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C.R. Evans
University of Southampton

A.P.M. Lockwood
University of Southampton

A.J. Evans
University of Southampton

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Field Studies of the Population Dynamics of the Spotted Spiny Lobster *Panulirus guttatus* (Latreille) at Bermuda

C. R. EVANS, A. P. M. LOCKWOOD, AND A. J. EVANS

Results of a study on the population dynamics of the spotted spiny lobster *Panulirus guttatus* (Latreille) at Bermuda are described. The annual growth coefficients (*K*) for male and female spotted spiny lobsters *P. guttatus* are estimated at 0.22 and 0.16 from size frequency analyses. Annual total mortality, fishing mortality, natural mortality, and recruitment coefficients (*Z, F, M,* and *R*) for 1987 were estimated at 0.79, 0.46, 0.33, and 0.79, respectively, based on length and weight data and the exploitation rate (E = 0.58) was estimated from population weight data. The catchability coefficient (q) for 1987 was estimated at 3.9×10^{-6}/trap-haul from the estimate of *F* and the 1987 data for total effort. The stock size (N_{1987}) of trappable *P. guttatus* lobsters at the start of calendar year 1987 was estimated at approximately 71×10^{3} individuals from q and industry catch and effort data. The population showed marked spatial preference with the density at the reef crest an order of magnitude greater than in the reef system as a whole.

Investigation of the factors that control the population in a fishery is a prerequisite for effective management (Schaeffer, 1954). In the Caribbean, the most common spiny lobsters fished include *Panulirus argus* (Latreille), *P. guttatus* (Latreille), and *P. laevicauda* (Latreille). *Panulirus argus* occupies coastal shallows and offshore reefs over a wide geographical range, extending from Brazil to Bermuda, whereas *P. guttatus* is known to chiefly occupy coral reef habitat through the Caribbean to Brazil. Studies of *P. guttatus* are few, but include those conducted in the Bahamas and Florida (Herrnkind, 1985), Bermuda (Sutcliffe, 1953), the French West Indies (Farrugio, 1976; Marfin, 1978), and Jamaica (Munro 1974), where *P. guttatus* is most abundant adjacent to the reef crest (Munro, 1974; Evans and Lockwood, 1994).

The Caribbean spiny lobster *P. argus* and the spotted spiny lobster (local name Guinea chick lobster) *P. guttatus* have in recent years been landed by fishermen in roughly the same proportions in Bermuda, although in the 1950s, one *P. guttatus* lobster was taken for every 20 *P. argus* (Sutcliffe, 1953).

Recently, the fishery for *P. argus* in Bermuda has experienced technological changes. Lobster-specific traps with escape gaps have been introduced (Hateley and Sleeter, 1983), and are replacing the old fin-fish/lobster trap used in the 1970s and 1980s. Having gained in importance and value, the *P. guttatus* fishery was targeted for study by the Overseas Development Administration, with the objective of deriving information on the population dynamics of *P. guttatus*.

MATERIALS AND METHODS

The principal fishing gear employed was the traditional Bermudan antillean arrowhead fish trap (1.2 × 1.1 × 0.5 m) consisting of a 38-mm hexagonal "chicken wire" mesh on a heavy spicewood frame (Sutcliffe, 1952). Traps were baited with the heads and tails of coral reef fish and set in the "white holes" (sand-floored depressions in the reef) for 2 or 3 days, with a marker buoy and a "header" buoy mid-depth to keep the line safely clear of the coral. Trapping was carried out in nine study areas of the principal northeastern spotted spiny lobster fishing grounds in the full range of habitats in which the species is found at Bermuda, viz. the outer reefs (patch reefs, reef flat, fore-reef slope, main terrace and outer terraces in the vicinity of the reef crest) (Fig. 1). The number of traps employed in each study area varied from 12 to 16. Study areas were visited once only, for a 2- or 3-mo block, except for St. David's Head study area which was visited for two 7-wk blocks, one in the late summer and one in the late autumn/early winter of 1986, and Kitchen Shoals, which was visited for 6 months May through October 1987. The periods of sampling were all in the summer or autumn periods of 1986 or 1987, except for the East Ledge Flat study area, which was visited in late winter 1987 for 8 weeks, Feb.–March. Further details of the depth and season of sampling for

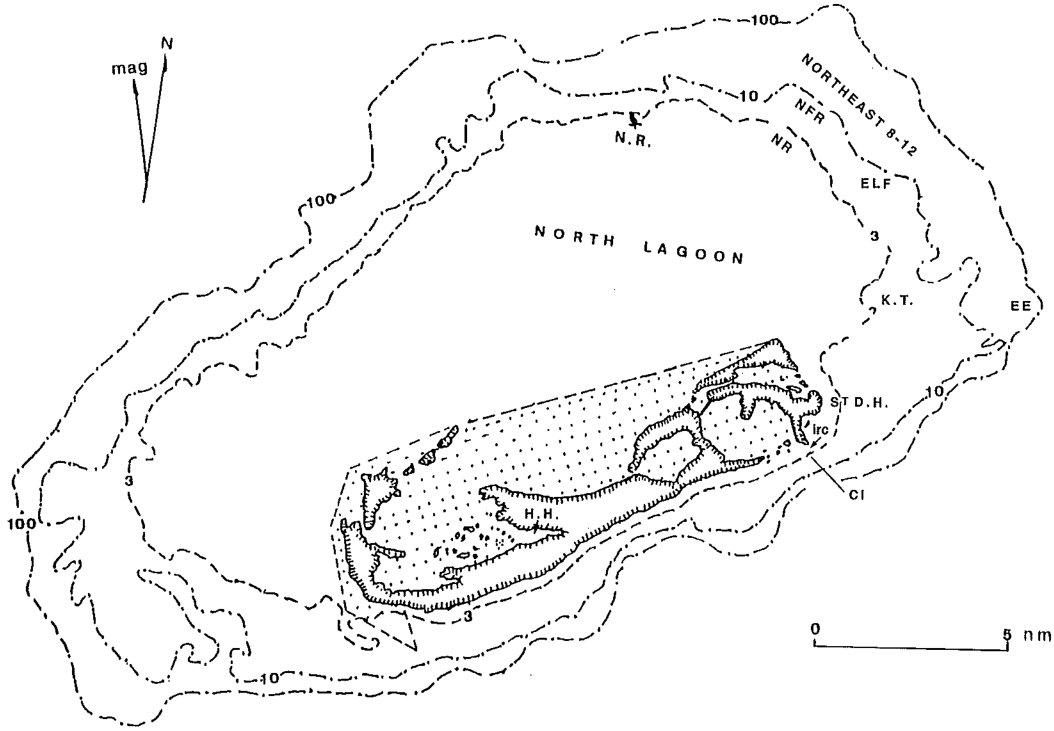

Fig. 1. Map showing the Bermuda Platform and the nine study areas in the fishing grounds. The fishing grounds lie chiefly outside of the 3-fathom (≈6 m) line. Stippled area = prohibited trapping zone; NR = North Rock; EE = eastern edge; CI = Cooper's Island (boiler reefs/reef crest); KT = Kitchen Tripod, location of the Kitchen Shoals study area; NFR = Northern fore-reefs between North Rock and Kitchen Tripod; NR = North Reefs (reef tract between North Rock and Kitchen Tripod); ELF = East Ledge Flat; St D H = St. David's Head; Northeast 8–12 = Main terrace associated with the North Reefs between North Rock and Kitchen Tripod; IRC = Cooper's Island, inside the reef crest.

each study area are given in the legend of Figure 2.

Carapace length (CL), the distance between the anterior and posterior margins of the carapace along the middorsal line, was measured with a vernier calliper to the nearest 0.1 mm. Live weight was measured using appropriate spring balances to the nearest 5 g.

Estimates of the annual growth (K) and total mortality (Z) coefficients of male and female *P. guttatus* lobsters were derived from integrated size-frequency analysis [modal length-at-age: Pauly's (1983) method] and by length frequency analysis [the Beverton and Holt (1956) method] of a relatively large sample of *P. guttatus* lobsters (Fig. 2) derived from K. The Allen (1953) weight equation (for exploitation rate) was used to estimate the annual fishing mortality, natural mortality, and recruitment coefficients from Z.

An approximate estimate of the annual mean population number (N_{1987}) for calendar year 1987 was derived by application of the estimate of the catchability coefficient (q) to the fishery statistics of catch and effort from the Nicholson and Bailey (1935) equation: $C_t = N_t(1 - \exp(-qf_t))$, where N_t is the population size at the start of the tth period and f_t is the total effort expended in the tth period to take the catch of C_t.

Results

The annual growth rates (K) of the fishable stock.—The size composition of males is polymodal as compiled from samples from the nine study areas (Fig. 2). The estimate of the annual growth coefficient (K) for males was 0.22 from Pauly's (1983) integrated method of size-frequency analysis (Fig. 3).

The carapace length measurement work on the females caught in the nine study areas also resulted in a polymodal size-frequency distribution (Fig. 4). The annual growth coefficient of females was estimated at 0.16 from similar analyses based on the smaller sample. The lat-

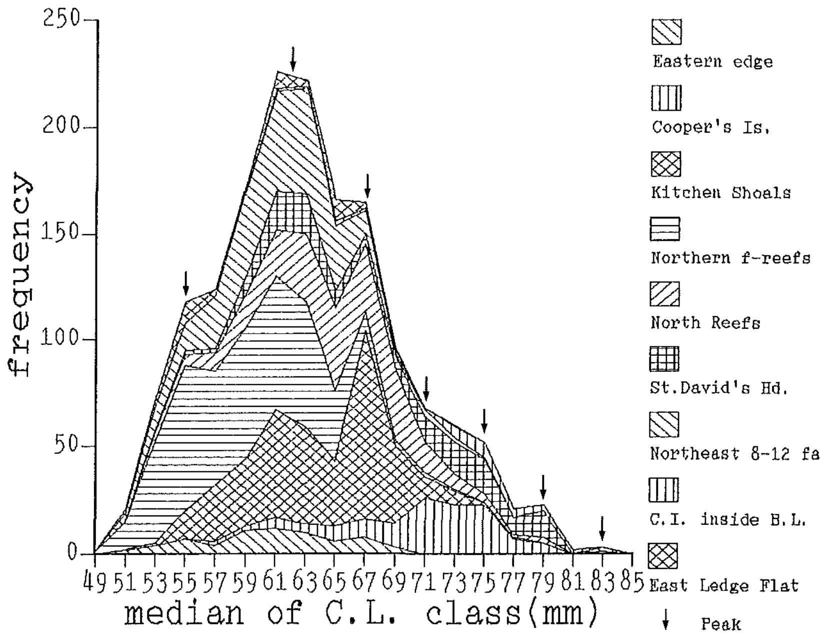

Fig. 2. The size-frequency distribution of Male *P. guttatus* from the fishing grounds. The size-frequency distribution is a combination of nine samples taken from various locations in the different physiographic environments occupied by *P. guttatus* lobsters, chiefly in the summer and autumn periods of 1986–87. The peaks were determined subjectively at 55, 62, 67, 71, 75, 79, and 83 mm CL. The area curves for the eastern edge, Cooper's Island and Kitchen Shoals are located nearest to the x-axis.

Key to Area: Depth and Season of Sampling

Area	Depth (fathoms)	Period
Eastern edge	10–22	Autumn
Cooper's Island (reef crest)	4–6	Autumn
Kitchen Shoals	3–5	Summer and autumn
Northern fore-reefs	7–9	Summer
North Reefs (between North Rock and Kitchen Tripod)	2–5	Autumn
St. David's Head (reef crest)	4–6	Autumn
Northeast	8–12	Summer
Cooper's Island (inside crest)	2.5–4	Autumn
East Ledge Flat	2–3.5	Winter

ter sample resulted from a disparity in the number of males and females caught in the study areas. A large number of males were caught in relation to females. The total number of males caught was 1,556 (Fig. 2) compared to 100 females (Fig. 4), or 16:1.

The total mortality rates of the fishable stock.—The annual total mortality coefficient (Z) was estimated at 0.81 for males and at approximately 0.77 for females based on the annual growth coefficients of 0.22 for males and 0.16 (0.155) for females from the length parameters in Tables 1 and 2 by the Beverton-Holt (1956) equation for annual total mortality:

$$Z = K(L_{maxasym} - L)/(L - L'),$$

where $L_{maxasym}$ is the maximum asymptotic length, L' is the mode of the size frequency distribution, and L is mean length of individuals of length greater than the mode.

$L_{maxasym}$ was estimated at 87.6 mm CL for males and at 86.0 mm CL for females from the equation given by Pauly (1983) for the determination of maximum asymptotic length from the Ford-Walford plot of the "length-at-age" data. A comparison may be made with the maximum length of males observed in the 1950s, which was 87 mm CL (Sutcliffe, 1953), in agreement with the estimate of 87.6 mm CL for the males. The sample of females in Sutcliffe's (1953) study was too small for comparison.

The other length parameter data were as fol-

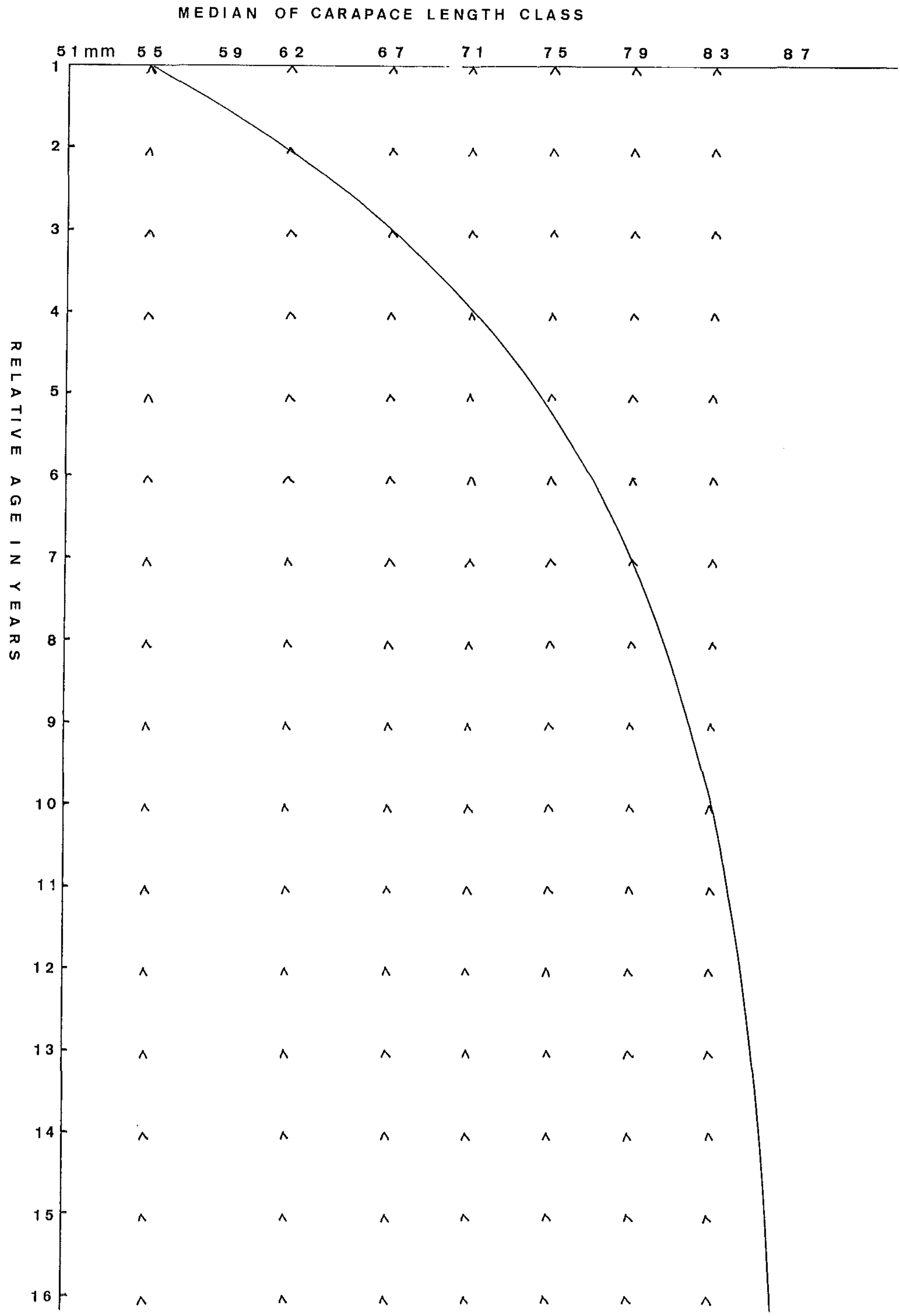

Fig. 3. Growth curve for the male spotted spiny lobster *P. guttatus* at Bermuda, based on the peaks of Figure 1 and on the Pauly (1983) integrated method of size frequency analysis. The observed peaks of the size-frequency distribution are repeated under one another on the assumption that the size frequency does not change significantly from year to year. A smooth curve is drawn through as many peaks as possible with a curved ruler. Sizes for each relative age are read off from the curve and a Ford-Walford plot is drawn from them by the method summarized in Pauly (1983). The annual growth coefficient K for males was thereby estimated at 0.22, and the maximum asymptotic length was estimated at 87.6 mm carapace length.

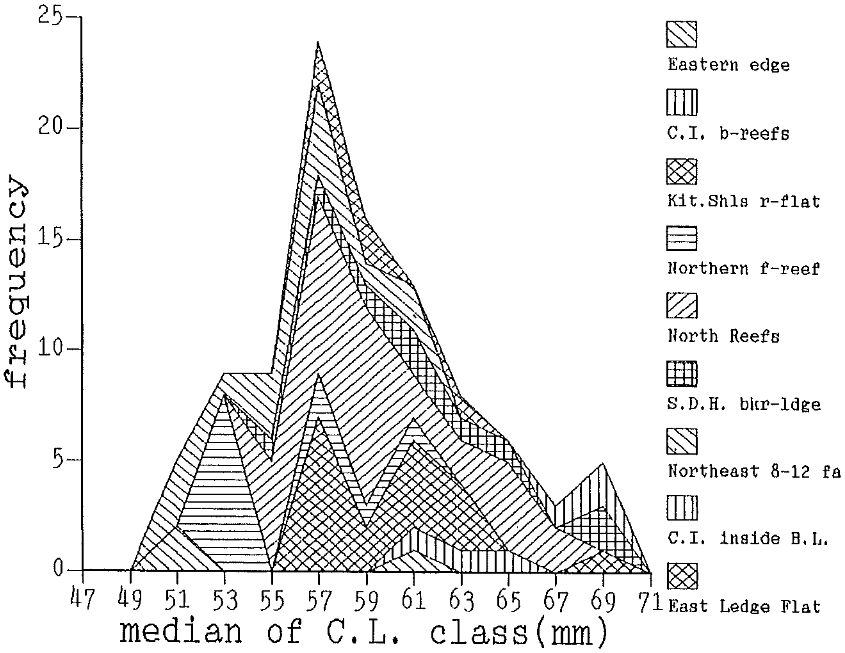

Fig. 4. The size-frequency distribution of female *P. guttatus* spiny lobsters. The size frequency was obtained by the same trapping effort, periods, and study areas as outlined in Figure 2. The total number of females caught in these nine study areas (100) was relatively very low compared to that of males (1,556). The peaks were subjectively determined at 52, 57, 61, 65, and 69 mm CL; the size-frequency analysis to determine the rate of growth of females was carried out by Pauly's (1983) integrated method.

TABLE 1. Male *Panulirus guttatus*: compilation of mean wt of animals in the exploited phase and of mean carapace length (CL) of fully recruited animals of ≥ 50 mm CL[a] and ≥ 60 mm CL[b] respectively (combined sample of nine different areas).

Sample	$\overline{W}_Y$ (exploited phase)[c] (g)	Sample size (n)	$\overline{CL}$ animals ≥ modal CL[b] (mm)	Sample size (n)
Eastern edge (10–28 fathoms, autumn)	199	67	63.5	39
Cooper's Island boiler reefs (B.L.[d], autumn)	287	123	71.4	119
Kitchen Shoals (reef flat, summer)	222.9	288	65.15	219
Fore-reefs around Northeast Breaker (7–9 fathoms, July–Aug.)	183.46	414	62.97	169
North Reefs (Sep.–Dec.)	234.2	223	65.99	189
St. David's Head boiler reefs (phase 1, Aug.–Oct.)	262.8	132	69.2	119
Main terrace around Northeast Breaker (8–12 fathoms, July–Aug.)	196.9	229	62.51	143
Off Soldier's Point, Cooper's Island inside B.L.[d] (autumn)	305	31	73.5	30
East Ledge Flat (reef flat Feb.–March)	201	49	64.3	28
Bermuda reef platform (Cooper's Island—North Rock)	218.6	1,556	65.9	1,055

[a] 50 mm CL is the estimated size-at-first-capture.
[b] 60 mm CL is the modal CL.
[c] Calculated from mean CL (exploited phase).
[d] B.L. = Breaker Line (reef-crest).

TABLE 2. Female *Panulirus guttatus*: compilation of mean wt of animals in the exploited phase and of mean carapace length (CL) of fully-recruited animals of ≥ 50 mm CL[a] and ≥ 56 mm CL[b] respectively.

Sample	$\overline{W}_Y$ (exploited phase)[c] x(g)	Sample size (n)	$\overline{CL}$ animals ≥ modal CL[b] (mm)	Sample size (n)
Eastern edge (10–28 fathoms, autumn)	145	3	60.8	1
Cooper's Island boiler reefs (B.L.[d], autumn)	200	3	63.2	3
Kitchen Shoals (reef flat, summer)	190	21	61.9	20
Fore-reefs around Northeast Breaker (7–9 fathoms, July–Aug.)	148	12	58.8	4
North Reefs (Sep.–Dec.)	177	31	60.4	26
St. David's Head boiler reefs (Phase 1, Aug.–Oct.)	192	9	62.7	8
Main terrace around Northeast Breaker (8–12 fathoms, July–Aug.)	156	13	58.2	8
Off Soldier's Point, Cooper's Island, inside B.L.[d] (autumn)	232	3	68.3	3
East Ledge Flat (reef flat Feb.–March)	172	5	58.7	5
Bermuda reef platform (Cooper's Island—North Rock)	176.0	100	61.0	78

[a] 50 mm CL is the estimated size-at-first-capture.
[b] 56 mm CL is the modal CL.
[c] Calculated from mean CL (exploited phase).
[d] B.L. = Breaker Line (reef-crest).

lows (Tables 1 and 2): males: $L' = 60.0$ mm CL, $L = 65.9$ mm CL; females: $L' = 56.0$ mm CL, $L = 61.0$ mm CL.

The median estimate of Z for males and females combined is 0.79, and is used as a population fisheries parameter below to derive M, F, and R.

The annual fishing mortality, natural mortality and recruitment coefficients (F, M and R) of the fishable stock.—The appropriate catchability coefficient for the fishery catch and effort data may be derived from the annual total mortality coefficient by application of the Allen (1953) equation to population weight data: exploitation rate (E) = W_c/W, where W_c is the weight-at-first-capture and W is the mean weight of the stock in the exploited phase.

This application is possible since, near the optimum level of harvest and exploitation, the Allen (1953) equation holds, $E = F/Z$ (Stevenson, 1981), and recruitment R is approximately the sum of parameters M and F. The fishery catchability coefficient (q) may then be derived from $F = q \cdot f$, where f is the total fishery effort, for the calendar year to which the carapace length frequency distributions and weight data refer (1987 in the case of the present field study, from 21 Aug. 1986 to 23 Oct. 1987).

The annual fishing mortality coefficient (F).—The weight data were as follows: males: $W_c = 110$ g, $W = 219$ g, and $E = W_c/W = 0.50$; females: $W_c = 117$ g, $W = 176$ g, and $E = W_c/W = 0.66$.

An exploitation rate of 0.50 indicates that an optimum level of harvest and exploitation has been achieved. An estimate for the rate of exploitation for the population as a whole (males and females combined) is the median 0.58, which may be used to estimate the annual fishing mortality coefficient for the combined male and female stock from the exploitation rate equation $E = F/Z$ (Stevenson, 1981). The annual fishing mortality coefficient of spotted spiny lobsters (male and female combined) on the Bermuda Platform in 1987 was $0.58 \times 0.79 = 0.46$.

The annual natural mortality coefficient (M).—From $Z = M + F$, the annual natural mortality coefficient M is estimated by substitution. Thus, the annual natural mortality coefficient (M) of fishable spotted spiny lobsters (male and female combined) on the Bermuda Platform in 1987 was 0.33.

The annual recruitment coefficient (R).—The exploitation rate for males in 1987 was 0.50 and for females it was 0.66. The median is 0.58, and this is close to the optimum rate of 0.50. Therefore, spotted spiny lobsters were harvested in the mid-1980s at approximately the same level as maximum sustainable yield, assuming that the island stock is either self-sustaining or making a significant contribution to sustaining itself. The annual recruitment coefficient (R) is approximately the sum of M and F in these circumstances (Smith and Greene, 1991). The annual recruitment coefficient of spotted lobsters into the fishable stock on the Bermudan island shelf in calendar year 1987 was thus estimated at ca. 0.8 (male + female). This may be transformed to a finite annual recruitment rate (A_R) using the equation: $A_R = 1 - e^{-R}$ (Krebs, 1978); the finite annual recruitment rate for 1987 was 0.5–0.6.

Stock size and mean population density on the Bermuda Platform.—The stock size of trappable *P. guttatus* lobsters on the Bermuda Platform at the start of calendar year 1987 was estimated from the Nicholson and Bailey (1935) catch equation (see *Materials and Methods*). The yield (C_t) and effort (f_t) in calendar year 1987 (the *t*th period) were 26,008 (individuals) and 116,719 trap-hauls (Department of Agriculture, Fisheries and Parks, Bermuda, 1992).

The catchability coefficient (q) is given by the equation $F = q \cdot f$, where f is the total effort. Substituting for F and f (1987), $q_{1987} = F_{1987}/f_{1987}$.

Catchability, $q_{1987} = 0.46/116{,}719$ trap-hauls $= 3.9 \times 10^{-6}$/trap-haul. Therefore, from the Nicholson and Bailey (1935) equation, the stock size (N_t) was approximately 71×10^3 spiny lobsters at the start of calendar year 1987.

The area of reef occupied by fishable *P. guttatus* lobsters in the reef system was estimated for 1987 at approximately 4.13×10^2 km^2 from an Admiralty chart entitled "The Bermuda Islands," 1965, and a map of the substrate types in Morris et al. (1977). The estimated annual mean population number for 1987 was approximately 71×10^3. An estimate of annual mean density of spotted spiny lobsters in the reef system at the start of calendar year 1987 is therefore 71,100/413 = 172 lobsters/km^2.

Carapace length/weight relationships.—From the carapace length and weight (wt) measurements, the CL/wt relationships for animals of 50–70 mm CL were as follows: males: wt (g) = −316 + 8.5 (±0.69) CL (mm) (95% confidence limits of the slope = ±0.69); females: wt (g) = −198 + 6.29 (±1.0) CL (mm) (95% confidence limits of the slope = ±1.0).

Summary of findings.—The population dynamics results from the present study and from related studies (Evans and Lockwood, 1994; Evans et al., 1995a) are summarized in Table 3, and represent the data base and conclusions from the O.D.A.-funded research project relating to *P. guttatus*.

TABLE 3. Summary of data on the population dynamics of spotted spiny lobster *Panulirus guttatus* at Bermuda.

	Males	Females
From the present study:		
Growth coefficient (K)	0.22	0.155
Maximum asymptotic carapace length	87.6 mm	86.0 mm
V.B.G.F third parameter (t_0)	−0.846 yr	−1.12 yr
Total mortality coefficient (Z)	0.81	0.77
Exploitation rate (E)	0.50	0.66
Fishing mortality coefficient (F)	0.40	0.51
Natural mortality coefficient (M)	0.41	0.26
Carapace length (CL) at entry to exploited phase	50 mm	50 mm
Weight at entry to exploited phase	110 g	117 g
Mean weight, exploited phase	219 g	176 g
Recruitment coefficient (R)	0.81	0.77

Mean population density, Bermuda reef system = 172 lobsters/km^2.

Biomass in reef system (413 km^2 occupied) = 34 kg/km^2.

Fishery catchability coefficient, based on the traditional arrowhead fish trap (q) = 3.9×10^{-6}/trap-haul.

From Evans and Lockwood (1994):

Habitat: reef flat and terrace adjacent to reef crest.

Most abundant at reef crest. Trapped sex ratio 14:1, male : female (n = 1,750). Mean density in favored reef crest habitat is 29 ± 7.6 lobsters/ha (95% confidence).

From Evans and Evans (1995):

Maximum sustainable yield = ca. 33,000 lobsters/yr.

From Evans et al. (1995a):

Estimate of female size at first physical maturity 59 mm (SD 4 mm) CL. Maturity for males was at 69.3 mm (SD 1.7 mm) CL.

[a] V.B.G.F. = Jon Bestallonfy Growth Formula.

DISCUSSION

As noted earlier, in the late 1980s, *P. guttatus* assumed a greater importance in the total spiny lobster catch at Bermuda than was reported by Sutcliffe in the 1950s. The present results cast some light on factors of importance in the population dynamics and catchability of this species. The annual growth coefficient *K* was estimated from size-frequency analysis based on the peaks in the size-frequency distributions. The integrated method is more accurate than either the Petersen method (1892) or the method of modal class progression analysis because it "integrates" the two methods (Pauly, 1983). Increments in carapace length per moult observed for six males of 60–68 mm CL that were tagged, released, and recaptured in the field were relatively small (approximately 0.9 mm) and the coefficient of growth per moult for these males was 0.014 (Appendix) (Evans, 1989), suggesting that growth rate may slow considerably when males approach maturity (69 mm CL: Evans et al., 1995a), or that handling and/or tag-insertion suppresses growth.

The Beverton-Holt (1956) equation is appropriate if a large, representative sample of the size frequency distribution has been obtained and the fishing intensity is even in the fishing grounds (Beverton and Holt, 1956). The wide range of habitats trapped in the principal fishing grounds satisfies the first of these criteria reasonably for males. However, the estimates of *K* and *Z* for females are approximate, because although the sample of females was taken by the same sampling program as that for males, it comprised much fewer animals. From personal observations in northeastern fishing grounds and around the reef system in 1986–87, fishing intensity appeared to be relatively even.

Differential trap ratios vary with depth on the Bermuda Platform in the summer and autumn, with the highest sex ratios (male to female) occurring in the deeper water seaward of the reef crest, and the lowest ratios occurring in the patch reefs and reef flat inside the crest (Evans and Lockwood, 1994). Differential trap-retention between the sexes probably accounts for the disparity in the sex ratio observed from trapping (16:1). Female spotted spiny lobsters are generally considerably smaller than males of the same age. The mean retention length of *P. argus* in antillean arrowhead traps is 50 mm CL (Munro, 1974). Young female or male spotted spiny lobsters of <49 mm CL were not caught in the present study; this agrees with Munro's estimate for *P. argus*. It is therefore very probable that all of the 0+ and most of the 1+ years age classes of males were excluded from the sample. The same bias would apply for females, but to the probable total exclusion of female yearlings (1+ years). However, estimation of growth rate was not affected by this effect since the Pauly integrated method utilizes relative age in years, rather than absolute age, to derive the curve.

Another possible source of bias which could affect results if males and females are combined is the fact that females have a lower catchability than males (Evans and Lockwood, 1994). This effect would not have biased the results of the present study, however, since separate analyses were carried out for males and females. The youngest females (0+ and 1+ years) are probably the most secretive, but are not captured in any case because of the 50-mm mean trap retention.

The population density of *P. argus* post-recruits in the reef areas of the Bermuda platform was estimated to be 290/km^2 (Evans and Evans, 1996), which is about twice that obtained for *P. guttatus* in the present study (172/km^2). The estimates convert to biomass estimates of 230 kg/km^2 and 34 kg/km^2, respectively, using estimates of the mean weights of individual members of the stock (0.80 kg and 0.20 kg, respectively). The average biomass of *P. guttatus* lobsters is thus approximately an order of magnitude less than that of *P. argus* lobsters.

The maximum sustainable yield (MSY) of spotted spiny lobsters was estimated by Evans and Evans (1995) and by Evans et al. (1995b) at approximately 33,000 spotted lobsters per calendar year (Jan.–Dec.). Evans and Evans (1995) estimated the MSY of *P. argus* at Bermuda at 37,000 ± 7,700 (SE) lobsters per lobster fishing season (Sep.–Mar.). The estimate of MSY for *P. guttatus* fits reasonably well with the estimated stock size of ca. 71,000 individuals, the annual catch of ca. 30,000, and the estimated exploitation rate of ca. 0.5–0.6

The principal habitat occupied by *P. guttatus* at Bermuda is the reef crest of the atoll's reef system, and the reef flat and ledge immediately landward and seaward, respectively (Evans, 1988, 1989; Evans and Lockwood, 1994). The average density of *P. guttatus* in these areas was estimated, from the mean of three estimates from different locations, at 29 ± 7.6 trappable lobsters/ha (95% confidence limits) (Evans and Lockwood, 1994). This represents 2,900 ± 760 lobsters/km^2 along the reef crest, which is an order of magnitude greater than that for the total reef area occupied (172/km^2) and infers a clumped distribution, with a concentration along the line of the reef crest.

The greater population density and biomass of *P. argus* than *P. guttatus* on the Bermuda Platform, where the reef area occupied and fishing mortality for each species is approximately the same (Evans and Evans, 1996), per-

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haps reflects a prominence of *P. argus* over *P. guttatus* in the Caribbean area generally. This prominence may be related to greater migratory ability in *P. argus* than in *P. guttatus* (Herrnkind, 1985; Evans and Lockwood, 1994; Evans et al., 1995a; Evans and Lockwood, 1996), which results in enhanced access to food and habitat (Herrnkind, 1985).

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DEPARTMENT OF OCEANOGRAPHY, UNIVERSITY OF SOUTHAMPTON, SOUTHAMPTON OCEANOGRAPHY CENTRE, WATERFRONT CAMPUS, EUROPEAN WAY, SOUTHAMPTON SO14 3ZH, UNITED KINGDOM. PRESENT ADDRESS: (AJE) DORSET NATURAL RESOURCES AND ENVIRONMENT CONSULTANTS, 2, EDGEHILL ROAD, BOURNEMOUTH, ENGLAND. Date accepted: February 26, 1996.

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Appendix

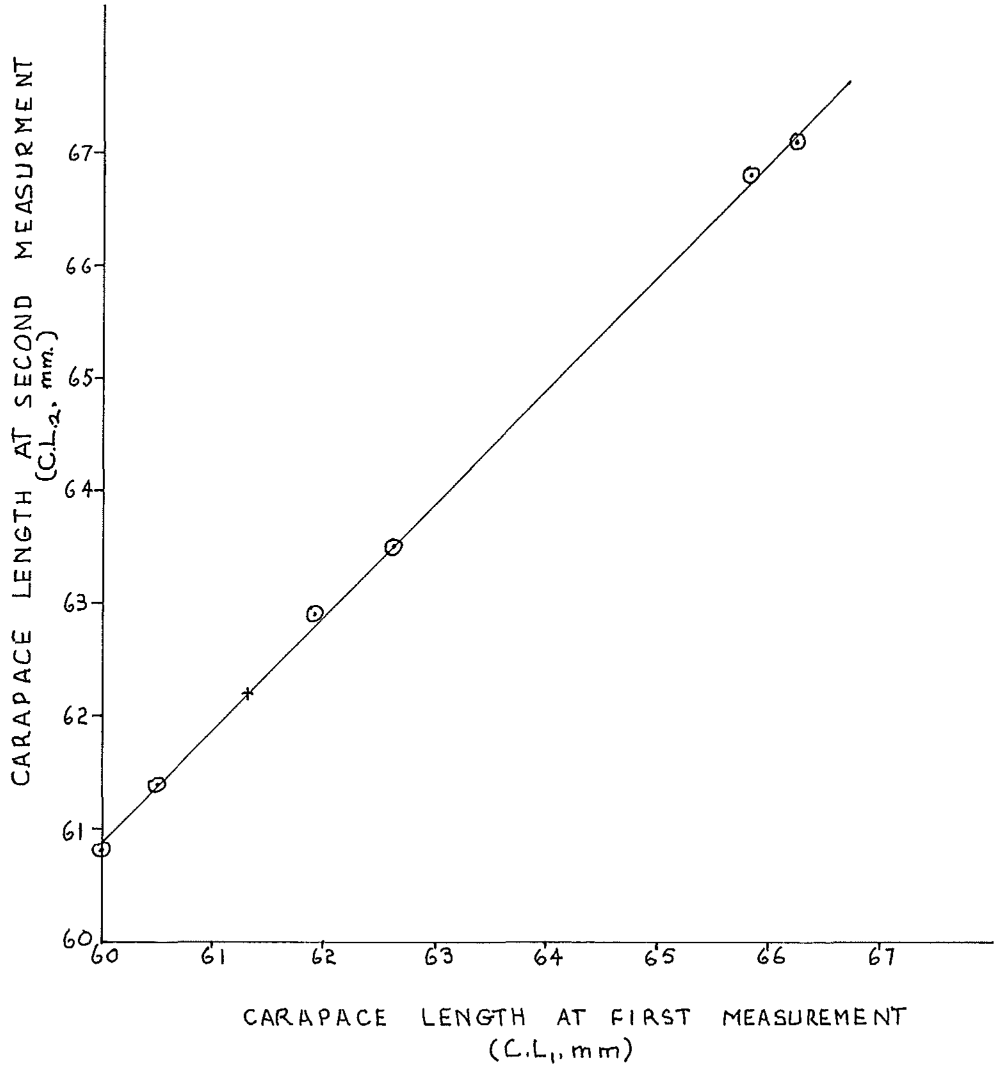

Figure showing the relatively slow growth achieved after one moult by tagged male adult *P. guttatus* lobsters from the reef-crest (Kitchen Shoals), during the Summer (May–Oct.) of 1987. Animals were of size 60–67 mm CL. The line was fitted by correlation/regression program of a progammable calculator. Intercept A = 0.043, slope (B) = 1.014, correlation coefficient (r) = 0.9997 (statistical significance at the 0.1% level) ($P = 0.001$). The equation is as follows: $CL_2 = 0.043 + 1.014 \cdot CL_1$. The circled points refer to tag-recaptures in the field, and the *x* point refers to an animal that moulted in a large (8 ft diameter) round aquarium tank. Animals' growth may be depressed somewhat from tagging, but the relatively slow rate of growth compared to that computed from the size-frequency analyses by the Pauly (1983) method ($K = 0.22$) is probably largely due to a slowing of the growth rate at maturity. Size at first physical maturity in males occurs at 69 mm CL.