Abstract. – Size-specific fecundities of spiny lobster *Panulirus marginatus* were compared for two time-periods: pre- and early exploitation or "before" (1978–81), and post-exploitation or "after" (1991). Fecundity was further evaluated within each time-period at two collection sites that represented the major lobster fishing grounds (Maro Reef and Necker Island) in the Northwestern Hawaiian Islands. Complementary data on egg size and spawning-frequency index were compared between study sites and time-periods.

Study sites and time-periods had no observable effects on egg size or spawning frequency, and there was no temporal effect on fecundity at Maro Reef. Fecundities at the two sites differed, however; "after" size-specific fecundity was an estimated 16±9% greater than "before" fecundity at Necker Island. Observations suggest that the recent increase in fecundity at Necker Island may reflect a compensatory (density-dependent) response to greater exploitation at this site. Results are discussed in terms of evidence for density-dependent responses in other, exploited spiny lobster stocks.

Comparisons of spiny lobster *Panulirus marginatus* fecundity, egg size, and spawning frequency before and after exploitation

Edward E. DeMartini
Denise M. Ellis

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street
Honolulu, Hawaii 96822-2396

Victor A. Honda

Southwest Enforcement, Pacific Area Office
National Marine Fisheries Service, NOAA
300 Ala Moana Boulevard
Honolulu, Hawaii 96850-0001

The spiny lobster *Panulirus marginatus* (Quoy & Gaimard) is endemic to the Hawaiian Archipelago and Johnston Island (Brock 1973, Uchida et al. 1980). This species supported a major commercial fishery in the main Hawaiian Islands (MHI) prior to the rapid increases in demand after World War II (Uchida et al. 1980). Not until the expansion of the fishery into the Northwestern Hawaiian Islands (NWHI) began in 1977 did the species again support a valuable commercial enterprise, complemented with bycatches of slipper lobster *Scyllarides squamosus* (H. Milne-Edwards) and *S. haanii* (De Haan). A fishery management plan was created in 1983 to regulate the fishery based on minimum size limits and limited entry.

Prior to 1990, annual landings averaged 1–2 million spiny lobster worth US$4–6 million ex-vessel. Beginning in 1990 and continuing until the fishery closure in early 1991, however, landings fell heavily, equaling one-fifth of the long-term average (Landgraf 1991). These decreases reflected real declines in abundance, as both research and commercial catch per trap-haul (CPUE) similarly declined (Landgraf 1991). The present belief is that recent declines in the spiny lobster CPUE reflect a combination of continued, heavy exploitation and the occurrence of a series of poor year-classes, particularly at Maro Reef, one of the two major NWHI fishing grounds (Polovina 1991).

Recent research by Polovina (1989) has indicated that a density-dependent decrease in the size-at-onset of egg production occurred in NWHI spiny lobster from 1977 to 1986–87. Additional types of compensatory responses to lower population densities may be operative and may have a major influence on the dynamics of these lobster populations, but data are lacking (Polovina 1989). Included among these compensatory mechanisms is an increase in size-specific fecundity, a phenomenon suggested for other species of spiny lobsters (Chittleborough 1976 and 1979, Beyers & Goosen 1987, MacDiarmid 1989).

With the *a priori* prediction that size-specific fecundities might have increased for NWHI spiny lobster

during the recent period of low population densities, we initiated a study of its fecundity and related reproductive life history. Prior to our study, little quantitative information existed on the fecundity of this species, and data were limited to the waters off Oahu in the MHI (Morris 1968, McGinnis 1972). Our objective is to compare the size-specific fecundities of NWHI spiny lobster between two time-periods: an early or pre-exploitation (hereafter referred to as "before") period in 1978–81, and a postexploitation ("after") period in 1991, when population densities had declined to a fraction of their pre-exploitation level.

Methods and materials

Specimen collection

Spiny lobster were collected using baited commercial traps at Maro Reef and on the offshore bank of Necker Island, the second of the two major NWHI fishing grounds (fig. 1, Polovina 1989). Lobsters were trapped during multiple cruises aboard chartered commercial vessels and the NOAA ship *Townsend Cromwell* during the summertime (May–August) breeding seasons of 1978–81 (the "before" period) and on a single cruise by the *Townsend Cromwell* during June–July 1991 ("after"). Commercial traps fished for a standard (overnight) soak period were used at each site during both time-periods. Specimens were similarly handled aboard the chartered vessels and the *Townsend Cromwell*.

Sample processing

Lobsters were sexed, carapace length (CL) measured, and the egg developmental stage of egg-bearing ("berried") females scored as either Stage 1 (orange = freshly extruded), Stage 2 (brown = late development), or Stage 3 (white = hatching imminent). The CL, defined as the distance along the middorsal line from the transverse ridge between the supraorbital spines to the posterior margin of the carapace, was measured to the nearest 0.1 mm. Berried female specimens were either processed fresh in the ship's wet lab or flash-frozen (damp) aboard ship for processing ashore.

In the laboratory, brood sizes were estimated using Stage-1 females whenever possible so as to minimize the effect of potential egg loss (Morgan 1972, Annala & Bycroft 1987). The eight pleopods including egg clusters (setae bearing the egg masses) were separated by dissection and placed on absorbent paper towels. Egg clusters were then stripped off the pleopods onto preweighed weigh boats. Each individual female's total egg complement was weighed (damp weight to 0.1 mg) and then reweighed following determination of egg subsample
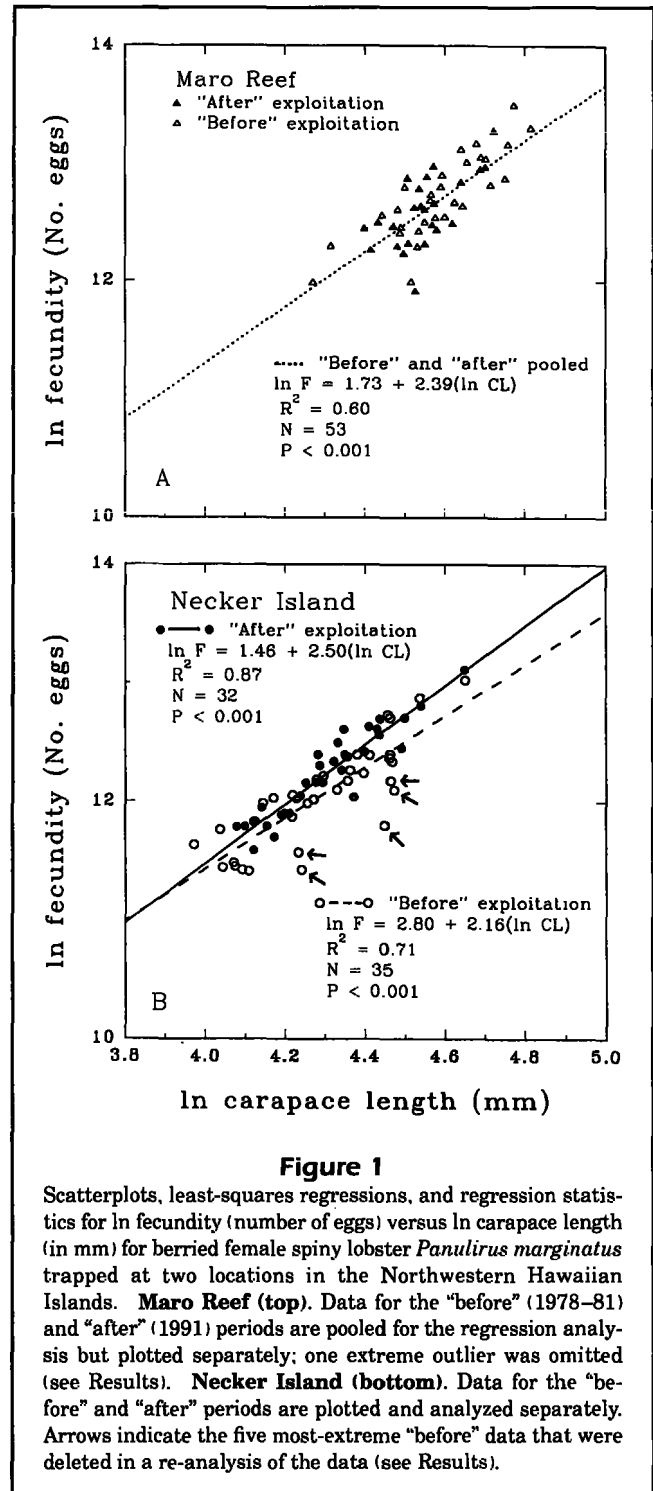

Figure 1

Scatterplots, least-squares regressions, and regression statistics for ln fecundity (number of eggs) versus ln carapace length (in mm) for berried female spiny lobster *Panulirus marginatus* trapped at two locations in the Northwestern Hawaiian Islands. **Maro Reef (top)**. Data for the "before" (1978–81) and "after" (1991) periods are pooled for the regression analysis but plotted separately; one extreme outlier was omitted (see Results). **Necker Island (bottom)**. Data for the "before" and "after" periods are plotted and analyzed separately. Arrows indicate the five most-extreme "before" data that were deleted in a re-analysis of the data (see Results).

weights; these two weighings were then averaged to provide a measure of the total egg mass. Random subsamples comprising a minimum (by weight) of 1% ($\bar{x}=1.5\%$) of the female's total egg mass were weighed (0.1 mg) and later enumerated to estimate fecundity (F_t=total number of eggs) by proportion:

$$F_t = F_s \cdot \left(\frac{W_t}{W_s}\right),$$

where F_s = number of eggs in subsample, W_s = weight of egg subsample, and W_t = total weight of eggs. Some frozen-thawed egg masses were fixed in 4% formaldehyde for 1 month to harden eggs prior to weighing and counting. A single subsample was used to characterize the fecundity of each "before" specimen. Three replicate subsamples were used to estimate the sampling error of "after" fecundity determinations; the three pooled subsamples provided the best estimate of "after" fecundity. Total eggs were counted for one of the "after" specimens to gauge the accuracy of the weighing and counting procedures.

Egg sizes were estimated to complement the fecundity data. For a subset of both "before" and "after" Stage-1 specimens, a minimum of 25 eggs per female were randomly chosen and measured (random axis, at 50×) using a dissecting microscope with calibrated eyepiece micrometer.

Total egg production is the product of the number of eggs produced per spawning (brood size) and the number of spawnings. For females above threshold body sizes at onset of egg production at each of the sites during the two time-periods (Polovina 1989), we indexed spawning frequency based on the relative frequencies of berried (to total) females present in historical catch data of the Honolulu Laboratory. We used records of catches made at Maro Reef and Necker Island on summertime cruises during years within pre- and postexploitation periods when sufficient data were available (1977, 1988–91).

Statistical analysis

Analysis of covariance (ANCOVA, SAS Proc GLM; SAS 1985) was used to compare mean fecundities between sampling periods; CL was used as a covariate to adjust for potential body-size differences between periods. As justified, central tendencies in fecundity were compared between periods ("before," "after") using least-square means (LSM) and their standard errors (SEM). Period and site (Maro Reef, Necker Island) were evaluated as class variables. Student's *t*-test, with degrees of freedom adjusted (as necessary) by Satterthwaite's approximation for unequal variances (Bailey 1981), was used to compare indices of spawning frequency between periods.

Results

Size-fecundity relationships

Paired CL and fecundity data were available for 54 spiny lobster from Maro Reef. At Necker Island, there were 67 analogous data pairs (Appendix A). Over 90% of the "before" specimens had Stage-1 eggs, and Stage-2 eggs were equally distributed among specimens from the two sites. Incidence of Stage-2 eggs appeared higher in the "after" samples from Maro Reef (8/24=33%) than in the analogous samples from Necker Island (3/32=10%). No lobsters with Stage-3 eggs were collected during either time-period. The coefficient of variation [CV=(SD/$\bar{x}$)·100] of the triplicate "after" fecundity estimates was about 2%. The accuracy of the mean of the two weighings of an entire egg mass was within 4% of a total count.

At Maro, slopes were indistinguishable between periods, regardless of whether an obvious outlier (whose residual deviated 8.5% from its predicted value) was included (ln CL × period interaction: $F_{1,50}=0.06$, $P=0.81$) or was deleted from the analysis ($F_{1,49} \leq 0.01$, $P>0.99$). Slopes also were indistinguishable between the two periods at Necker Island ($F_{1,63}=1.17$, $P=0.28$).

Intercepts did not differ between periods at Maro Reef ($F_{1,50}=0.22$, $P=0.64$), but the period (intercept) effect at Necker Island was significant ($F_{1,64}=10.17$, $P=0.002$). Greater size-specific fecundity in the "after" period at Necker Island persisted, even if the five most-extreme "before" values (noted by the arrows in Fig. 1) were deleted and the analysis rerun ($F_{1,59}=4.40$, $P<0.05$). Using all available data, the power (1 minus Type-II error) of the test for period differences at Necker Island was 84%, for a critical Type-I error of 5% ($\alpha_2=0.05$).

CL significantly influenced fecundity at both Maro Reef ($F_{1,50}=70.6$, $P<0.001$; Fig. 1) and at Necker Island ($F_{1,64}=215.6$, $P<0.001$; Fig. 1). After adjustment for period differences in CL, the fecundity of lobsters at Necker Island was an estimated 16±9% greater during the "after" versus the "before" period (LSM±SEM of lnF = 12.224±0.034 and 12.072±0.033, respectively). Unlike the case at Necker Island, mean fecundity at Maro Reef differed only by <3% between the "before" and "after" periods (LSM±SEM = 12.680±0.041 and 12.651±0.046, respectively).

Egg size

The median egg diameters of 22 females collected from Maro Reef and Necker Island during the "before" period were 0.58–0.69 mm. The analogous data for 53 "after" females were 0.61–0.73 mm, with a grand median of 0.66 mm.

Slopes of female body size/egg size (median diameter) relations were indistinguishable between sites (CL × site interaction: $F_{1,51}=0.55$, $P=0.46$). Intercepts also were indistinguishable: egg size was uninfluenced by site ($F_{1,52}=2.75$, $P=0.10$). Carapace length had no

effect when sites were evaluated separately ($F_{1,52}$=0.11, P=0.75). However, female size significantly but weakly (R^2=0.08) affected egg size when data for the two sites were pooled (CL effect: $F_{1,53}$=2.104, P=0.04; median egg diameter=30.2 EPU+0.039 CL_{mm}; N=55; EPU= 0.0197mm).

Spawning frequency

The relative frequency of berried/total adult females collected at Maro Reef and Necker Island during the summer of 1988 (N=3085 adult females), 1990 (1198), and 1991 (1165) was 0.246±3.401 ($\bar{x}$±1SD, N=6 site-year combinations). This index of the spawning frequency of females did not differ (t'=0.01, P>0.9) from 0.230±0.510, the estimated frequency for 3037 females collected during the summer of 1977 (N=2 site-years).

Discussion

Fecundity-body size relations

Exponents of the curvilinear, $F=a \cdot CL^b$, relations observed in this study ranged from 2.16±0.241 (statistically equal to 2.0) to 2.50±0.175 (2.0<b<3.0; Fig. 1). Perhaps both area of egg-bearing surface and volume (female body mass) influence fecundity in this species. Prior data on size-specific fecundity for an Oahu population of *P. marginatus* allow us to estimate the exponent in the equation $F=a \cdot CL^b$ as 2.96±0.31SE (N=11; table XV, Morris 1968).

A variety of linear:cubic relationships are available for other spiny lobster species. The following values of the exponent b in the power equation are either known or calculable for: *Panulirus interruptus* (1.0, Lindberg 1955), *P. homarus* (1.0, Berry 1971), *P. cygnus* (1.0, Morgan 1972); *Jasus verreauxi* (1.0, Kensler 1967), *J. edwardsii* (1.0, Kensler 1968; 3.01, McDiarmid 1989; 2.11–3.75, Annala & Bycroft 1987), *J. lalandii* (1.0, Beyers & Goosen 1987 and Pollock 1987; 3.58, Zoutendyk 1990), *J. tristani* (1.0, Pollock & Goosen 1991), *Nephrops norwegicus* (2.35, Thomas 1964 in Aiken & Waddy 1980). Best fits thus vary from linear to cubic both among species and among geographic populations within species. The only apparent pattern is the generally linear relationship between length and egg number in other *Panulirus* spp.

Parameter interrelations

Although size-specific fecundity clearly changed between the "before" and "after" periods of exploitation for Necker Island lobster, neither egg size nor spawning frequency appeared to differ between the two sampling periods at either study site. Theoretically, size-

specific fecundity might be expected to co-vary with egg size and spawning frequency (Gadgil and Bossert 1970). However, in many organisms, offspring size and number often do not track one another simultaneously or to an equivalent extent (Capinera 1979, Roff 1982). Therefore, our observation that egg size did not co-vary with egg number in *Panulirus marginatus* should not be surprising. Perhaps strong selection for planktonic larvae of relatively invariant body size is typical within particular populations of spiny lobster, even though average egg sizes might differ among populations of some species. This speculation is consistent with our observation that estimated egg volume varied only about 50% among female *P. marginatus* of a large range of body sizes from either site. This value is low compared with those of most marine teleosts (Bagenal 1971).

Site and period comparisons

The site (geographic population) differences observed in this study of NWHI spiny lobster are not without precedent in other spiny lobsters. Annala & Bycroft (1987) and Beyers & Goosen (1987), for example, observed geographic differences in the size-specific fecundities of *Jasus edwardsii* and *J. lalandii*, respectively. For *J. edwardsii*, differences in size-specific fecundity were detected for populations ranging from extreme southern to northern New Zealand (Annala & Bycroft 1987). The spatial scale of the geographic pattern noted by Beyers & Goosen (1987) for *J. lalandii* was 600 km. Approximately 650 km separate Necker island and Maro Reef.

Unlike the Necker Island population, the fecundity of lobsters from Maro Reef was indistinguishable between the two sampling periods. The absence of a period effect at Maro Reef was not due to larger variance at a similar effect size (Cohen 1988); rather, the standard deviation of the residuals of lnF at Maro Reef (0.217) resembled that for Necker Island (0.206). There is the possibility, though, that size-specific fecundity has increased at Maro Reef too, but we were unable to detect it because of an artifact that particularly affected the fecundity estimates of "after" specimens from this site. Many of our "after" specimens from Maro Reef had Stage-2 eggs. Greater egg loss might have occurred during the handling of these specimens, because eggs at later stages of development may be more prone to dislodgement (Annala & Bycroft 1987). Anecdotal observations of the integrity of egg masses of the "after" females from Maro Reef suggest that, even though some additional egg loss might have occurred, it is unlikely to have been sufficient to obliterate an increase in size-specific fecundity of a magnitude similar to that observed for Necker Island lobster.

A significantly greater size-specific fecundity persisted at Necker Island in the "after" period even if the most-likely outliers from the "before" data were excluded from the analysis. This conservative re-analysis strongly suggests that period differences in the size-specific fecundities of Necker Island lobster are real. The magnitude of our best estimate of this difference (16%) further suggests that it represents a biologically meaningful change. A much more extensive series of before-and-after data would be necessary to resolve this issue beyond a reasonable doubt.

On balance, then, our data suggest that the size-specific fecundity of NWHI spiny lobster has increased at Necker Island, but likely not at Maro Reef, following a decade of heavy exploitation at both fishing grounds. Why and how can this be?

The data of Polovina (1989) suggest one possible explanation. The density-dependent decrease in mean carapace length-at-onset of egg production has been proportionately greater for female lobsters at Necker Island (10–15%, 67.8 to 57.9–60.8 mm) than at Maro Reef (6–9%, 74.8 to 68.2–70.5 mm; table 3, Polovina 1989). In 1977, the pre-exploitation densities (catch per trap-haul) of adult lobsters were higher at Necker Island ($\bar{x}\pm$SEM = 5.76±0.75) than at Maro Reef (3.89±0.45); yet by 1986–87, densities had declined more at Necker Island (to 2.14±1.24) than at Maro Reef (2.65±0.67; tables 1&2, Polovina 1989). By decreasing densities to a greater extent (thereby making more shelter or food resources available per lobster), it is possible that the effects of more intense cropping may now extend beyond decreased size-at-maturity to greater size-specific fecundity for Necker Island lobster.

Other factors besides exploitation might be somehow influencing the density and size-specific fecundity of *P. marginatus* at Maro Reef. Relatively few small lobsters were present at Maro Reef compared with Necker island during either of the time-periods used in our fecundity comparison (Polovina 1989; Fig. 1). Even so, disproportionately low recruitment at Maro Reef during 1986–88 might have recently exaggerated long-term baseline differences in the body-size distributions of exploitable *P. marginatus* at the two banks (Polovina & Mitchum 1992). Of the several possible reasons for higher pre-exploitation densities at Necker Island (more productive bottom habitat, fewer adult lobster predators), none is presently substantiated. Studies are in progress to evaluate the quality and distribution of bottom habitats among Maro Reef, Necker Island, and other NWHI lobster grounds.

Density-dependent reproduction in lobsters

Density-dependent changes in egg production have been described or suggested for several other species of spiny

lobster. Examples include changes in the number of spawnings (duration of spawning season) for individual females (Chittleborough 1976, 1979) as well as increases in size-specific fecundities (Thomas 1964, Beyers & Goosen 1987, MacDiarmid 1989) in response to lower population densities or otherwise greater food availabilities. Body size at onset of sexual maturity has responded in qualitatively different fashion to changes in lobster densities among different populations and species of lobsters. Several studies of *Jasus lalandii* (e.g., Pollock & Goosen 1991) have observed smaller body sizes at first maturation in stunted or physiologically stressed, high-density populations. As mentioned previously, Polovina (1989) has demonstrated the opposite response to reductions in adult densities resulting from exploitation. A fundamental, biological difference is whether size-at-maturity is an age- or size-dependent trait for a particular species and population. It is reasonable to expect species differences in the determination of maturation, and comparative studies of the mechanisms regulating the onset of maturation in different spiny lobsters would be informative.

Statistical considerations

Several studies have evaluated, but been unable to detect, geographic variations in fecundity (Thomas 1964, Morgan 1972). The study by Morgan (1972) represents a case in which sample sizes were small and power was low despite nontrivial effect sizes. Future studies of lobster fecundity should report statistical power, especially when tests are unable to reject null hypotheses of no difference among populations.

Acknowledgments

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Appendix A

Body size (carapace length, CLmm) and fecundity (F, no. eggs×10³) data for individual spiny lobster *Panulirus marginatus* collected during "before" and "after" exploitation periods at Necker Island and Maro Reef. Data are ordered by increasing CL within period at each site.

Maro Reef				Necker Island			
Before		After		Before		After	
CL	F	CL	F	CL	F	CL	F
71.5	161	81.3	262	53.1	113	59.1	134
74.7	220	82.6	222	56.7	128	60.3	134
85.0	286	84.2	284	57.0	93	61.6	110
88.3	300	87.4	271	58.6	97	61.6	138
88.8	246	88.2	223	58.8	94	62.8	157
89.0	258	89.6	212	59.9	91	63.7	134
89.9	363	90.6	399	60.9	90	64.9	124
91.4	162	90.7	230	61.8	137	66.1	148
92.8	219	92.2	309	63.0	160	66.6	148
93.1	250	92.4	157	64.7	167	67.5	147
94.5	270	93.3	367	67.9	172	68.6	169
95.9	325	93.7	318	67.9	143	69.2	174
96.1	341	94.5	308	68.9	106[b]	70.2	192
96.8	316	94.6	231	69.5	91[b]	72.0	196
97.1	280	95.2	407	70.5	160	72.4	243
98.5	364	96.4	269	71.6	166	72.7	226
98.8	402	96.8	438	72.1	196	73.2	194
99.4	282	97.1	108[a]	73.4	202	75.3	232
101.9	319	97.5	260	75.9	180	76.1	273
103.7	499	101.4	275	77.8	238	76.8	216
104.0	308	103.7	382	78.0	194	77.3	303
105.2	448	108.9	433	78.5	212	77.4	251
107.6	525	110.2	442	79.8	242	79.1	172
109.0	467	112.4	595	81.2	207	81.4	250
110.3	460			82.4	241	82.3	308
111.6	370			85.6	133[b]	84.0	303
115.7	391			86.3	339	84.5	285
116.4	522			86.6	235	84.6	328
118.2	730			86.7	330	89.2	258
123.2	601			86.7	243	90.0	336
				86.8	194[b]	93.7	368
				87.2	228	104.5	499
				87.5	179[b]		
				93.4	390		
				104.6	454		

[a] Extreme outlier deleted from final analysis.
[b] One of five most-extreme values deleted from conservative re-analysis (see Results).