70 to 95 mm CL (mean CL = 80.8 mm), similarly showed molting but no reproductive activity, although reproduction was evident among similarly sized females collected offshore at that time

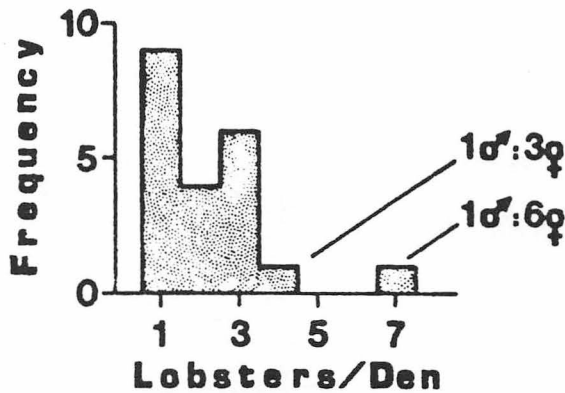


Figure 4.

Table 4. Analysis of variance results for spiny lobster size (log-transformed carapace length) with sex and habitat (three areas: Figure 3: offshore, inshore, shallow Bank) as factors.

Source of Variation	SS	df	MS	F
Sex	0.031	1	0.0310	3.92*
Habitat	0.689	2	0.3445	43.61****
Sex by Habitat	0.012	2	0.0060	0.76 ns
Error	0.994	126	0.0079	

\*\*\*\*P<0.001; \*P<0.05; ns P>0.05

(compare Figures 3a and 3c). Offshore collections throughout the year were characterized by relatively large animals (mean males, 114.4—120.3 mm CL; mean females, 98.5—106.2 mm CL) with few below 90 mm CL; reproductively active females (egg-bearing) were found only in such habitats.

We interpret these data as indicating differentiation of the local lobster population by habitat and location according to age, molt state, and reproductive condition. The pattern at Lee Stocking Island resembles superficially that of areas at Bimini and Florida with similar habitat distribution, where juveniles occupy shallow bank areas dominated by seagrass and algal patches (Kanciruk and Herrnkind, 1976). Subadults and transient, or molting, adults seasonally occupy the fringe of offshore islands, while large adults, and those in reproductive condition, occur throughout offshore reef habitats (Kanciruk and Herrnkind, 1976; Davis, 1977; Warner *et al.*, 1977; Lyons *et al.*, 1981).

The size-frequency pattern of the offshore population (and combined) closely resembles that of a commercially taken sample in the same general region in 1966 (Simpson, 1976). The Lee Stocking Island pattern also resembles that of the U.S. Virgin Islands (Olsen, 1981), and Bimini (Kanciruk and Herrnkind, 1976, 1978). Populations in the latter areas show modes in the 75-90 mm CL range compared to modes in the range of 90-110 mm CL at Lee Stocking Island. Variability in size structure may result from differences in either juvenile recruitment and mortality rates or fishing pressure, or both. We believe the former to be consequential because the Bank region appeared to have a relatively low density of juvenile lobsters, compared to Bimini and the Florida Keys (where we have collected extensively), suggesting a low rate of juvenile recruitment. Fishing pressure seemed generally moderate (by free diving and trapping) and especially low in Bank areas. Davis (1977) documented significant fishery impact upon a previously unfished spiny lobster population (Dry Tortugas). Heavy fishing in our offshore areas would likely reduce density and possibly modify the existing size frequency pattern.

### Sex-Specific Patterns

Offshore, males were characteristically and significantly larger than females at all seasons (Figure 2; Tables 2 and 3), matching the conditions described for Exuma area lobsters in 1966 (Simpson, 1976) and typical of other spiny lobster populations in reproductive habitats (Kanciruk, 1980). In addition, the offshore sex ratio pattern (by size class; Figure 5; 5 mm CL intervals) shows a trend typical of many long-lived decapods in which, after sexual maturity, males grow faster than females (Wenner, 1972). Immature males and females show similar growth rates and typically constitute a 1:1 sex ratio. Thereafter, females theoretically invest metabolic input in egg production while males invest relatively little in sperm production, the rest going to somatic growth (Lipcius, 1985). Males theoretically also reach larger maximum size than females. Figure 5b matches the trend, predicted by theory, that in size classes just after sexual maturity, females dominate, *i.e.*, slower growth maintains females in those size classes and thus, the proportion of males declines. This effect is offset with age as males grow into size ranges obtained only by very old females or those beyond female growth potential. Therefore, males become proportionately dominant and, at the extreme, make up to 100% of the size class complement.

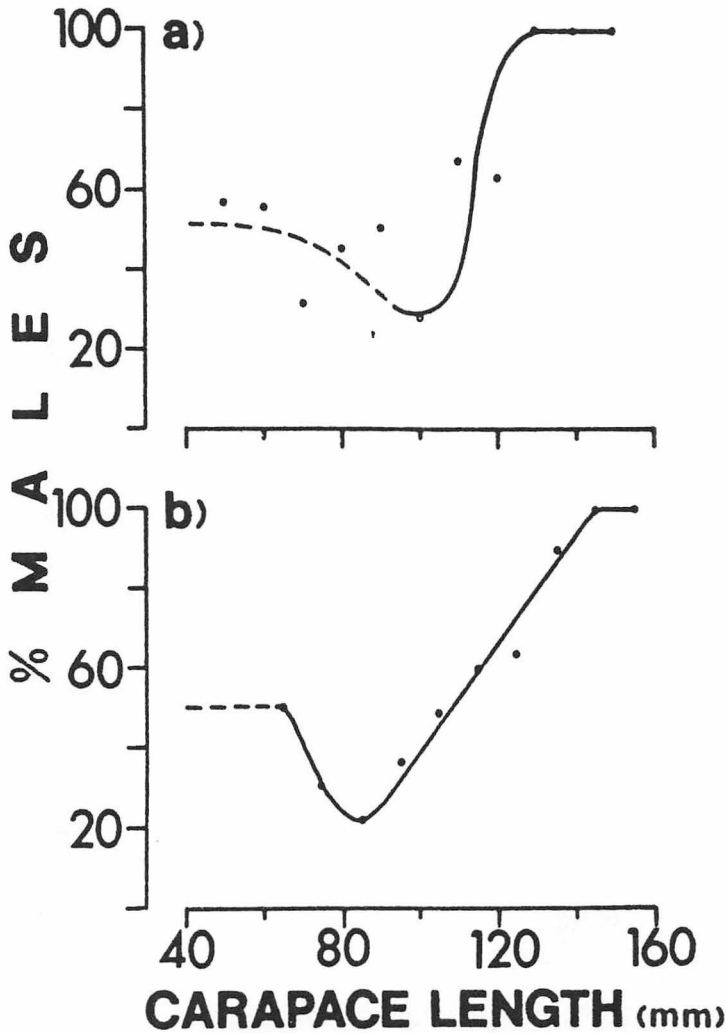


Figure 5.

The size-related effect of sexual maturity upon sex ratio is unclear in the June sample, which included collections from offshore, inshore, and bank areas. The sex ratios of size classes near maturity (70—100 mm CL) approximates 1:1 (Figure 5a), whereas for offshore areas it is 30 males: 7 females (Figure 5b). We conclude that collections from non-reproductive habitats will bring an overall sex ratio closer to unity because sex differences in growth rate become minimal. Thus, size-related sex ratio is a function of habitat differences in sex-dependent growth rates as a consequence of female reproductive and molting patterns. The overall offshore sex ratio was 54% males : 46%

females compared with 58% males for the Exumas in 1966(Simpson, 1976) and 60% males for the U.S. Virgin Islands offshore (Olsen *et al.*, 1975). Because the data collection methods differed among these reports, statistical comparisons are inappropriate. However, the present Lee Stocking population sex ratio falls within the range of variation of other populations in similar habitats.

**Reproduction**

Offshore females carried external, fertilized eggs primarily during spring with the incidence declining through mid-autumn (Figure 6). Egg-bearing females comprised nearly 80% of offshore females in June, matching peak levels in the Dry Tortugas (80%; Davis, 1977), Bermuda (70%; Sutcliffe, 1953) and U.S. Virgin Islands (80%; Olsen *et al.*, 1975). Those females carrying eroded spermatophores during winter had not necessarily spawned recently but

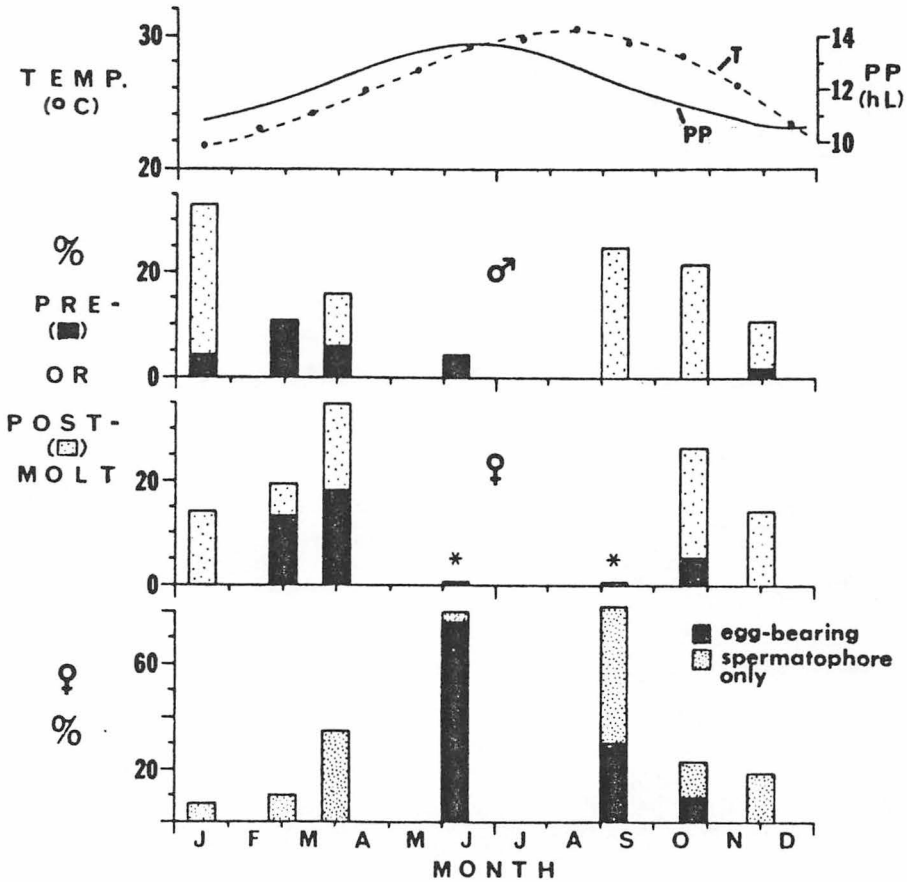


Figure 6.

rather, might not molt until the next spring (Figure 6). Peak reproduction in spring is typical of other northern subtropical spiny lobster population (Kanciruk, 1980). The continued incidence of spawning into autumn resembles the situation in the offshore areas of Bimini (Kanciruk and Herrnkind, 1976), U.S. Virgin Islands (Olsen *et al.*, 1975) and Florida Keys (Lyons *et al.*, 1981).

### Molting

Offshore males and females molted primarily between September and March, *i.e.*, the non-reproductive period (Figure 6, Table 5). Males appeared to begin molting earlier in autumn and finish earlier in spring than females. We found no females molting offshore between April and October. However, females and males in the reproductive size range molted during summer in the inshore and Brigantine Cay habitats (where no reproductive activity occurred). These differences in molting and reproduction concur with observed population size variation in the various habitats.

Table 5. Chi-square analysis of molting and reproductive condition over time. Lobsters were classified as pre- and postmolt or intermolt for molting, and as egg- and spermatophore-bearing or clean for female reproduction.

Process	Sex	N	df	X <sup>2</sup>
Molting	Males	215	5	12.45*
	Females	182	2	12.34***
Reproduction	Females	182	2	90.66****

\*P<0.05; \*\*\*P<0.005; \*\*\*\*P<0.001

### Movement Patterns

Lack of tagging data limits our interpretations to those based on indirect signs of migration. Clearly, young lobsters must move to the offshore areas during the season of their pubertal molt; it is uncertain whether this occurs just before or after that point. Once offshore, adult lobsters may remain there more or less permanently with some occasionally moving back inshore, perhaps to molt. This would explain the presence of large individuals (well past the normal reproductive minimum size) in incipient molt state inshore during June when all offshore adults were in intermolt and 80% of females bore eggs. We propose that inshore-offshore transit by individuals is phased with:

1. Initial onset of reproduction.
2. Linked to onset of summer molting, although large inshore lobsters may simply represent the extremes in size distribution of a subadult age class.

Movements by inshore juveniles can only be speculated to resemble the progressive ontogenetic habitat shift from post-settlement nursery areas, in shallow algal habitat, to slightly deeper seagrass/patch reef habitat and, eventually, to the fringes of the shallow bank bounding the deeper reefs (Herrnkind, 1980). Seasonal climatic patterns including sharp onset of autumnal cold periods or hurricanes probably induce major movements in locally affected areas (Kanciruk and Herrnkind, 1978). Within offshore areas of several square kilometers, we noted apparent nomadism wherein isolated

reefs, unpopulated at one time, were repopulated several weeks later. The local area is not apparently one of extensive population turnover, nor recruitment, such as the Florida Keys where the offshore (adult) habitat borders an extensive nursery.

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