

Density Dependence in Spiny Lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands

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A positive linear relationship between the ratio of natural mortality to von Bertalanffy growth and catch per unit effort (CPUE) and a negative relationship between asymptotic length and CPUE were observed for the spiny lobster, *Panulirus marginatus*, among seven banks in the Northwestern Hawaiian Islands prior to the development of a fishery (1977-81). Resampling two of these banks in 1986-87 after heavy fishing indicated an increase in the asymptotic length and a decrease in the length at onset of egg production.

Il existait une relation linéaire positive entre le ratio de la mortalité naturelle à la croissance von Bertalanffy et la prise par unité d'effort (PUE) ainsi qu'une relation négative entre la longueur asymptotique et la PUE chez la langouste, *Panulirus marginatus*, dans sept bancs de la partie nord-ouest de l'archipel hawaïen avant l'établissement d'une pêcherie (1977-81). Un nouvel échantillonnage de ces bancs en 1986-87, après une pêche intense, a indiqué un accroissement de la longueur asymptotique et une diminution de la longueur au moment de la production d'oeufs.

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Density-dependent relationships affecting growth, natural mortality, asymptotic size, and size at onset of sexual maturity in some lobster stocks have been difficult to rigorously document because of limitations in data bases and analytic methods (Chittleborough 1979; Morgan 1980; Munro 1983; Addison 1986). However, documenting these relationships is frequently cited as research critical to understanding lobster population dynamics (e.g. Cobb 1986). Addison (1986) hypothesized that, if a significant relationship between density and population parameters exists as a result of the lobster's use of shelters, management measures derived from changes in size-frequency distributions and standard yield-per-recruit models may be incorrect since they assume population parameters do not change with density.

Density-dependent relationships are examined for population parameters of the spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands (NWHI), a chain of small islands, banks, and reefs on the northwestern portion of the Hawaiian Archipelago (Fig. 1). Based on research sampling data from 1977 to 1981, estimates of density, in terms of catch per unit effort (CPUE); asymptotic length (L_{∞}); and the ratio of natural mortality to growth (M/K) for the spiny lobster are determined for seven NWHI banks prior to the development of a commercial fishery. Nine years after this initial sampling, an annual research program was initiated to resample the spiny lobster populations at Necker Island and Maro Reef, both having experienced heavy commercial fishing and reductions in lobster density. The changes in density, measured as changes in CPUE, are compared with changes in total mortality to growth (Z/K), L_{∞} , and size at onset of egg production.

Analytic Methods

Catch Rates

Standardized lobster sampling was conducted in 1977-81 at 26 banks in the NWHI and again in 1986-87 at Necker Island and Maro Reef, the two most productive and heavily fished banks. Lobster habitat at each bank was partitioned into 0.01 nmi² quadrats, and a randomly selected subset of the quadrats was fished at 20-90 m depths with California wire mesh, two-chambered lobster pots. The percent of the 0.01 nmi² quadrats sampled ranged from 60 to 90%; typically a greater proportion of the habitat was sampled at the smaller banks. At least eight strings of eight traps per string were baited and set overnight in each quadrat sampled. The trapped lobsters were measured and released at the trapping site. For each quadrat, the CPUE was computed as the number of lobsters trapped divided by the number of traps recovered. The bank CPUE and standard error were computed as the mean and standard error of the CPUE's from all the quadrats sampled.

The research sampling covered all seasons and at some banks extended for several years. However, neither seasonal factors nor trap selectivity appear to bias the trap data. Specifically, in a study on selectivity of traps as population sampling gear, MacDonald and Stimson (1980) compared lobster catch rates and size structure between trap and diver catches and observations at Kure Atoll in the NWHI. Their study concluded that (i) trap CPUE does not seem to be influenced by seasonal or lunar factors, (ii) trap catches do not appear to be influenced by a dominance hierarchy based on size, (iii) size distributions

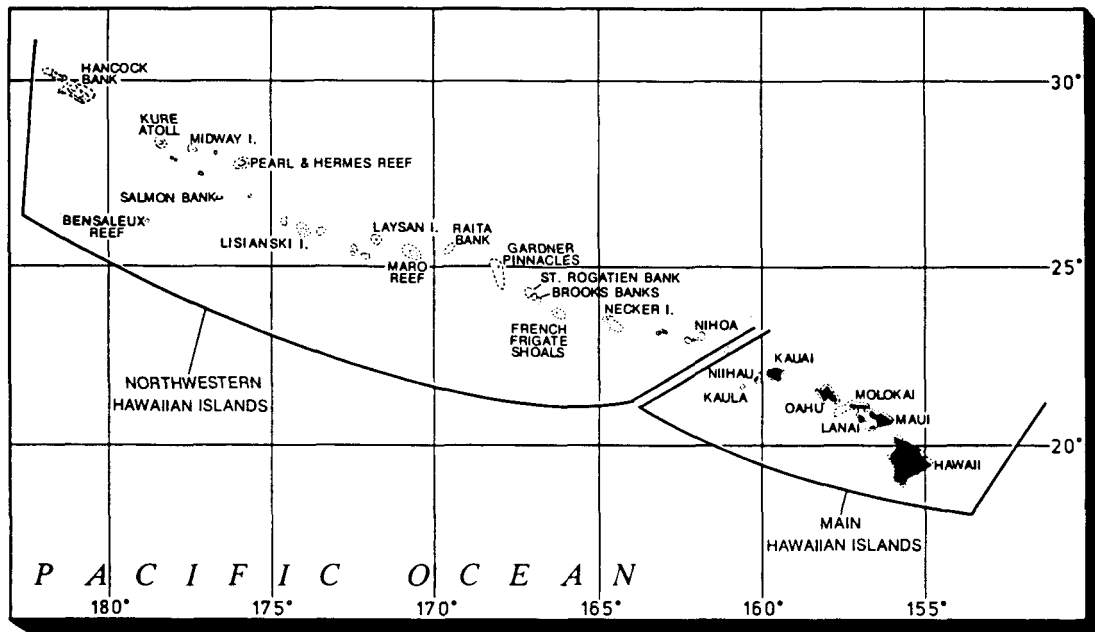


FIG. 1. The Hawaiian Archipelago, including the Northwestern Hawaiian Islands.

TABLE 1. Estimates of mean M/K , L_{∞} , and catch per unit effort (CPUE) (SE in parentheses) for lobster populations at seven banks in the Northwestern Hawaiian Islands. N denotes sample size.

Bank	Year	N	Mean CPUE	Mean L_{∞}	Mean M/K
Necker Island	1977	6474	5.76 (0.75)	113.8 (1.3)	4.22 (0.27)
Gardner Pinnacles	1977-80	390	1.68 (0.41)	115.0 (2.1)	2.20 (0.51)
Raita Bank	1977-80	384	1.13 (0.36)	128.1 (1.7)	1.56 (0.44)
Maro Reef	1977	2318	3.89 (0.45)	127.1 (1.9)	3.56 (0.30)
Laysan Island	1977	954	1.79 (0.39)	125.1 (2.5)	2.72 (0.49)
Pearl and Hermes Reef	1977-79	543	0.63 (0.20)	137.0 (2.2)	2.17 (0.39)
Midway	1977-79	896	1.48 (0.51)	117.2 (1.9)	2.55 (0.48)

of trap and diver-caught lobsters above about 85 mm carapace length show no difference, and (iv) trap CPUE appears to be a reliable measure of adult density.

Mortality to Growth Ratio and Asymptotic Length

Estimates of mortality and growth were computed as a ratio rather than separately because a recently developed estimator using length-frequency data permits estimates of this ratio that are more precise than if either parameter is determined separately (Wetherall et al. 1987). If growth and natural mortality vary with density, it will likely be a positive density and mortality relationship and an inverse density and growth relationship (Cobb and Phillips 1980). The ratio of mortality to growth is sensitive to both these relationships.

Although lobsters grow incrementally rather than continuously, the von Bertalanffy growth curve with parameters K and L_{∞} adequately approximates a lobster growth curve (Morgan 1980). In the absence of fishing mortality under the assumptions of von Bertalanffy growth and a constant natural mortality rate (M) for lobsters above the smallest length fully represented in the catch (L_c), the length-frequency data can be used to estimate

the ratio of instantaneous natural mortality to growth (M/K), with a relationship derived from the equation (Beverton and Holt 1957)

$$M/K = (L_{\infty} - \bar{l})/(\bar{l} - L_c),$$

where \bar{l} is the mean length of all lobsters greater than L_c . Rearranging this equation to express \bar{l} as a linear function of L_c gives

$$\bar{l} = L_{\infty}/(M/K + 1) + L_c(M/K)/(M/K + 1).$$

Now instead of treating L_c as a single value, a sequence of L_c and corresponding \bar{l} values is constructed by beginning with the smallest L_c fully represented in the catch and increasing it in a regular fashion to the largest fish in the sample and computing an \bar{l} for each. In practice, the lower limit of the first size class after the mode of the length-frequency distribution is used as the first L_c value, and each subsequent L_c value is taken as the lower limit of each progressively larger size class. Regressing the sequence of \bar{l} values on the corresponding L_c values (weighted by the standard errors of \bar{l}) gives estimates of the slope and intercept of equation (1), which can be solved for L_{∞} and M/K (Wetherall et al. 1987). When fishing mortality (F) is

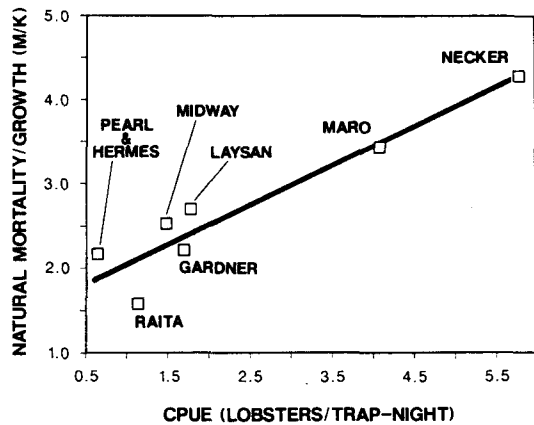


FIG. 2. Plot of the ratio of natural mortality to growth (M/K) against catch per unit effort (CPUE) for seven banks in the Northwestern Hawaiian Islands. The line is the regression equation $M/K = 1.63 + 0.46 \cdot \text{CPUE}$.

TABLE 2. Estimates of mean catch per unit effort (CPUE), Z/K , and L_{∞} (SE in parentheses) for lobster populations at Necker Island and Maro Reef in 1986–87. N denotes sample size.

Location	N	Mean CPUE	Mean L_{∞}	Mean Z/K
Necker Island	2106	2.14 (1.24)	158.2 (5.3)	6.28 (0.57)
Maro Reef	2351	2.65 (0.67)	132.7 (0.63)	3.16 (0.10)

present, this method estimates the ratio of total mortality ($Z = M + F$) to growth (Z/K) and L_{∞} .

Because of differences in the length-frequency distributions between males and females, estimates of M/K and L_{∞} were first computed for males and females separately, then averaged for a mean bank estimate.

Length at Onset of Egg Production

The research sampling recorded whether females were carrying external eggs. A function of the hyperbolic tangent (Tanh) is fit to the proportion of females with eggs (Y), where carapace length class (X) is the independent variable and parameters A , B , and C are estimated with the model

$$Y = A(1 + \text{Tanh}[B(X - C)]).$$

A weighted least squares estimation is used, where the weights are the number of females in the length class. The parameter C is the carapace length, where the percent of the females with eggs equals one-half the asymptotic level ($2A$), and this is taken as the estimate of length at onset of egg production (L_m).

Results

Although 26 banks were sampled in the NWHI for spiny lobsters (Uchida and Tagami 1984), only seven banks met the minimum sample size requirement based on a simulation analysis with the M/K and L_{∞} estimation procedure (see Wetherall et al. 1987). Thus, the analyses used only the seven banks where size-frequency samples of at least 150 lobsters were measured for each sex, from a period prior to any significant fishing effort. Estimates of mean M/K , L_{∞} , and CPUE for each of the seven

banks are in Table 1. A regression of mean bank M/K estimates on mean bank CPUE shows a significant positive relationship ($P < 0.001$, $R^2 = 0.88$; Fig. 2). Lobsters at banks with high CPUE have significantly higher natural mortality or lower growth or both than at banks with low CPUE.

A regression of L_{∞} on mean CPUE suggests that these variables are negatively correlated, but the result is not statistically significant ($P = 0.27$). However, simulation studies show that the estimates of L_{∞} can be negatively biased for small sample sizes (Wetherall et al. 1987). When L_{∞} is regressed on CPUE with a weighted regression where the weights correspond to the sample size of lobsters measured at each bank, the coefficient of CPUE is estimated as -2.6 , which is statistically significant ($P = 0.08$) and indicates L_{∞} varies inversely with CPUE.

Necker Island and Maro Reef experienced considerable fishing effort after 1980; the greatest decline in CPUE occurred at Necker Island, which is closer to the fishing port in Honolulu and has a smaller area of productive habitat than Maro Reef. The 1986–87 mean CPUE's were 37 and 68% of their 1977 levels at Necker Island and Maro Reef, respectively (Table 1, 2). At Necker Island, the mean L_{∞} was estimated at 158.2 mm for 1986–87 and at 113.8 mm prior to the fishery. The difference in L_{∞} between the two periods is statistically significant ($P < 0.05$) (Table 1, 2; Fig. 3). At Maro Reef, even though initially L_{∞} was relatively large there was a statistically significant increase in L_{∞} , although much less than that observed at Necker Island, after the reduction in CPUE ($P < 0.05$) (Table 1, 2).

Although estimates of M/K are unavailable for Maro Reef and Necker Island for 1986–87, estimates of M/K for 1977 compared with estimates of Z/K for 1986–87 strongly suggest that M/K declined at both banks as CPUE declined. At Maro Reef, M/K for 1977 and Z/K for 1986–87 did not significantly differ. Because the 1986–87 CPUE is 68% of the 1977 level, fishing mortality must be substantial, and hence, M/K must have declined in 1986–87. At Necker Island, Z/K is greater than the 1977 M/K ; however, if F/M is estimated as the difference between the 1986–87 Z/K and 1977 M/K divided by the 1977 M/K , an F/M estimate of 0.49 is obtained. This estimate very likely underestimates the ratio of fishing mortality to natural mortality, given that 1986–87 CPUE is 37% of the 1977 level.

Using the Beverton and Holt (1957) yield equation to estimate the reduction in population biomass of a stock relative to its unexploited level as a function of F/M (Beddington and Cooke 1983), when $M/K = 3$, the exploitable biomass will be reduced to 55 and 37% of the level prior to exploitation when $F/M = 0.5$ and 1.2, respectively. Thus, at Necker Island, the reduction of the 1986–87 CPUE to 37% of the unexploited level suggests F/M exceeded 1.0 and certainly the 0.49 estimated under the assumption that M/K is density independent. If F/M were 0.50, the 1986–87 CPUE would be expected to be about 50% of the 1977 level. The M/K , which corresponds to the 1986–87 CPUE level of 2.14, can be calculated from the equation derived from the regression of M/K on CPUE for the seven banks (Fig. 2). This equation estimates $M/K = 2.73$ at Necker Island in 1986–87. With this estimate of M/K and Z/K of 6.28, F/M is estimated to be 1.3, which is consistent with the estimate from the Beverton and Holt (1957) equation given the level at 1986–87 CPUE relative to 1977.

The percentage of females sampled with external eggs increased as a function of carapace length from zero to an asymptotic level (Fig. 4). By 1987, carapace lengths at onset of egg production at both Necker Island and Maro Reef were

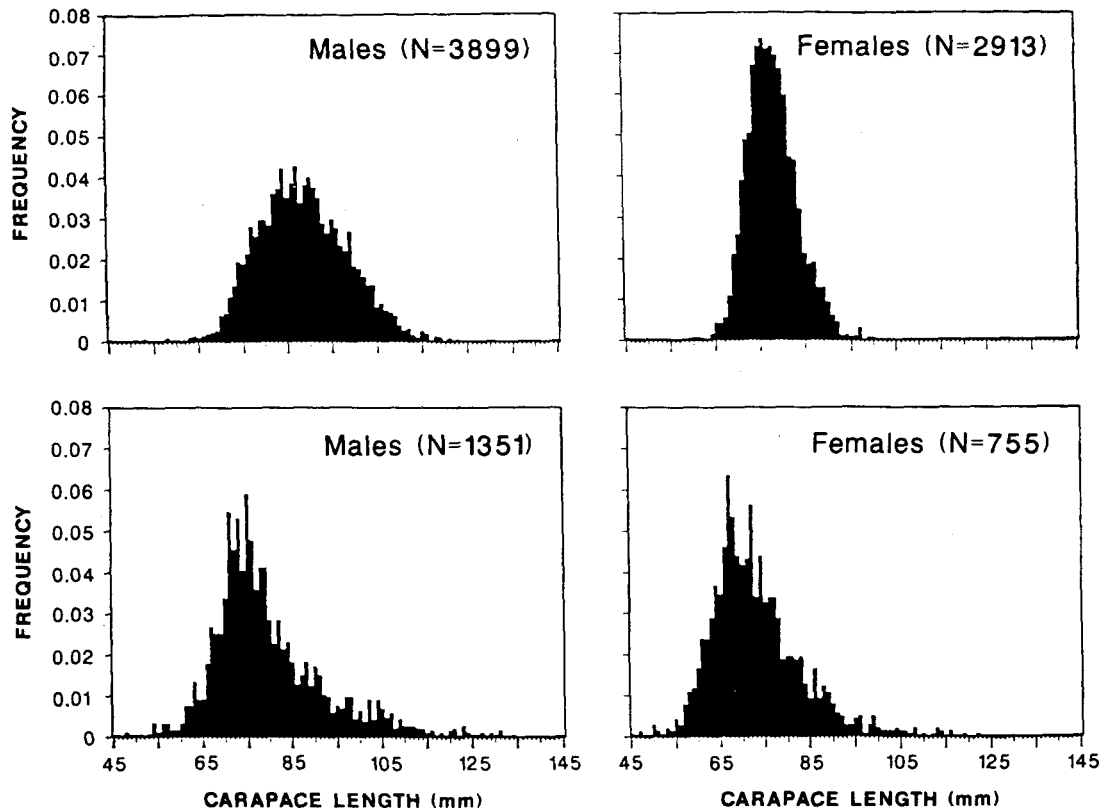


FIG. 3. Plots of length-frequency samples for male and female lobsters from Necker Island obtained from 1977 (top) and 1986-87 (below) sampling periods. (N denotes the number of lobsters in each sample.)

significantly lower than in 1977 ($P < 0.05$) (Table 3). At Necker Island, the length declined from 67.8 mm in 1977 to 60.8 mm in 1987 (Table 3). At Maro Reef, the length declined from 74.8 mm in 1977 to 68.2 mm in 1987 (Table 3).

Discussion

A positive relationship has been shown to exist between M/K and CPUE over seven banks. The similarity in coral reef habitat and reef fauna between these banks (Grigg 1984; Hobson 1984), the evidence that trap catches are a reliable measure of adult abundance and size structure (MacDonald and Stimson 1980), and the indication that M/K decreases with CPUE at Necker Island and Maro Reef when density is reduced due to fishing — all argue that this relationship is likely not due to other factors, which might differ between banks, and further indicate a positive relationship between M/K and density. As to whether the change in the ratio of M to K is due to changes in M or changes in K or both, the separate estimates of the parameters needed to address that issue are not available. However, studies on other species of spiny lobsters suggest that it is likely that both M and K change with density. Munro (1983) estimated the natural mortality coefficient (M) for *P. argus* was 0.52 for an unexploited stock, 0.23 for a moderately exploited stock, and 0.14 for a heavily exploited stock. A similar relationship between density and natural mortality was indicated in *P. cyg-*

nus (Cobb and Phillips 1980). Likewise, growth can be influenced by food and space availability, which change as density changes (Cobb and Phillips 1980).

The inverse relationship between L_{∞} and CPUE, both between banks and over time at Necker Island and Maro Reef, is consistent with the hypothesis that asymptotic size changes inversely with density. Differences in the volume of shelters at two areas in England have been suggested as the cause of marked differences in the size structure of the lobster, *Homarus gammarus*, populations: the area where large shelters are abundant also has more large lobsters (Howard 1980). In the NWHI, the banks all have the same coral reef habitat, so it is unlikely that the size structure of the habitat differs between banks. However, when density is high, crowding may occur even in large shelters and effectively reduce shelter size.

Changes in the length at onset of maturity apparently due to changes in density have been observed in some fish populations. Shelton and Armstrong (1983) documented a 3-cm decline in the length at maturity of the South African pilchard, *Sardinops ocellata*, during a period of substantial population decline. By contrast, there was a 1-cm increase in the length at onset of sexual maturity in the South African anchovy, *Engraulis capensis*, after a period of population increase. Rothschild (1986) suggested that, when a population experiences a reduction in density, the increase in available food for each individual will result in an increase in the rate of sexual development and

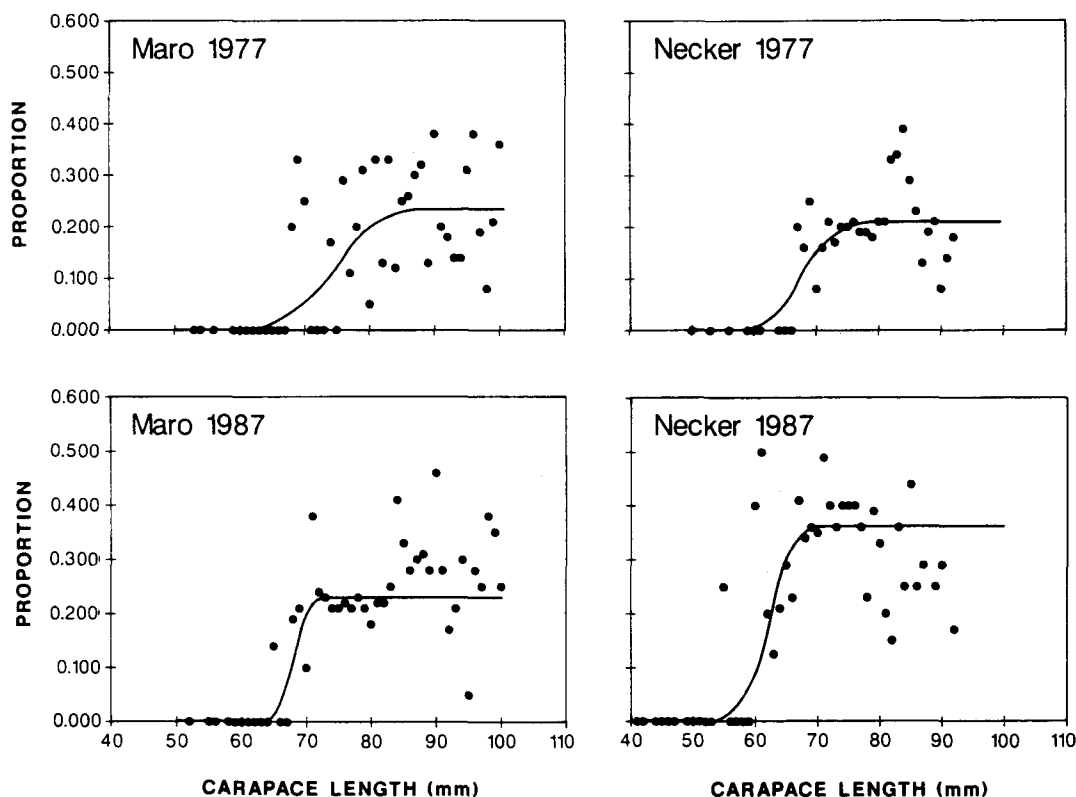


FIG. 4. Proportion of female spiny lobsters at Necker Island and Maro Reef with eggs as a function of carapace length for 1977 and 1987.

TABLE 3. Length at onset of egg production for 1977, 1985-86, and 1987. CL = carapace length (mm) (SE in parentheses), L_m/L_∞ = ratio of length at onset of egg production to female asymptotic length, and N denotes sample size.

Location	1977			1985-86			1987		
	N	CL	L_m/L_∞	N	CL	L_m/L_∞	N	CL	L_m/L_∞
Necker Island	1955	67.8 (1.5)	0.66	1491	57.9 (1.0)	0.41	797	60.8 (1.1)	0.47
Maro Reef	630	74.8 (2.5)	0.61	1614	70.5 (1.9)	0.59	873	68.2 (0.8)	0.54

hence an attainment of the onset of sexual maturity at a smaller size. However, it is also possible that behavioral interactions are important and smaller females are responding not just to a reduction in density but also to a reduction in number of larger females. The observed reductions in length of egg-bearing females at Necker Island and Maro Reef are consistent with both these hypotheses.

A hypothesis that the size at onset of egg production is determined exclusively by age has been used to explain differences in the size at onset of egg production for the rock lobster, *Jasus lalandii*, in different areas of the Benguela ecosystem (Beyers and Goosen 1987). It is argued that the differences in the size at onset of egg production result from differences in growth, so faster growing lobsters are larger when they reach the age at onset of sexual maturity. If the onset of egg production is determined exclusively by age and if growth increases when density is reduced by fishing, then the size at the onset of egg production should increase as fishing increases and not decrease

as observed in the NWHI. An explanation for the difference between this hypothesis and the NWHI findings is that the NWHI fishery only harvests lobsters above the size at onset of egg production; hence, there is no reduction in juvenile lobsters and perhaps no increase in juvenile lobster growth, even though total lobster density decreases.

A management implication of the finding that M/K and L_∞ vary with density is that the application of static yield-per-recruit models can be misleading. Suppose managers want to determine the minimum length at which spiny lobsters should be harvested to maximize the yield-per-recruit at Necker Island when F/M is at 1.3 (estimated 1986-87 level). The Beverton and Holt (1957) yield-per-recruit model can be formulated in terms of M/K , L_r/L_∞ , and F/M , where L_r is the length at entry to the fishery (Beverton and Holt 1966). If this model is used with the 1977 data ($M/K = 4.22$; $L_\infty = 114$ mm), the minimum length to maximize yield-per-recruit will be set at 41 mm. However, based on the estimated values of M/K and L_∞ (M/K

estimated from the M/K versus CPUE regression) in 1986–87, the minimum length should be 67 mm. The fishery operating with a minimum length of 41 mm will have a yield-per-recruit that is 20% lower than the maximum achieved with the 67 mm minimum length under the 1986–87 population parameters.

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