Temporal changes in population density, fecundity, and egg size of the Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, Northwestern Hawaiian Islands

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Abstract—Fecundity (*F*, number of brooded eggs) and egg size were estimated for Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, Northwestern Hawaiian Islands (NWHI), in June 1999, and compared with previous (1978–81, 1991) estimates. Fecundity in 1999 was best described by the power equations $F = 7.995\,CL^{2.4017}$, where *CL* is carapace length in mm ($r^2=0.900$), and $F = 5.174\,TW^{2.758}$, where *TW* is tail width in mm ($r^2=0.889$) (both $n=40$; $P< 0.001$). Based on a log-linear model ANCOVA, size-specific fecundity in 1999 was 18% greater than in 1991, which in turn was 16% greater than during 1978–81. The additional increase in size-specific fecundity observed in 1999 is interpreted as evidence for further compensatory response to decreased lobster densities and increased per capita food resources that have resulted either from natural cyclic declines in productivity, high levels of harvest by the commercial lobster trap fishery, or both. The density decline is well-documented by a fivefold decrease in commercial catch-per-trap-haul (CPUE) during the late 1980s to early 1990s and by a similar decrease in research CPUE for all-sized (including juvenile) *P. marginatus* through the 1990s. Fecundity increases are consistent with decreases in median body size at sexual maturity, first described from comparisons of 1977–81 and 1986–87 specimens and consistently observed thereafter during the 1990s. Egg size covaried with fecundity; in 1999, individual eggs within broods had a 11% greater mass (15% greater volume) than eggs brooded in 1991. Implications of these observations are discussed in relation to possible future management measures for a commercial lobster fishery in the NWHI. More generally, our findings argue for the need to routinely reevaluate compensatory responses in exploited stocks of lobsters and other resources.

The endemic Hawaiian spiny lobster (*Panulirus marginatus*) has been the principal target of the Northwestern Hawaiian Island (NWHI) commercial trap fishery since the mid- to late 1970s (Uchida and Tagami, 1984; Polovina, 2000). Landings and exvessel (wholesale) value have fluctuated greatly over the years, in part because of annual variations in trapping effort and a 1-yr fishery closure in 1993, but have been generally lower during the 1990s because of declines in oceanic productivity and recruitment and increased exploitation (Polovina and Moffitt, 1995; Polovina et al., 1995). The fishery was closed in 2000 because of increasing uncertainty in the population models used to assess stock status. In December 2000 President Clinton, through Executive Order (EO) 13178 and later through EO 13196, established the Northwestern Hawaiian Islands Coral Reef Ecosystem Reserve which may prohibit commercial lobster fishing in the NWHI for at least 10 years. Annual research surveys of the National Marine Fisheries Service (NMFS), Honolulu Laboratory, have demonstrated a decline (Fig. 1) in spiny lobster density (CPUE, catch-per-trap-haul) at Necker Bank, NWHI, one of the sites at which spiny lobsters have been consistently targeted since about the mid-1970s.

Polovina (1989) first described a density-dependent decrease in median body size at sexual maturity and an increase in asymptotic body size for spiny lobster at Necker Bank, based on a contrast between specimens collected during 1977–81 and 1986–87. DeMartini et al. (1993) observed an increase in size-specific fecundity for specimens collected in 1991, used to further characterize the Necker Bank population's status after-exploitation. Compensatory increases in juvenile growth and survival and increases in size at maturity as responses to decreased density following increased fishery exploitation have been observed for other spiny lobster stocks (e.g. see Pollock, 1995a, 1995b).

In this article, our objectives were to estimate recent (1999) berried female fecundity and egg size for the Hawaiian spiny lobster at Necker Bank and to relate these to prior, analogous estimates for lobsters collected in 1991 and 1978–81, analyzed by DeMartini et al. (1993). We then use the 1999 fecundity estimates and 1999 commercial catch data to characterize recent egg production by the Necker Bank population. We conclude with a brief discussion of the management implications of compensatory reproductive responses by the population.

Methods and materials

All specimens used in this study were trapped from Necker Bank surrounding Necker Island (23°34′N, 164°42′W), NWHI, during the species' mid-spring to mid-summer peak period of egg brooding at mid-archipelago latitudes (Uchida and Tagami, 1984). Specimens

for 1999 were collected on a cruise of the NOAA ship *Townsend Cromwell*. Details of specimen collection and processing of the 1978–81 and 1991 samples are described by DeMartini et al. (1993). The 1999 samples were collected during 9–22 June 1999 from the bank terrace at a median 27-m depth by using molded plastic ("Fathom Plus") traps baited with 1 kg of mackerel (*Scomber japonicus*) and fished with a standard (overnight) soak.

Shipboard processing

Specimens were processed identically to those collected in June 1991. All specimens were processed alive within minutes of trap retrieval. Both carapace length (CL: defined as the straight line distance between the anterior edge of the supraorbital ridge and the posterior edge of the carapace along the dorsal midline) and tail width (TW: defined as the straight line distance across the abdomen at the widest spot between the first and second abdominal segments) of each specimen were measured to 0.1 mm with dial calipers. TW is the present metric of choice for lobster management in the NWHI trap fishery. CL was the metric used to characterize body size in many prior research and management studies of the species, and its measurement was needed for comparison with results of studies made prior to the mid-1980s. Berried (ovigerous) females were scored for egg developmental stage by using a gross visual proxy (brooded eggs noted as either orange or brown in color to the unaided eye). Berried specimens were individually flash-frozen for laboratory evaluation ashore.

Laboratory analyses

Fecundity, here defined in the limited sense of a single brooded egg mass (see Chubb, 2000), was estimated for 5–10 females per 5-mm TW class in order to provide at least 40 total specimens spanning the entire size range for analyses. Except for sample sizes, procedures were identical to those used for the 1991 collection. Only females bearing orange egg clusters with embryos lacking visible melanin pigment (early embryonic development) were considered in order to minimize the probability of physical damage, egg loss, and fecundity underestimation during capture and handling, which is an apparent problem only for broods of heavily pigmented (brown), late-development eggs with soft capsules (DeMartini, unpubl. data). Frozen specimens were thawed overnight at 3°C. All four pairs of egg-bearing pleopods were then removed from the abdomen, gently blotted (damp-dry) on a paper towel, and weighed individually to 0.1 mg on an electric
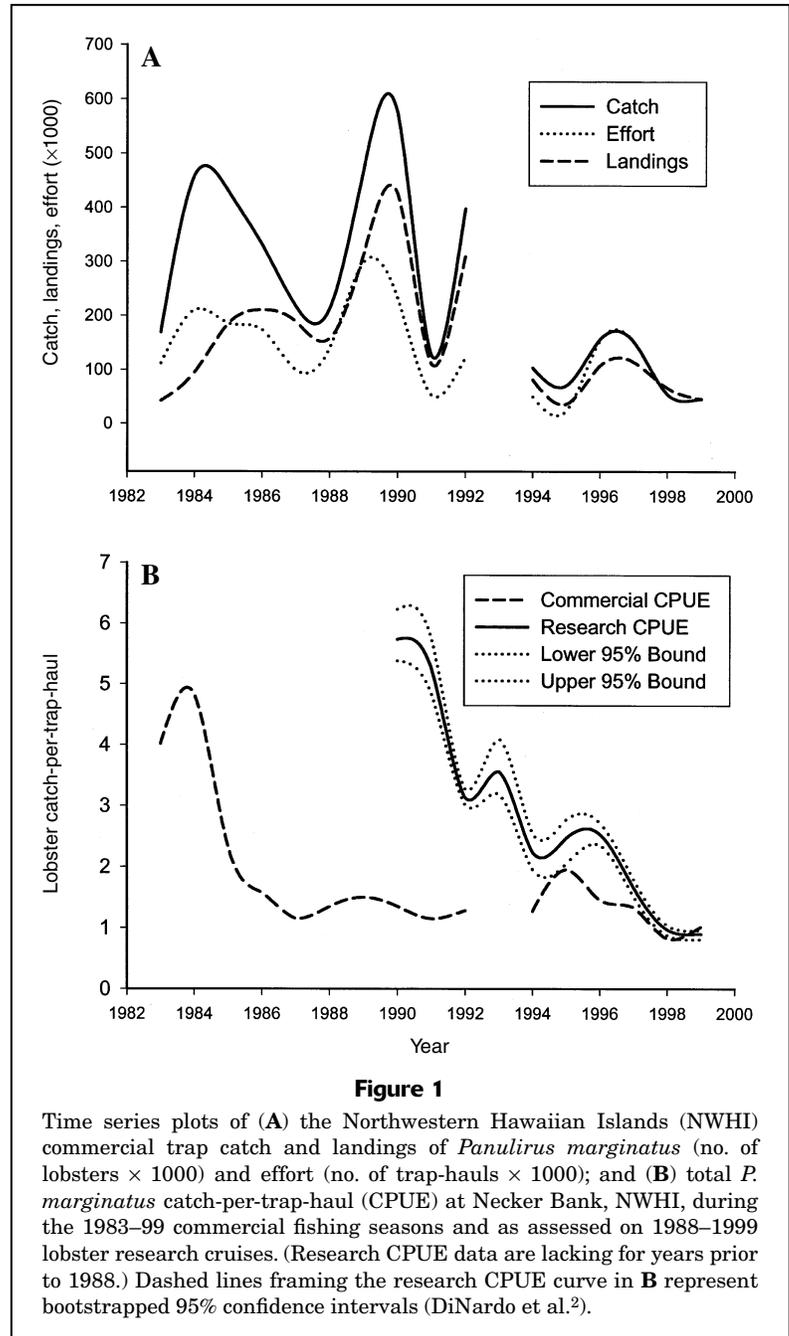

Figure 1

Time series plots of (**A**) the Northwestern Hawaiian Islands (NWHI) commercial trap catch and landings of *Panulirus marginatus* (no. of lobsters × 1000) and effort (no. of trap-hauls × 1000); and (**B**) total *P. marginatus* catch-per-trap-haul (CPUE) at Necker Bank, NWHI, during the 1983–99 commercial fishing seasons and as assessed on 1988–1999 lobster research cruises. (Research CPUE data are lacking for years prior to 1988.) Dashed lines framing the research CPUE curve in **B** represent bootstrapped 95% confidence intervals (DiNardo et al.[2]).

microbalance. Eggs were then carefully teased off pleopod setae with jeweler's forceps and stored after being wrapped in cool, damp paper towels to minimize evaporative weight loss. Individual pleopods were then reweighed and the weight of each pleopod's egg complement was calculated by difference. Three subsamples of 0.1–0.2 g, each comprising about 700–1000 eggs total (about 100 eggs per pleopod, pooled over all 8 pleopods), were next weighed to 0.1 mg, their component eggs counted, and relative fecundity (RF, number of eggs per gram of brooded eggs) was calculated as a simple ratio, with the three subsamples used to calculate a mean and standard error of RF. Fecundity (*F*, defined

Table 1

(**A**) Summary catch statistics (*Townsend Cromwell* research cruise, Necker Bank, June 1999) and (**B–D**) fundamental linear-mass interrelationships for body and egg sizes of female Hawaiian spiny lobster (*Panulirus marginatus*) at Necker Bank, Northwestern Hawaiian Islands.

A Female catch statistics	Total		Berried		$TW_{\text{all females}}$		TW_{berried}	
	n	%	*n*	%	median	range	median	range
	834	54.6	350	42.0	50.1	24–72	51.1	38–72

B Relation of tail width to carapace length and vice versa; model: $Y = aX + b$

$$TW = 0.6087\,CL + 4.44 \text{ and } CL = 1.5772\,TW - 4.00, \qquad [r^2=0.963, n=825, P<0.001]$$

where TW = tail width in mm, CL = carapace length in mm, and *a* and *b* are fitted constants.

C Relation of body weight to carapace length; model: $Y = aX^b$

$$BW = 0.00090\,CL^{2.9952}, \qquad [\text{range: } 51.9–114.7 \text{ mm CL}, n= 197, P<0.001]$$

where BW = total body weight in g, and CL = carapace length in mm, for unberried females (source: Uchida and Tagami [1984]).

D Relation of egg weight to egg diameter; model: $Y = aX^b$

$$EW = 0.3985\,ED^{2.2472}, \qquad [r^2=0.833, n=40, P<0.001]$$

where EW = egg weight in 0.001 mg, and ED = egg diameter in mm.

as the total number of pleopod-brooded eggs) was calculated as the product of mean RF and total weight of the brooded egg mass. Pilot tests indicated that this procedure estimated *F* with coefficients of variation (CV, SD/mean × 100%) consistently <5%. Subsamples of 25 eggs were randomly taken from each female's total egg complement and the diameter of individual eggs were measured (random axis) at 500× magnification by using a dissecting microscope and an optical micrometer. Average individual egg weight was also independently derived as the ratio of the weight to numbers of eggs present in the parent sample.

Statistical analyses

Relations of female body size to fecundity and body size to egg size were evaluated for the 1999 samples by using both linear and nonlinear least squares procedures (proc REG, proc NLIN) of PC SAS for Windows v. 6.12 (SAS Institute, 1990a, 1990b). Analysis of covariance (ANCOVA; proc GLM; SAS Institute, 1990c; Chubb, 2000) was used to compare size-specific fecundity estimates of Necker Bank *P. marginatus* among the three exploitation periods: 1978–81, 1991, and 1999. Subseasonal variation within spawning seasons was controlled by the aforementioned restriction on month of specimen collection, and single collections were assumed to provide accurate characterizations within exploitation periods. Fecundity data used to characterize the 1978–81 and 1991 periods at Necker Bank are listed in Appendix A of DeMartini et al. (1993). Analogous comparisons of size-specific egg sizes were limited to the 1991 and 1999 periods because no data on variance of egg sizes were available for the 1978–81 samples

(DeMartini et al., 1993). Body-size–fecundity relations were allometric, hence log-linear (see Somers, 1991); natural logarithms were used for ANCOVAs and regressions of log-linear relations.

An index of reproductive potential (IRP; Kanciruk and Herrnkind, 1976) was computed for the 1999 specimens in order to determine the size classes of females that contributed most to population egg production. The IRP was constructed by using data for female *P. marginatus* caught by the commercial fishery at Necker Bank during 1999, collected by several contracted fishery observers.

Results

Fecundity and egg size of lobsters in 1999

Fecundity A number of the female *Panulirus marginatus* trapped on the research cruise at Necker Bank during June 1999 were berried (Table 1). The estimated fecundity of 40 females, spanning 54.3 to 105.4 mm CL (39.3–67.4 mm TW, see CL-TW relation; Table 1), ranged more than fivefold, from 109,865 to 590,530 eggs (Appendix A). Fecundity was positively and nonlinearly related to TW (Fig. 2) and CL and best described by the power equations $F = a\,TW^b$ and $F = a\,CL^b$, respectively, as

$$F = 5.1743\,TW^{2.7580}, \qquad [r^2=0.889]$$

and

$$F = 7.9952\,CL^{2.4017}$$
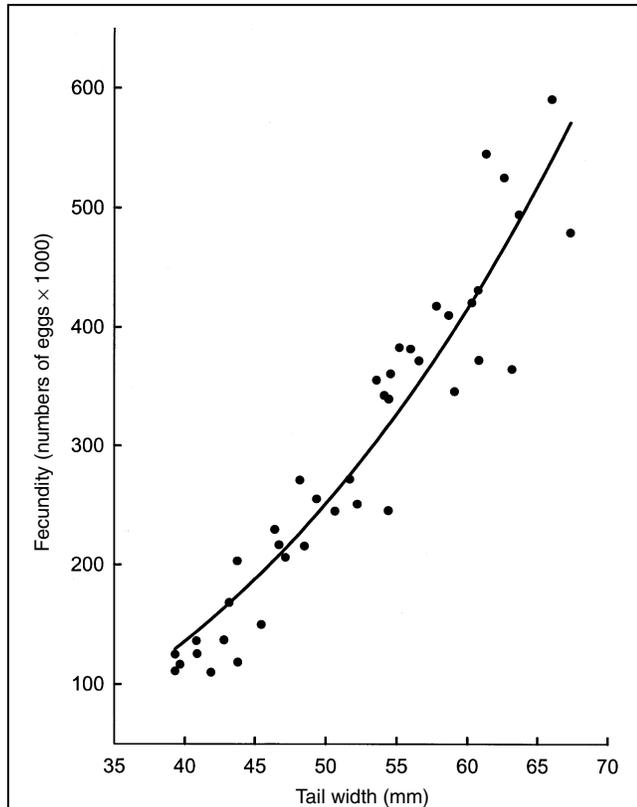$$[r^2=0.900, \text{ both } n=40, P<0.001.]$$

Figure 2

Scatterplot and fitted power curve describing the relation between fecundity (no. of brooded eggs×1000) and tail width (TW, in mm) for *Panulirus marginatus* collected at Necker Bank, 1999.
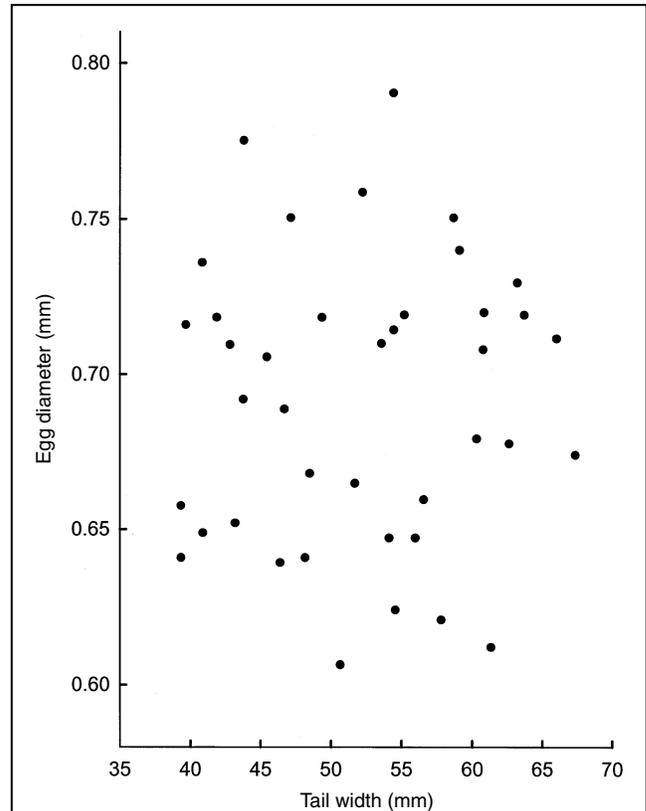

Figure 3

Scatterplot describing the relation between egg diameter (mm) and tail width (TW, in mm) for *Panulirus marginatus* collected at Necker Bank, 1999.

The standard errors of *b* were 0.1787 and 0.1472, respectively. A log-linear fit of the F-CL data (LnF=2.5533 LnCL +1.3977) was nominally inferior (r^2=0.886) to the curvilinear fit but was required for the general linear model used in the ANCOVA comparisons that follow below. Fecundity subsamples averaged 1.5 ±0.14(SE)% of total brooded egg mass weight. Brooded egg masses weighed an average 51.4 g and ranged from 15.8 to 109.2 g. CVs of the three replicate estimates of RF averaged 1.2 ±0.11%. Mean RF was 5882 ±160(SE) eggs per g of brooded eggs and ranged nearly twofold from 4030 to 7930 eggs per g of eggs among the 40 females. Based on the aforedescribed nonlinear best fit, the fecundity of the median-size (53.8 mm TW, 80.9 mm CL) female caught at Necker Bank in 1999 by the commercial trap fishery was an estimated 306,400 ±90,200 (95% CI) eggs.

Egg size   The mean (±SE) diameter of early-stage eggs carried by the 40 berried females was 0.69 ±0.007 mm, with a range of 0.61 to 0.79 mm. Analogous median (25th, 75th percentile) diameters were 0.70 (0.65, 0.72) mm. The corresponding egg weights were 0.17 ±0.005 and 0.18 (0.15, 0.20) mg (range: 0.13–0.25 mg). Individual egg size

(diameter: Fig. 3; weight) was unrelated (both *P*>0.63) to female body size (TW). Individual egg weight was a power function of egg diameter (Table 1).

Temporal comparisons of fecundity and egg size

Fecundity   Size-specific fecundities differed among the three periods, and body-size–adjusted means differed for each period (Table 2, Fig. 4). Size-adjusted mean fecundity in 1999 was 18% greater than in 1991, which in turn was 16% greater than during 1978–81. Lobster in 1999 thus exhibited a cumulative 36% increase in size-specific fecundity over that described for lobster collected during 1978–81. The statistical power (1 minus *β*, where *β* is the probability of making a type-II error) to detect an effect size equal in magnitude to the changes observed between 1978–81, 1991, and 1999 was estimated as >97% at *α* = 0.05.

Egg size   Brooded eggs on average were about 5% greater in diameter (equivalent to 15% greater volume assuming the volume of a sphere, *V*=4/3 πr^3) and were 11% heavier in 1999 compared to 1991 (Table 3). The precision of our

Table 2

(**A**) ANCOVA and (**B**) component least squares regression statistics for log-linear (LnY = ln$a$ + bLnX) relations of fecundity (F) to carapace length (CL) for *P. marginatus* caught at Necker Bank during three periods: 1978–81, 1991, and 1999. Natural logs are used throughout. Underlines illustrate that the least-square means for each period differ from one another. MSE = mean square error.

A ANCOVA model: LnF = LnCL + period (r^2=0.855; root MSE=0.1843)

Factor	df	MS	F	P
Model	3	6.82	199.6	0.0001
LnCL	1	17.16	502.1	0.0001
Period	2	0.87	25.5	0.0001
LnCL × period (P=0.27—ns; not included in final model)				
Error	105	0.03		
Total	108			

$$\frac{12.426 > 12.284 > 12.119}{1999 \quad > 1991 \quad > 1978{-}81}$$

B Regression models: LnY = Lna + bLnX

1978–81　　LnF = 2.7994 + 2.1569 LnCL,
　　　　　　r^2=0.708,
　　　　　　n=35,
　　　　　　P<0.001,
　　　　　　SE a=1.0367,
　　　　　　SE b=0.2412

1991　　　LnF = 1.5859 + 2.4778 LnCL,
　　　　　　r^2=0.881,
　　　　　　n=34,
　　　　　　P<0.001,
　　　　　　SE a=0.6934,
　　　　　　SE b=0.1607

1999　　　LnF = 1.3977 + 2.5533 LnCL,
　　　　　　r^2=0.886,
　　　　　　n=40,
　　　　　　P<0.001,
　　　　　　SE a=0.6452,
　　　　　　SE b=0.1485

Table 3

(**A**) ANCOVA and (**B**) component least squares regression statistics for linear relations of egg diameter (ED, in eye-piece units, × 0.020=mm) to carapace length (CL, mm) of *P. marginatus* caught on research cruises to Necker Bank during 1991 and 1999. See Table 2 caption for additional details.

A ANCOVA model: $ED = CL$ + period (r^2=0.142; root MSE=2.193)

Factor	df	MS	F	P
Model	2	27.36	5.69	0.005
CL	1	3.33	0.69	0.41
Period	1	46.85	9.74	0.003
CL × period (P = 0.81—ns; not included in final model)				
Error	69	4.81		
Total	71			

$$\frac{0.691 > 0.658}{1999 \ > 1991}$$

B Regression models: $ED = a + b\,CL$

1991　　　ED = 31.1646 + 0.0230 CL,
　　　　　　r^2=0.021,
　　　　　　n=32,
　　　　　　P<0.001,
　　　　　　SE a=2.1224,
　　　　　　SE b=0.0282

1999　　　ED = 33.5760 + 0.0128 CL,
　　　　　　r^2=0.006,
　　　　　　n=40,
　　　　　　P<0.001,
　　　　　　SE a=2.1768,
　　　　　　SE b=0.0274

measurements was sufficient for the observed change in egg diameter to have had an 87% chance of being detected at α = 0.05.

Individual and population egg production

Based on the IRP of Kanciruk and Herrnkind (1976), most egg production by the Necker Bank population of *P. marginatus* in 1999 was by small adults (<60 mm TW) that now dominate the population (Table 4). Large adults (>60 mm TW), although highly fecund, are now too rare to contribute substantially to total population egg production (Table 4).
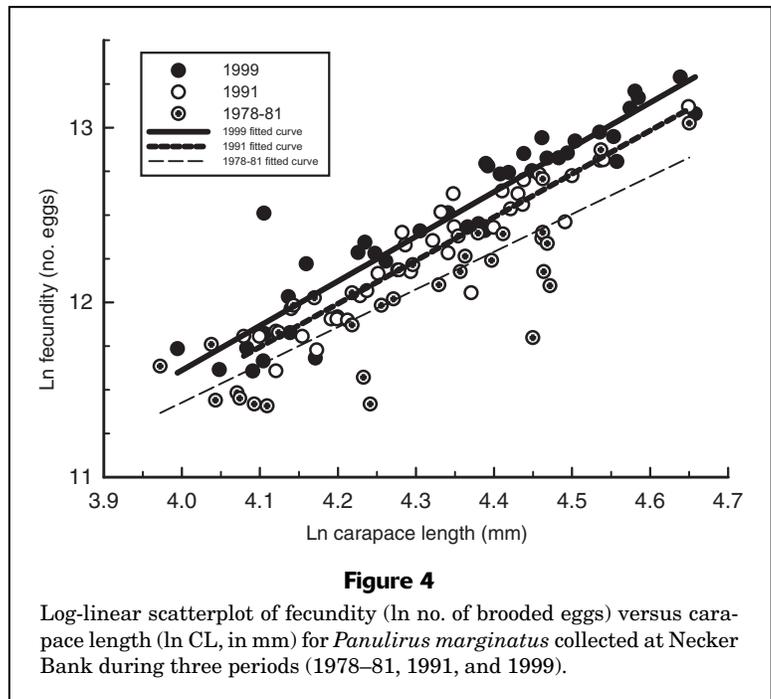
Discussion

Size-specific fecundity and egg size

Fecundity　The initial 16% increase in body size-specific fecundity between 1978–81 and 1991 occurred while commercial CPUE decreased fivefold. Unlike commercial data, research CPUE data were collected at fixed stations (including juvenile habitat), were uninfluenced by increased catchability (the targeting of larger adult lobster in more productive habitats by commercial fishermen), and continued to show a decline of similar magnitude during the 1991–99 period when size-specific fecundity increased an additional 18% (Fig. 1B). Thus both observed fecundity responses occurred simultaneously with declining lobster densities. The cumulative 36% increase in size-specific fecundity observed for Necker Bank *P. marginatus* over a >20-yr period of exploitation is not unreasonable given the evidence for concurrent, compensatory declines in body size at sexual maturity in this population (Polovina,

1989; DeMartini et al.[1]). Density-dependent changes in somatic growth, survival rates, and body sizes at sexual maturity have been described for numerous other palinurid species (Pollock, 1995a, 1995b). At least one case study provides further evidence for reproductive compensation. Chittleborough (1979) documented a decreased interval between broods as a response to increased exploitation in the Western Australian rock lobster, *P. cygnus*. Prior to the present study, the study of De-Martini et al. (1993) was the only published record of changes in size-specific fecundity in a spiny lobster, perhaps attributable to density declines resulting from exploitation, although perhaps only reflecting natural interannual variation independent of fishing (Pollock, 1995b).

The fecundity update for 1999 in this article further supports DeMartini et al.'s (1993) original interpretation of an increase in size-specific fecundity as a density-dependent response at lower population densities. Other data on body size at sexual maturity for the period 1988–99, to be reported elsewhere (DeMartini et al.[1]), extend the temporal pattern of smaller body size at sexual maturity first documented during 1986–87, after 10 years of exploitation, by Polovina (1989). The observed decrease in size at maturity could have been caused by slower growth (Pollock, 1995a) resulting from lower levels of oceanic productivity (Polovina et al., 1994, 1995). However, if smaller size at maturity has been a proximal response to decreased rather than increased per capita food availability, it is inconsistent with the simultaneous increases in size-specific fecundity and egg size which have occurred. Evidence for changes in the nutritional status of *P. marginatus* at Necker Bank during 1991–95 is equivocal (Parrish and Martinelli-Liedtke, 1999). Resolution of whether the lower densities of spiny lobsters at Necker Bank have resulted from natural declines in productivity, increased fishery exploitation (or both) would require comparative evaluations for lobsters collected from fished as well as unfished control areas at the bank; unfortunately, as of 1999 unfished lobster habitat at Necker Bank does not exist.

The observed increase in size-specific reproductive output of *P. marginatus* probably has been a phenotypic response to lower densities and higher per capita food availabilities at Necker Bank. It is unlikely, given the 3-yr generation time of *P. marginatus* (Uchida and Tagami, 1984) and relatively short (20+ yr) period over which the responses have occurred, that a genetic, rather than phenotypic, dynamic has been involved. More extensive comparisons of the egg productions of *P. marginatus* populations among Necker and other NWHI banks differing in natural and fishery-induced densities would be necessary

Figure 4

Log-linear scatterplot of fecundity (ln no. of brooded eggs) versus carapace length (ln CL, in mm) for *Panulirus marginatus* collected at Necker Bank during three periods (1978–81, 1991, and 1999).

to further distinguish natural variation from fishing effects. Complete resolution of this issue would require quantitative comparisons of growth rates and ages at maturity for a lengthy series of year classes of *P. marginatus* at Necker Bank and elsewhere.

Egg size Our data demonstrate that egg size can vary substantially among same-size *P. marginatus* collected during the midpoint of a single breeding season, as does fecundity among same-size females. It should not be surprising, then, that average population egg size has covaried with fecundity, even if egg size is body-size independent. The observed change in mean egg size between 1991 and 1999 could not have been due to either developmental or subseasonal changes because we evaluated egg size by consistent methods, using only early-development broods collected during the month of June. It is possible, although unlikely, that the larger eggs (hence larvae) produced in 1999 were somehow of inferior quality and had lower hatching success and poorer subsequent survival.

Intraspecific variation in egg size has rarely been described in spiny lobsters (Pollock, 1995a, 1997). Annala (1991) suggested that egg size increases with body size for a cold-temperate species, *Jasus edwardsii*, from mainland New Zealand. Egg size is unrelated to female body size in tropical *Panulirus argus* (Fonseca-Larios and Briones-Fourzan, 1998). In one particularly detailed study of the egg size dynamics of a small-bodied Caribbean palinurid, *P. guttatus*, Briones-Fourzan and Contreras-Ortiz (1999) detected no relation of egg size to female body size, even though egg size varied nearly twofold among females ranging over twofold in carapace length.

Few studies have documented temporal changes in egg size for palinurid lobsters. A seasonal decline in egg size

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[1] DeMartini, E. E., R. B. Moffttt, and P. Kleiber. 2002. Unpubl. data. Honolulu Laboratory, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.

Table 4

Index of reproductive potential (IRP) calculated for female *Panulirus marginatus* caught by the Northwestern Hawaiian Islands commercial trap fishery at Necker Bank in 1999. IRP = $(A×B×C)/D$, where A= proportion of total females in each 1-mm TW class ($×100\%$), B = proportion of berried females per 1-mm class ($×100\%$), C = estimated brood size of the median-size female in each class ($×10^3$ eggs), and D = a constant (0.015788) used to standardize the most productive size class to 100% (Kanciruk and Herrnkind, 1976). E = % of total egg production; $F = E/A$, a class-specific measure of egg productivity.

TW class (mm)	Total no. of females	No. of berried females	A	B	C	IRP	E ($×10^3$)	F ($×10^3$)
<39	27	1	0.42	0.43	114	0.00	0.03	35.17
39–40	20	4	0.32	0.17	131	0.05	0.13	40.59
40–41	28	5	0.45	0.21	140	0.09	0.20	43.48
41–42	32	4	0.51	0.17	150	0.08	0.24	46.51
42–43	41	8	0.66	0.34	160	0.23	0.33	49.67
43–44	52	10	0.84	0.43	171	0.39	0.44	52.96
44–45	74	20	1.19	0.85	182	1.17	0.67	56.38
45–46	117	30	1.88	1.28	193	2.95	1.13	59.95
46–47	152	40	2.44	1.71	205	5.43	1.55	63.65
47–48	233	81	3.74	3.46	218	17.88	2.53	67.50
48–49	301	100	4.83	4.27	231	30.20	3.46	71.49
49–50	358	132	5.75	5.64	244	50.15	4.35	75.63
50–51	453	178	7.28	7.61	258	90.43	5.82	79.92
51–52	442	176	7.10	7.52	272	92.09	5.99	84.36
52–53	441	171	7.08	7.31	287	94.13	6.30	88.96
53–54	425	170	6.83	7.26	302	95.00	6.40	93.71
54–55	363	147	5.83	6.28	318	73.84	5.75	98.62
55–56	395	174	6.34	7.44	335	100.0	6.58	103.7
56–57	367	159	5.89	6.79	352	89.19	6.42	108.9
57–58	297	117	4.77	5.00	369	55.74	5.45	114.3
58–59	313	119	5.03	5.08	387	62.66	6.03	119.9
59–60	250	88	4.02	3.76	405	38.78	5.04	125.6
60–61	227	99	3.65	4.23	425	41.48	4.80	131.5
61–62	194	84	3.12	3.59	444	31.47	4.29	137.6
62–63	142	57	2.28	2.44	464	16.34	3.28	143.9
63–64	119	37	1.91	1.58	485	9.29	2.87	150.3
64–65	105	36	1.69	1.54	507	8.32	2.65	156.9
65–66	64	27	1.03	1.15	529	3.97	1.68	163.7
66–67	53	18	0.85	0.77	551	2.29	1.45	170.7
67–68	43	18	0.69	0.77	574	1.93	1.23	177.9
68–69	33	14	0.53	0.60	598	1.20	0.98	185.3
69–70	26	6	0.42	0.26	622	0.42	0.80	192.8
70–71	16	5	0.26	0.21	647	0.23	0.52	200.6
71–72	7	2	0.11	0.09	673	0.04	0.23	208.5
72–73	9	1	0.14	0.04	699	0.03	0.31	216.7
>73	7	2	0.11	0.09	782	0.01	0.08	242.3
Total	6226	2340	100.00	100.00		100.00		

for all-sized females has been observed in two Caribbean species, *Panulirus inflatus* (Gracia, 1985) and *P. argus* (Fonseca-Larios and Briones-Fourzan, 1998). Briones-Fourzan and Contreras-Ortiz (1999), however, could detect no difference in egg size among *P. guttatus* sampled during three consecutive years. Mean egg size declined within the spawning season, but this decline reflected a loss in mass caused by embryonic development within individual eggs rather than the production of smaller eggs later in the breeding season (Briones-Fourzan and Contreras-Ortiz,

1999). Pollock (1995c) noted that *P. guttatus* produces unusually few, but large eggs for a shallow-water tropical palinurid.

Using the CL-to-body-weight regression listed in Table 1, we estimated an inverse index of egg size (Pollock, 1997) for Necker Bank *P. marginatus* in 1999 that was 660 eggs per g total body weight. Such small eggs are typical within the derived lineage of shallow-water, subtropical and tropical members of the genus (Pollock, 1997).

We could find no other studies documenting changes in egg size as a response to density fluctuation in palinurid lobsters. Prior to the mid-1990s, information on temporal and size-related patterns of fecundity and egg size were largely restricted to cold- and warm-temperate members of the genus *Jasus* and *Panulirus* (Pollock, 1995c, 1997). Perhaps egg size, like size-specific fecundity, is phenotypically labile in tropical reef species of the genus *Panulirus* for which high and variable predation pressure makes such plastic responses adaptive. More research on size-specific, individual reproductive output is needed for *P. marginatus* and other tropical reef species of spiny lobsters.

It is unknown whether egg size lability in *P. marginatus* has a genetic or environmental basis. One could perhaps evaluate this for individual females by repetitively measuring egg subsamples from successively brooded egg masses of berried tagged and recaptured females. Fixed but differing egg sizes among individual females would be consistent with a genetic basis. On the other hand, changes in the size of eggs produced by the same individual female in successive broods would suggest that environmental factors are involved.

Management implications

One of our observations has major relevance to the management of *P. marginatus* in the NWHI lobster fishery. Based on the IRP of Kanciruk and Herrnkind (1976), egg production by the Necker Bank population of *P. marginatus* was dominated by the 50–57 mm TW classes in 1999, which together contributed >43% to population egg production (Table 4). Even though each large (>60 mm TW) individual produces a disproportionately great number of eggs, large females are now so poorly represented in the population that they no longer drive population egg production (Table 4). The eggs produced by smaller (50–57 mm TW) females are more important to the population now than before exploitation. In 1996 a "retain all" size policy was established for the commercial fishery, replacing a 50-mm-TW minimum size limit used previously, in part because of the high mortality of discarded lobsters (DiNardo et al., 2002). If a commercial lobster fishery with a minimum size limit were to be reinstated in the NWHI, a minimum size larger than the previous (50 mm TW) should be considered. Our findings on the size distribution of population egg production indicate that smaller adult females, which now produce most of the population's eggs, should be further protected, perhaps by using larger escape vents in traps. Doing so would increase total population egg production and might assist in countering recruitment overfishing (Botsford, 1991; Pollock, 1993). *Panulirus mar-ginatus* production at Necker Bank historically and presently dominates archipelago-wide production by the species; this production is supported by empirical catch data (DiNardo et al.[2]) as well as modeling of its recruitment dynamics (Polovina et al., 1999). Augmenting egg production by the Necker Bank population might significantly bolster stock-wide productivity. The body size distribution of egg production by *P. marginatus* at other NWHI banks is presently unknown, however, and egg production by large females elsewhere possibly could partly offset the deficit in production at Necker. Our observations on the size distribution of egg production at Necker Bank nonetheless merit important consideration for setting size limits for spiny lobster management.

By necessity we calculated the IRP assuming that all size classes produced the same (single) brood per spawning period because data on size-specific spawning frequency were lacking. We caution that, if females >60 mm TW (whose size-specific egg production is greatest) produce broods more frequently than smaller females (Lipcius, 1985), we have proportionately underestimated the contribution of larger females to population egg production.

Individual *Panulirus marginatus* of all sizes likely produce multiple broods per individual spawning season, based on the protracted period during which females are berried (Uchida and Tagami, 1984; Polovina and Moffitt, 1995) and the occasional presence of new, intact (unused) spermatophore plates on spent females (unpubl. data, Honolulu Laboratory, NMFS). (The latter observation in fact suggests that Necker Bank *P. marginatus* can produce more than one brood per molt [like *P. argus*; Sutcliffe, 1953].) There are no time-series growth-rate data available with which to evaluate whether females of a given body size might now be producing larger broods at more frequent intervals than previously. If females are now growing faster, it is likely that the rates of both molting and brood production are now greater. Accurate estimates of individual spawning frequencies and how these might differ among females of varying body sizes, would be needed to fully describe the compensatory increase in reproduction which has occurred for the Necker Bank population of *P. marginatus*.

Acknowledgments

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[2] DiNardo, G. T., W. R. Haight, and J. A. Wetherall. 1998. Status of lobster stocks in the Northwestern Hawaiian Islands, 1995–97, and outlook for 1998. Southwest Fish. Sci. Cent. Admin. Rep. H-98-05, 35 p. Honolulu Laboratory, Southwest Fish.Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.

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Appendix A

Two body size metrics (carapace length, CL; tail width, TW) and fecundity (F, number of brooded eggs) data for 40 individual spiny lobster (*Panulirius marginatus*) collected during 1999 at Necker Bank, Northwestern Hawaiian Islands. Data are ordered by increasing CL.

CL	TW	F
54.3	39.3	124,860
57.3	39.3	110,815
59.3	40.9	125,324
59.8	41.9	109,865
60.6	39.7	116,385
60.6	48.2	271,153
60.7	40.8	136,116
62.6	43.2	168,210
62.7	42.8	136,786
64.0	43.8	203,026
64.8	43.8	118,303
66.6	45.5	149,753
68.4	46.7	216,477
69.0	46.4	229,561
69.9	48.5	215,502
70.9	47.2	206,099
74.1	50.7	245,037
76.8	51.7	271,830
78.8	52.2	250,885
79.8	49.4	255,240
80.5	54.4	245,510
80.6	54.6	360,611
80.8	53.6	355,366
82.1	54.5	339,466
83.0	54.2	342,488
84.6	56.0	381,494
85.5	59.1	345,755
86.6	57.8	417,662
87.2	56.6	371,609
88.5	60.8	372,148
89.5	55.2	382,667
90.4	58.7	409,864
93.2	60.8	431,027
94.9	60.3	420,458
95.3	63.2	364,508
97.0	63.7	494,282
97.6	61.3	545,059
98.0	62.6	525,173
103.4	66.0	590,530
105.4	67.4	479,197