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FURTHER OBSERVATIONS ON THE BREEDING AND MIGRATION OF THE BERMUDA SPINY LOBSTER, *PANULIRUS ARGUS*¹

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ABSTRACT

Some results of investigations of breeding, distribution, and migration of *Panulirus argus* in Bermuda during 1951 and 1952 are given. A graphic schedule of breeding events for females includes the times of appearance of the first and second spermatophores and the first and second eggs. Certain aspects of mating and the shedding of pleopodal setae by females are discussed. Lobsters larger than 145 mm carapace length are found most frequently in the lagoon and are in notably small proportions outside the reefs. This distribution is particularly noticeable during the breeding season when most of the smaller mature lobsters migrate to the periphery of the reefs. Data indicate a correlation of color of lobster and environment.

INTRODUCTION

While the observations presented here are based in part upon investigations begun in 1949 by E. P. Creaser, they are mainly a continuation of work published in a previous paper dealing with breeding and migration of the Bermuda spiny lobster (Sutcliffe, 1952). The work was supported throughout by a grant from the Bermuda Government and has constituted a staff project of the Bermuda Biological Station.

The author gratefully acknowledges the assistance of Mr. Jack O'Connor, Mr. Michael Scott, and the rest of the staff of the Bermuda Biological Station. Thanks are also due Mr. Edric Spurling, who furnished much valuable information.

METHODS

The lobsters for this investigation were obtained from traps confined mostly to a two-mile wide section across the Bermuda plateau, including North Rock to the north, Ferry Reach, Castle Harbor, and Nonsuch Island on the south shore (Fig. 1). During the summer of 1952 correlative material was obtained from traps located at various other places (see Fig. 1). All measurements are in terms of carapace length in millimeters.

¹ Contribution No. 196 from the Bermuda Biological Station.

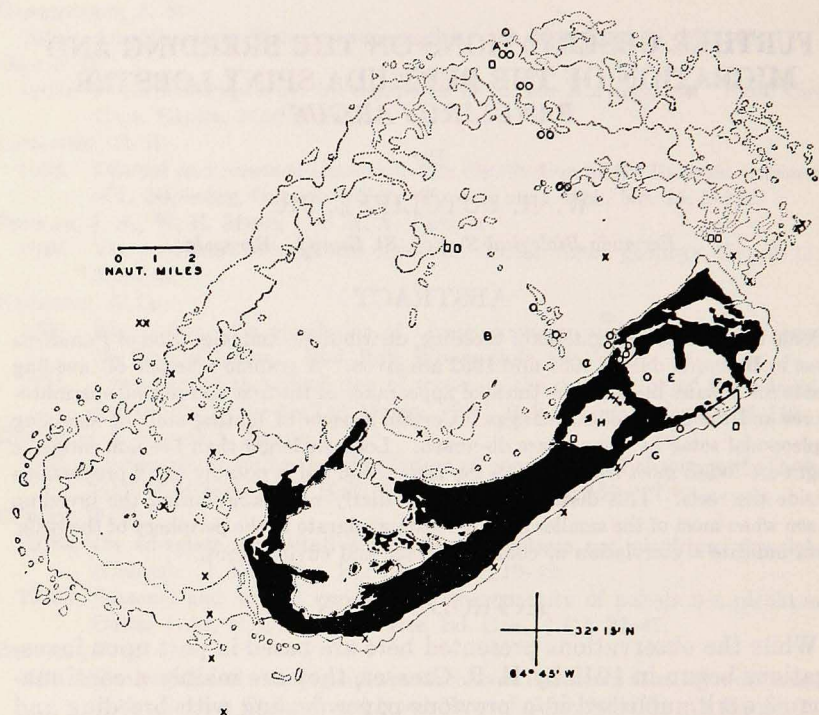


Figure 1. Bermuda and reefs showing locations of traps: enclosed area near Nonsuch Island represents seven or more traps maintained the year round; O, isolated year-round traps; X, maintained summer 1952; □, maintained intermittently; A, North Rock; B, lagoon; C, North Shore; D, Ferry Reach; E, Castle Harbor; F, Nonsuch Island; G, South Shore; H, Harrington Sound. The dotted lines represent the three-fathom contour.

RESULTS AND DISCUSSION

Breeding. Females are seldom found in breeding condition at carapace lengths of less than 90 mm; sexual maturity is attained at 90 to 95 mm (Sutcliffe, 1952). Percentages of females 95 mm or larger in the various phases of breeding are shown in Fig. 2. It may be seen that although all of the females laid their first brood, they were not all carrying their first eggs at any one time. The mode of the second laying is of lesser magnitude, possibly because all of the females did not lay eggs a second time. Also, it is possible that females carried the second set of eggs for a shorter length of time because of rising temperatures (maximum in August), thus making the percentage of females carrying the second eggs smaller at any one date. The percentage of females showing signs (see Sutcliffe, 1952) of having carried

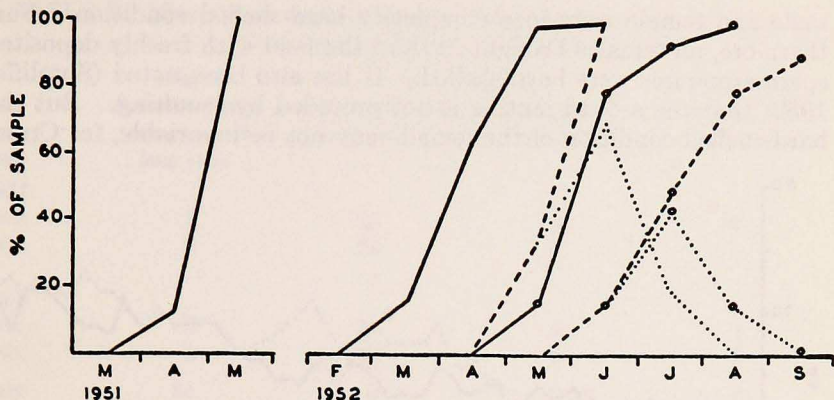


Figure 2. Percentages of females 95 mm and larger (539 specimens) in various phases of breeding: — with first spermatophore; —○— with second spermatophore; actually carrying first eggs; ..o.. actually carrying second eggs; — — — showing signs of having carried first eggs; —○— showing signs of having carried second eggs.

eggs in September may not be indicative of a true percentage value of the total fecund population, for by this time some of the females had undergone ecdysis following the breeding season and thereby obliterated the criteria for determining the previous breeding history.

Repetitive egg laying has been noted for *P. argus* by Creaser (1950) and Sutcliffe (1952) and for *P. japonicus* by Ino (1950). In the last case only four of the 61 lobsters retained in the laboratory laid eggs for the second time. However, the attenuation and shape of the curve given by Ino, expressing percentages of egg-bearing females during the breeding season, suggest that a considerable number of Japanese lobsters may lay a second time. Smith (1951) has given a graph of percentages of egg-bearing females for *P. argus* in the Bahamas, as has Bradstock (1950) for *Jasus lalandii* in New Zealand. In Smith's and Bradstock's material the curves are essentially bimodal, thus indicating a second laying. In both cases the second peaks are smaller than the first, hence these observations tend to agree with those in Bermuda.

If the appearance of the first spermatophore in 1951 is compared with the first in 1952 (Fig. 2), it may be seen that active mating for the majority of lobsters took place about a month earlier in 1952. A possible explanation for this may be seen in Fig. 3, which shows that surface temperatures as recorded in Ferry Reach during March and April were higher earlier in 1952 than in 1951.

Ten matings involving the deposition of the first spermatophore were obtained in the laboratory, although the matings were not actually observed. All laboratory matings took place when both

male and female were in a completely hard-shelled condition. Furthermore, all females brought in from the field with freshly deposited spermatophores were hard-shelled. It has also been noted (Sutcliffe, 1952) that the second mating is not preceded by moulting. But the hard-shelled condition of the female may not be invariable, for Craw-

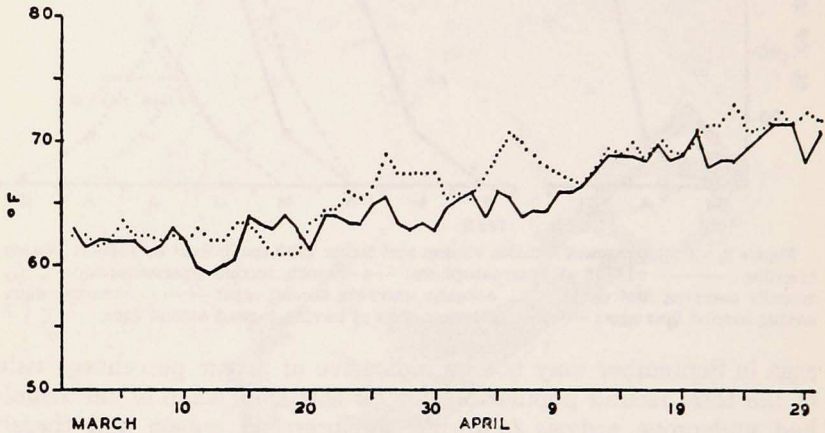


Figure 3. Daily surface water temperatures in Ferry Reach in March and April: —, 1951; ·····, 1952.

ford and De Smidt (1922) reported the case of a female carrying a spermatophore while the shell was "quite soft," which indicates that mating took place soon after moulting. Sheard (1949) says of *P. longipes*, "To be successful mating must occur immediately after the moult of the female while the shell is still soft." The mating of *Jasus lalandii* takes place when the female is in a soft-shelled condition (von Bonde, 1936). Thus, although the soft-shelled condition of the female during mating is known for two related species, the hard-shelled condition of females during mating seems to prevail with *P. argus*.

It is possible that the stimulus for the extrusion of the eggs is not a function of mating with *P. argus*, for laying occurred from a few days to a month after mating in the laboratory. Two unmated females retained in the laboratory laid unfertilized eggs. These remained attached only a few days. Unmated females of *Palaemonetes* are known to lay eggs as well (Burkenroad, 1947). Field results indicate that egg-laying by lobsters occurred a little over a month following mating (Fig. 2).

Starting in November 1951, females were examined as to the condition of the endopodal setae of the pleopods which carry the eggs. The hatching of the second eggs in August was followed by an ecdysis

TABLE I. MONTHLY CATCHES OF FEMALE LOBSTERS (95 mm or more) AND CONDITION OF PLEOPODAL SETAE

Date	Premoult	Postmoult		Percentage of postmoult with short setae
	Spermatophore remnants and long setae	No spermatophore remnants Long setae	Short setae	
<i>1951</i>				
Nov.	5	12	6	33
Dec.	0	21	1	5
<i>1952</i>				
Jan.	0	51	4	7
Feb.	0	76	0	0
July	84	0	0	0
Aug.	39	1	0	0
Sept.	36	2	2	50
Oct.	9	7	1	13
Nov.	5	10	3	23
Dec.	0	37	4	10
<i>1953</i>				
Jan.	0	50	0	0

starting in September, as indicated by the disappearance of the remnants of the used spermatophores (see Table I). In decided contrast to the long setae of breeding females, a number of adult females subsequently appeared with the pleopodal setae reduced to short bristles, a reduction on the average from 13 to 1 mm in length. This condition is not found to be restricted to any particular size of adult animal. The shedding of the female abdominal breeding plumage, not unusual in decapods, has been reported for *Panulirus japonicus* by Nakamura (1940); but apparently this is not the case with *Jasus lalandii*, for Bradstock (1950) has pointed out that reduced setae are found only in the immature of this species. Of five females of *P. argus* which were kept in the laboratory and which underwent the first ecdysis after hatching of eggs, one retained the long setae essentially unchanged except for somewhat lighter color. The other four moulted to the short-seta condition. The three females which had long setae in August and September 1952 (Table I) could have undergone only one moult after egg hatching because of the short lapse of time involved; therefore they must have retained the setae. Thus, there would seem to be some variation with respect to the shedding of pleopodal setae among the females of *P. argus*. It is not known whether the cause is genetic or environmental.

Note also in Table I the progressive decline in the relative numbers of females with short setae in both 1951 and 1952. No females 95 mm or longer with short setae were observed from January 1952 until September 1952, which indicates that the females with reduced pleopodal setae (if not the entire adult female population) undergo a subsequent moult, evidently in the late fall or winter, which restores the long setae.

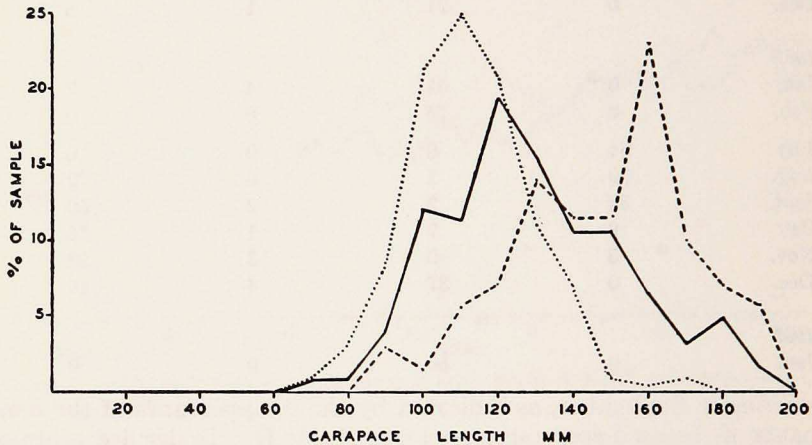


Figure 4. Comparison of length-frequencies: — lagoon population, September through April, 1951, 1952 (124 specimens); - - - lagoon population, May through August 15, 1951, 1952 (70 specimens); south shore population, November through February, 1951, 1952 (259 specimens).

Distribution and Migration. Sutcliffe (1952) has shown that certain sizes of the Bermuda spiny lobster become assorted at different depths or localities. The smallest immature lobsters are found in the shallowest protected inshore waters while the mature populations are more widely scattered. It is evident that there is further sorting with respect to lobsters of the largest sizes. Fig. 4 represents length-frequencies of animals sampled in two localities, the south shore and the lagoon. The dotted line shows the size composition of a representative sample of the population taken on the south shore in the Non-such area from November through February 1951. This is a fairly typical picture of the lobsters in waters less than 20 fathoms deep at the edges of the reefs, for samples taken at various times from the edges of the reefs of the east, northeast, northwest, and southwest were essentially similar. The south shore population varies slightly throughout the year with respect to the groups of greatest frequency,

and if the mode shifts at all, it is only between 115 and 120 mm in carapace length.²

The lagoon population contains considerably more lobsters of a larger size than does the population of the south shore (Fig. 4). Lobsters larger than 145 mm constituted about 26% of the fall-winter lagoon sample but only 3% of the south shore population; this discrepancy was even greater in summer. Although the south shore is moderately fished, this difference is not necessarily the result of fishing pressure, for a sample of 136 lobsters taken commercially from the reef edge to the northeast where there is relatively little lobster fishing showed that only 8% was 145 mm or larger. Furthermore, while the more central portions of the lagoon have long been known as a source of very large lobsters, none of the fishermen interviewed can remember having caught high percentages of large specimens on the outer reefs or beyond. Identical trapping methods are used in both places. Whether this concentration of large lobsters in the lagoon is a result of selective action on the part of the lobsters or is a matter of differential survival is not known. It is possible that the frequently heavy wave action at the reef edges could have deleterious effects on large individuals.

Further evidence of the peripheral breeding migration already discussed (Sutcliffe, 1952) may be seen in Fig. 4. If the sample taken in the lagoon from May to mid-August is compared with that taken there from September through April, a decided population shift is noted. Many of the lobsters smaller than 130 mm are lacking in the lagoon in summer; presumably they migrated to the reef edges. The remaining ones in the lagoon are mostly large males which do not migrate (82% in summer, 53% in fall-winter). Only an occasional female with eggs was encountered in the lagoon in summer, most of them having migrated to the reef edges and beyond. Correlative information from lobster collections obtained from a series of traps across the western end of the plateau (see Fig. 1) in the summer of 1952 confirmed this distribution. Egg-bearing females and males of a similar size were taken at the reef edges and down to 20 fathoms, while the lagoon was occupied mostly by large males and a thin scattering of immature specimens of both sexes. Very large males (190–200 mm) may be seen also in inshore situations such as Harrington Sound, Castle Harbor, and Ferry Reach.

The size composition of populations inhabiting water much deeper than 20 fathoms on the shelf of the Bermuda plateau is as yet unknown because of the practical difficulties of maintaining traps at such depths.

² This point will be discussed in a forthcoming paper entitled "Observation on the growth rate of the immature Spiny Lobster, *Panulirus argus*."

A few catches have been made at 50 fathoms, but the records are too scanty to warrant presentation at this time. From information given by Creaser and Travis (1950), it is apparent that lobsters can survive depths of at least 250 fathoms. According to Bradstock (personal communication), fishermen report large males and no females of *Jasus lalandii* in depths of 10–60 fathoms off New Zealand.

TABLE II. PERCENTAGES OF LIGHT AND DARK LOBSTERS FROM FIVE LOCALITIES IN BERMUDA (see Fig. 1)

Locality	% Dark	% Light	No. Specimens
South Shore	53	7	327
Ferry Reach and Castle Harbor	1	80	94
North Shore	5	42	77
Lagoon	11	25	168
North Rock	53	10	59

Certain practical aspects of this distribution of large and small lobsters come to mind. Inasmuch as there are indications that lobsters mate with others of a similar size, it would seem that the large males found in the lagoon contribute little with respect to breeding (females much larger than 140 mm are uncommon). The closed season on Bermuda lobsters (April 15–September 1) might be modified to trapping such males in the lagoon. Populations cannot be described as “overfished” purely on the basis of size composition without a careful search for possible distribution patterns such as those found in Bermuda, since the selection of certain areas at given seasons may furnish samples composed of lobsters of almost any size.

Both color and size seem to follow a marked distribution. Lobsters were divided into three arbitrary categories with respect to color—light, intermediate, and dark. The percentages of the extremes of variation are given in Table II for representative samples from five localities.

In general the coloration varies from very light (almost yellow) to nearly black and is characteristic of a given type of locality. This agrees with the findings of Crawford and De Smidt (1922) and Smith (1948) for *P. argus* and with those of von Bonde and Marchand (1935) for *Jasus lalandii*. Lobsters from the outside edges of the reef are characterized most frequently by an extremely dark hue while lobsters from inshore areas or inside the reefs assume lighter shades. As has been noted by Crawford and De Smidt (1922), it is definite that this is not a function of sex or size with *P. argus*, for the range of color variation has been observed in appropriate localities for all sizes of

both sexes. A similar conclusion was drawn for *P. interruptus* by Allen (1916). Sheard (1949) considers the extremely light-colored individuals of *P. longipes*, occurring most frequently in sandy areas adjacent to the reefs, to be "recently moulted virgin adults."

One might expect a seasonal change in percentages of dark and light animals in the south shore catches which would correspond to the migratory pattern. That is, during summer one would expect to find a greater number of light-colored lobsters in this area, but this does not seem to be the case. Although the total number of lobsters

TABLE III. NUMBERS OF LOBSTERS MOULTING IN THE LABORATORY, SHOWING FIELD COLORATION OR COLOR ASSUMED UNDER LABORATORY CONDITIONS (D. TRAVIS, PERSONAL COMMUNICATION)

<i>Number of moults in laboratory</i>	<i>Field coloration retained</i>	<i>Laboratory coloration attained</i>
0	15	1
1	3	5
2	5	14
3	1	26
4	0	5

rises considerably as shown by increased catch per unit-of-effort, the percentage of light-colored individuals remains much the same. As has been suggested (Sutcliffe, 1952), it is possible that the outward summer migration from the lagoon may be opposed by an inward migration from the deep water of the shelf, thus canceling out changes in color percentages.

When a lobster is kept in the laboratory there is no readily apparent change of color until after the first moult. Even though lobsters of contrasting color are used, the original hue is invariably retained until after one or more laboratory moults. The coloration of lobsters after ecdysis in the laboratory tended to a light bluish-gray or lavender with considerable individual variation. Table III shows noticeable color changes in animals maintained in indoor tanks. It may be seen that with an increasing number of laboratory moults there is an increasing tendency toward the bluish or lavender cast. This suggests that the previously mentioned variations in field color would be a result of the animals' existence for a certain length of time under different conditions. Of lobsters taken in the field, the nearest approach to the laboratory type of coloration was found on those that inhabit caves.

SUMMARY

1. A graphic schedule of breeding events for females of *Panulirus argus* in Bermuda for the summer of 1952 includes the times of appearance of the first and second spermatophores and of the first and second eggs as well as the approximate lengths of time that the two sets of eggs are carried. Repetitive egg laying is discussed with respect to this and some other species.

2. Active mating, as indicated by the appearance of the first spermatophores, began earlier in 1952 (March) than in 1951 (April). It is suggested that an earlier rise in temperature in 1952 may have been a contributing factor.

3. Available evidence indicates that *P. argus* mates while both sexes are in a hard-shelled condition. In two related species the female is soft-shelled during mating.

4. It is possible that mating is not a stimulus for the laying of the first set of eggs, since females in the laboratory laid eggs from a few days to a month after mating; two unmated females laid eggs.

5. Part of the adult female population sheds the pleopodal setae with the first moult following breeding. These setae are restored on a subsequent moult. The percentage of females that shed the setae is not known with certainty.

6. In addition to the localization of immature lobsters there is a sorting of large lobsters, particularly males. Thus far the latter individuals have been found most frequently in the lagoon. Adequate information is lacking for waters deeper than 20 fathoms outside the reefs.

7. The size distribution of large lobsters is most noticeable in the breeding season when the great majority of mature females and smaller mature males migrate to the periphery of the reefs. Certain practical aspects of this distribution are discussed.

8. Data show that the majority of lobsters in a given area tend to assume a characteristic color which may vary from nearly black to almost yellow. Darkest lobsters are found at the reef edges; lightest individuals are found inshore and in the lagoon. These color variations are not a function of size or sex and are probably a result of their existence for a certain length of time in a given type of locality.

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