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FECUNDITY AND EGG SIZE OF *SCYLLARIDES SQUAMMOSUS* (DECAPODA: SCYLLARIDAE) AT MARO REEF, NORTHWESTERN HAWAIIAN ISLANDS

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ABSTRACT

The body size-specific fecundity of *Scyllarides squammosus* is described based on the numbers of eggs carried externally on the pleopods of "berried" (ovigerous) females collected during June 1999, at Maro Reef, located mid-chain in the Northwestern Hawaiian Islands (NWHI). Fecundity was positively and nonlinearly related to "tail" (abdomen) width (TW); fecundity ranged from 53,807 to 227,489 eggs in 43 females spanning 52–77-mm TW. The smallest berried female encountered at Maro Reef in 1999 was larger than the smallest berried female observed during most previous years' (1986–97) lobster research cruises. Fecundity of the median-sized (60-mm TW) female caught at Maro Reef in 1999 by the NWHI commercial lobster trap fishery was an estimated 89,660 ± 3,980 (SE) eggs. Brooded eggs averaged 0.67 ± 0.006-mm diameter (range: 0.61–0.77 mm), equivalent to 0.17 and 0.13–0.24 mg, respectively. Egg size was unrelated to female body size. Fecundity and egg size estimates and their body size relationships are briefly compared with other scyllarid lobsters.

Compared to palinurid (spiny) lobsters, sparse fecundity or other reproductive biology data exist for scyllarid (slipper) lobsters (Stewart and Kennelly, 1997). The few exceptions are estimates of fecundity for scyllarids of the Mediterranean Sea (*Scyllarides latus* (Latreille, 1803): Almog-Shtayer, 1988 (cited in Spanier and Lavalli, 1998)) and the oceanic Azores Islands (Martins, 1985); the Indian Ocean (*Thenus orientalis* (Lund, 1793): Hossain, 1979; Jones, unpubl. Ph.D. thesis); and the southwestern Pacific Ocean off Australia (*Ibacus peronii* Leach, 1815: Stewart and Kennelly, 1997). No published data on fecundity currently exist for *Scyllarides squammosus* (H. Milne Edwards, 1837), a scyllarid abundant on insular banks of the Northwestern Hawaiian Islands (NWHI) in the central North Pacific Ocean.

Scyllarides squammosus has recently become an important, targeted component in the NWHI commercial lobster trap fishery, comprising 63–64% of the numbers of lobsters landed in 1998–99 and 44% of ex-vessel revenue in the1998 fishery (Kawamoto and Pooley, in press). Previously dominated by catches of the endemic Hawaiian spiny lobster *Panulirus marginatus* (Quoy and Gaimard, 1825), the NWHI lobster fishery increasingly needs explicit assessment and management of *S. squammosus*. Key life-history data needed for stock assessment include size and age at sexual maturity, growth rate, and the numbers (fecundity) and sizes of eggs produced by females of different sizes and ages.

Our objectives in this note are to provide quantitative estimates of size-specific fecundity and egg size for *Scyllarides squammosus* at Maro Reef, a major NWHI trapping grounds at which this species is targeted, as part of the suite of input parameters needed for its stock assessment.

MATERIALS AND METHODS

Field Collection.—All specimens used in this study were trapped at Maro Reef (25°25′N, 170°35′W) during June 25–30, 1999 (following the peak breeding period of *S. squammosus* in May–June), on an annual lobster cruise of the U.S. National Oceanographic and Atmospheric Administration (NOAA) ship *Townsend Cromwell*. Specimens were collected from bank terraces at 13–37-fm (median = 15-fm) depths using molded-plastic ("Fathom Plus") traps baited with 1 kg of mackerel, fished with a standard (overnight) soak.

Shipboard Processing.—All specimens were processed alive within minutes of trap retrieval. 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 was measured to 0.1 mm using dial calipers. "Berried" (ovigerous) females were scored for egg developmental stage 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 was estimated for a maximum of 10 females per 5-mm TW class. Fecundity estimates were based on the numbers of pleopod-brooded eggs; no attempt was made to estimate ovarian fecundity. Only females bearing orange egg clusters whose embryos lacked visible melanin pigment ("early" embryonic development) were considered. Doing so minimized the probability of physical egg loss during capture and handling, and consequent fecundity underestimation, which is an apparent problem only for broods of heavily pigmented ("brown"), late-development eggs with soft capsules (E. DeMartini, unpublished observation). 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 microbalance. Using jeweler's forceps, eggs were then carefully teased off pleopod setae and stored 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 calculated by difference. Three subsamples of 0.1–0.2 g, each comprising approximately 700–1,000 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 (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 relative fecundity. Total fecundity (defined as the total number of pleopod-brooded eggs) was calculated as the product of mean relative fecundity and total weight of the brooded egg mass. Pilot tests indicated this procedure yielded total fecundity estimates whose coefficients of variation (CV, SD/mean × 100%) were consistently less than 5%. Subsamples of 25–100 eggs (n = 25 in 41 of 43 cases, with 75 and 100 eggs measured in two cases in which the median was indistinct based on 25 measurements) were randomly taken from each female's total egg complement, and the diameter of individual eggs measured (random axis) at 500× magnification 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. No fresh eggs were available for relating weights of fresh and frozen-thawed eggs. Differences between fresh and frozen-thawed weights should have been minimal because only early development eggs were used, and these were thawed slowly while under refrigeration to avoid the rupturing of capsules. Nonetheless, egg weights should be considered approximations which at least provide quantitative bases for future spatial and temporal comparisons among estimates made using the same method.

Analyses.—Female body size-fecundity and body size-egg size relationships were evaluated using both linear and nonlinear least squares procedures (REG, NLIN) of PC SAS for Windows v. 6.12.

Results

Size-specific Fecundity

Of 2,450 total *Scyllarides squammosus* trapped at Maro Reef during June 25–30, 1999 (Table 1), the fecundity of 43 ovigerous females spanning 52.4–76.8-mm TW ranged from an estimated 53,807 to 227,489 eggs. Fecundity was positively and nonlinearly related to TW (Fig. 1), and best described by the power equation, $F = 0.0724 \cdot TW^{3.4265}$ ($r^2 = 0.813$, $n = 43$, $P < 0.001$). The 95% confidence interval on the slope was ±0.5643. A double log-linear fit of the data ($\log_{10} F = 3.2596 \cdot \log_{10} TW - 1.9397$), provided for ready comparison with most other reported lobster size-fecundity relations (e.g., DeMartini *et al.,* 1993), was nominally inferior ($r^2 = 0.794$). Fecundity subsamples averaged 2.1 ± 0.12 (SE)% of total brooded egg-mass weight. The CVs of the three replicate estimates of relative fecundity averaged 1.9 ± 0.18%. Based on the aforementioned non-linear best fit, the fecundity of the median-sized (60-mm TW) female caught at Maro Reef by the 1999 commercial trap fishery was an estimated 89,660 ± 3,980 eggs.

Table 1. Summary statistics for *Scyllarides squammosus* (H. Milne Edwards, 1837) trapped at Maro Reef, Northwestern Hawaiian Islands, during research operations of the NOAA ship *Townsend Cromwell,* during June 25–30, 1999. (TW = total abdomen width.)

Total number trapped	2,450
Male body size (range in TW, mm)	40–78
Female body size (range in TW, mm)	42–82
Number (%) female	1,061 (43.3)
Number (% of females) berried	319 (30.1)
Smallest berried female (TW, mm)	52
Largest berried female (TW, mm)	80

Brooded Egg Size

The median size of early-stage eggs was 0.67 ± 0.006-mm diameter (range: 0.61–0.77 mm) and 0.17 ± 0.004 mg (range: 0.13–0.24 mg). Individual egg size (diameter, Fig. 2; weight) was unrelated (both $P > 0.6$) to female body size.

Discussion

The strongly positive body size-fecundity relationship observed in this study for *S. squammosus* resembles those described for other scyllarids. *Scyllarides latus,* for example, exhibits a positive body size-to-egg number relationship in both the southeastern Mediterranean (Almog-Shtayer, unpubl. thesis) and in the Azores (Martins, 1985), although the relationship was not statistically significant in the latter study due to a small sample size (n = 20 lobsters). In the most thorough and quantitative previous evaluation of fecundity in a scyllarid (n = 75 lobsters), Stewart and Kennelly (1997) characterized

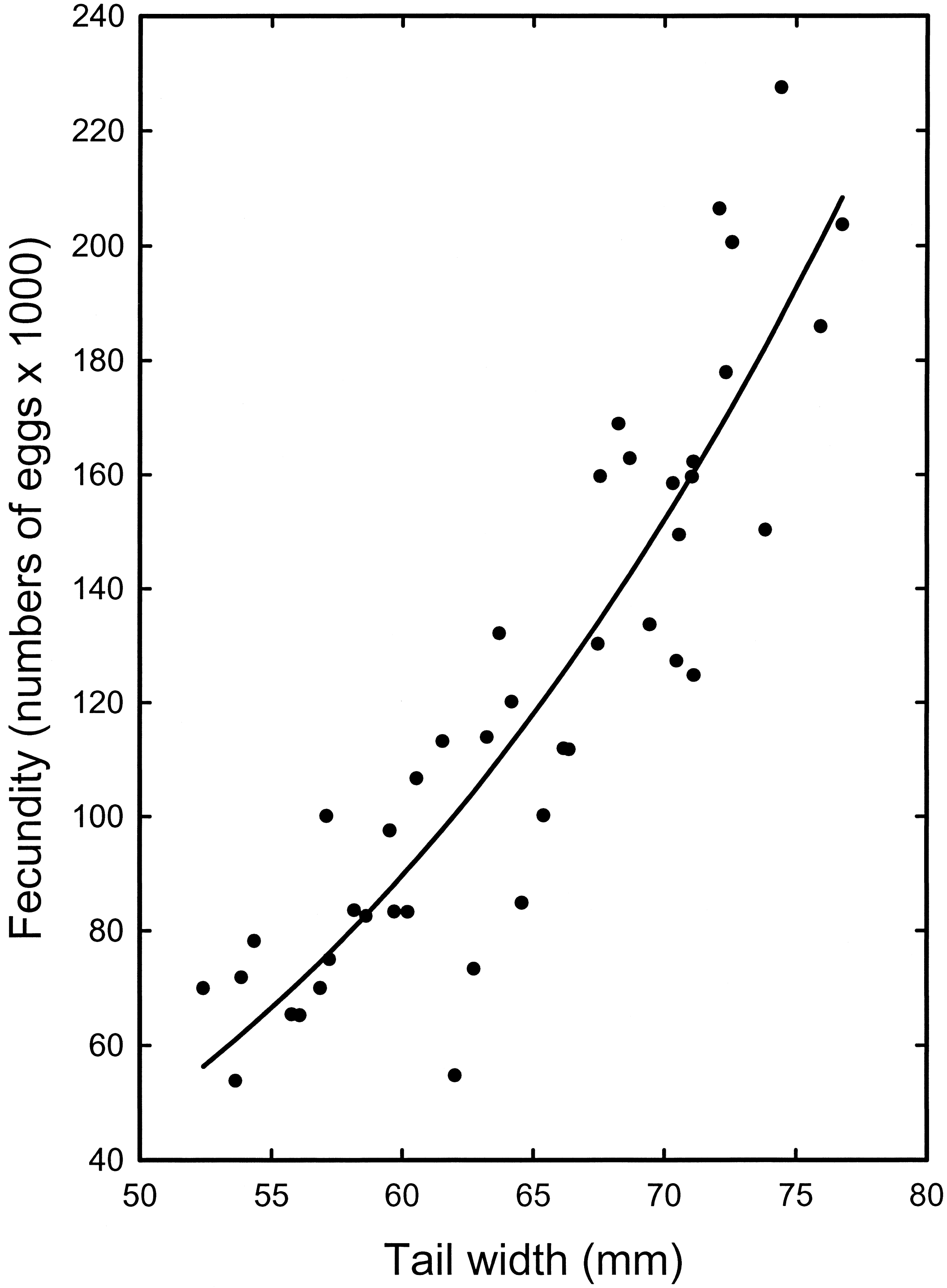

Fig. 1. Scatterplots and best fit (nonlinear) relationship between fecundity (F, the number of eggs present on pleopods) and tail (abdomen) width (TW, mm) of *Scyllarides squammosus* (H. Milne Edwards, 1837) from Maro Reef, Northwestern Hawaiian Islands, in June 1999.

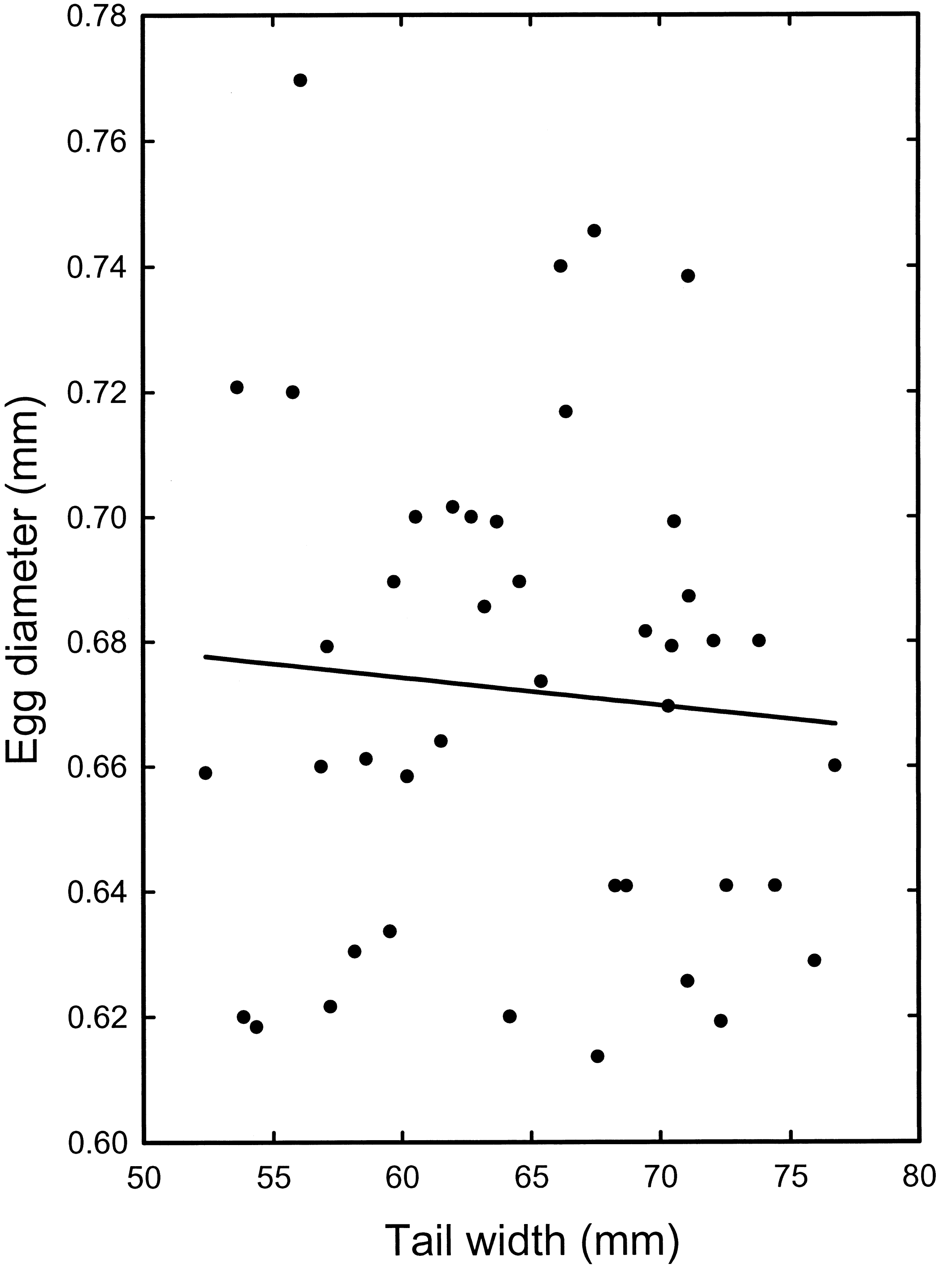

Fig. 2 Scatterplot and trend line (P = 0.62, ns) for relationship between egg diameter (mm) and tail (abdomen) width (TW, mm) for ovigerous *Scyllarides squammosus* (H. Milne Edwards, 1837) from Maro Reef, Northwestern Hawaiian Islands, in June 1999.

Table 2. Relative frequency and size of berried *versus* unberried female *Scyllarides squammosus* (H. Milne Edwards, 1837), trapped on annual research cruises of the NOAA ship *Townsend Cromwell* at Maro Reef, Northwestern Hawaiian Islands, in 1986–97[a] *versus* 1999. All trapping was conducted at the same grid of stations during late June to early July in each year. Source of 1986–97[a] data: DeMartini and Kleiber (1998). (TW = total abdomen width.)

Period or year	TW (mm) class	Reproductive state	Number females
1986–97[a]	< 52	berried	79
		unberried	343
1986–97[a]	≥ 52	berried	1,363
		unberried	2,641
1999	< 52	berried	0
		unberried	29
1999	≥ 52	berried	319
		unberried	713

[a]Excluding 1989, when no research cruise was conducted.

the fecundity of *Ibacus peronii* as strongly ($r^2 = 0.676$) positive and linearly related to body size. It is likely that scyllarids, like palinurid lobsters, produce eggs as some positive function of body size (pleopod capacity), although the exact shape (e.g., linear, cubic) of the relation may vary among populations and species (Chubb, 1994). Scyllarids like *S. squammosus* may also retain eggs in numbers proportional to pleopod capacity.

The minimum body size for which we were able to describe fecundity was limited by the smallest berried female *S. squammosus* (52-mm TW) among 1,061 females caught on the 1999 research cruise (Table 1). Median body size at sexual maturity was about 50-mm TW for *S. squammosus* at Maro Reef during 1986–97 (DeMartini and Kleiber, 1998), when 18.7% of all females smaller than 52-mm TW were berried. Hence, berried females smaller than 52-mm TW should have been present in the 1999 catch (3-way G-test (Zar, 1984): $P < 0.0001$; Table 2). We speculate that the relatively large body size at first sexual maturity observed in 1999 may represent a recent density-related increase in size at maturity, as the *S. squammosus* population at Maro Reef has expanded (as evidenced by increasing catch per trap-set) to replace the declining population of Hawaiian spiny lobster, *Panulirus marginatus*, at this bank (DiNardo *et al.,* 1998). Temporal patterns in size-at-maturity and fecundity-female size relationships for *S. squammosus* at Maro Reef appear to be opposite those for *P. marginatus* at Maro Reef and at Necker Island, NWHI, where adult *P. marginatus* densities have declined. For *P. marginatus* at Necker Island, female body size-at-maturity has decreased and body size-specific fecundity has increased in compensatory, density-dependent fashion over a period of two decades of commercial harvest (Polovina, 1989; DeMartini *et al.,* 1993; E. DeMartini, unpubl. data).

The insignificant body size-to-egg size relationship observed herein for *S. squammosus* has parallels in the literature. Body and egg sizes are unrelated, for example, in *S. latus* (Martins, 1985). Stewart and Kennelly (1997) also were unable, despite a large sample size, to detect any influence of body size on egg size in *Ibacus peronii*. Constancy of egg size among all-sized female *S. squammosus* may indicate, as suggested for *I. peronii* by Stewart and Kennelly (1997), that the eggs of all-sized females are equally viable.

Contrasts in fecundity-egg size tradeoffs between oceanic and coastal scyllarids are informative (Stewart and Kennelly, 1997). Like *S. latus* in the Azores (Martins, 1985), *S. squammosus* produces broods of many (10^4–10^5) small eggs (< 1-mm diameter). Coastal species like *Thenus orientalis* (Hossain, 1979; Jones, unpublished thesis) and *Ibacus peronii* (Stewart and Kennelly, 1997) are relatively less fecund (10^3–10^4 eggs) but produce relatively large (> 1-mm diameter) eggs. Perhaps, as suggested by Stewart and Kennelly (1997), the opposing fecundity-egg size tradeoffs in oceanic *versus* coastal scyllarids reflect the higher per capita mortality rates of larvae in open-ocean environments in which local larval retention is low. As lobster fisheries expand to target both slipper and spiny lobsters, and the life histories of additional scyllarids are described, body size-egg size relations should be reevaluated for coastal and oceanic species of both families. Doing so might provide important insights into fundamental egg-per-recruit relationships and thereby assist in the management of lobster fisheries.

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Literature Cited

Almog-Shtayer, G. 1988. Behavioral-ecological aspects of Mediterranean lobsters in the past and of the slipper lobster *Scyllarides latus* in the present.—M.A. thesis, University of Haifa, Israel. 165 pp. [In Hebrew, English abstract.]

Chubb, C. F. 1994. Reproductive biology: issues for management. Pp. 181–212 *in* B. F. Phillips, J. S. Cobb, and J. Kittaka, eds. Spiny Lobster Management. Blackwell Scientific Publications, Ltd, Oxford.

DeMartini, E. E., D. M. Ellis, and V. A. Honda. 1993. Comparisons of spiny lobster *Panulirus marginatus* fecundity, egg size, and spawning frequency before and after exploitation.—Fishery Bulletin (U.S.) 91:1–7.

———, and P. Kleiber. 1998. Estimated body size at sexual maturity of slipper lobster *Scyllarides squammosus* at Maro Reef and Necker Island (Northwestern Hawaiian Islands), 1986–97.—Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA. Honolulu, Hawaii 96822-2396. Administrative Report H–98–02. 14 pp.

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.—Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA. Honolulu, Hawaii 96822–2396. Administrative Report H–98–05. 35 pp.

Hossain, M. A. 1979. On the fecundity of the sand lobster, *Thenus orientalis* from Bay of Bengal.—Bangladesh Journal of Scientific Research 2(A): 25–32.

Jones, C. B. 1988. The biology and behaviour of Bay Lobsters, *Thenus* spp. (Decapoda: Scyllaridae) in northern Queensland, Australia.—Ph.D. thesis, University of Queensland, Brisbane.

Kawamoto, K. E., and S. G. Pooley. 2000. Annual report of the 1998 western Pacific lobster fishery (with preliminary 1999 data).—Honolulu Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service (NOAA), Honolulu, Hawaii. Administrative Report H–00–02. 38 pp.

Martins, H. R. 1985. Biological studies of the exploited stock of the Mediterranean locust lobster *Scyllarides latus* (Latreille, 1803) (Decapoda: Scyllaridae) in the Azores.—Journal of Crustacean Biology 5: 294–305.

Polovina, J. J. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands.—Canadian Journal of Fisheries and Aquatic Sciences 46: 660–665.

Spanier, E., and K. L. Lavalli. 1998. Natural history of *Scyllarides latus* (Crustacea; Decapoda): a review of the contemporary biological knowledge of the Mediterranean slipper lobster.—Journal of Natural History 32: 1769–1786.

Stewart, J., and S. J. Kennelly. 1997. Fecundity and egg-size of the Balmain bug *Ibacus peronii* (Leach, 1815) (Decapoda, Scyllaridae) off the east coast of Australia.—Crustaceana 70: 191–197.

Zar, J. H. 1984. Biostatistical Analysis, Second edition. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.

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