ASPECTS OF THE REPRODUCTIVE BIOLOGY, SPATIAL DISTRIBUTION, GROWTH, AND MORTALITY OF THE DEEPWATER CARIDEAN SHRIMP, *HETEROCARPUS LAEVIGATUS*, IN HAWAII

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ABSTRACT

The recent rapid development of fisheries for the *Heterocarpus laevigatus* in Hawaii and elsewhere in the tropical Pacific has created the need for biological information to manage the resource. This study reports on a 16-month sampling program of commercial shrimp catches in Hawaii, during which the depth of capture, carapace length (CL), sex, and reproductive condition of 7,368 *H. laevigatus* were determined.

The overall sex ratio of *H. laevigatus* was 1:1.16 in favor of females and depended on the depth sampled; there were relatively fewer females as depth increased. Seasonal variation in sex ratio was evident which may have been due to changing catchability and availability or a sex related dispersion pattern. Sex ratio also depended on size category, displaying a standard pattern with no evidence of protandry.

Females mature at 40 mm CL (64% of asymptotic length) and ovigerous individuals are found year round. However, the main reproductive season is from August-February, with over 50% of females carrying eggs from October-January. Mature shrimp may undergo a depth related seasonal migration in synchrony with breeding. Mature males and females were found deeper (700 m) during the reproductive season than not (550 m). Females apparently settle in deep water and migrate gradually to shallower water as they grow.

Seasonal length-frequency data suggest *H. laevigatus* is not semelparous. Separate analyses of CL-frequency distributions of male and female shrimp indicate their von Bertalanffy asymptotic sizes are 57.9 and 62.5 mm CL, respectively. Growth coefficients (K) estimated by modal progression were 0.35 and 0.25 per year for males and females, and total instantaneous mortality rates were 1.51 and 0.73 per year, respectively.

The deepwater caridean shrimp, also known as "ono" or smooth nylon shrimp, *Heterocarpus laevigatus*, (Family Pandalidae) occurs throughout the tropical Pacific Ocean, where it is found in benthic deepwater habitats (450-900 m) (Wilder 1977; King 1983). While early trapping surveys in the Hawaiian Islands revealed its local abundance (Clarke 1972; Struhsaker and Aasted 1974), little information was available concerning its biology. These early studies did show, however, that *H. laevigatus* was potentially of commercial importance, with a preliminary maximum sustained yield estimate of 454-907 metric tons (t) derived for the Hawaiian Archipelago (Department of Land and Natural Resources 1979). More recently the Western Pacific Regional Fishery Management Council[3] (WPRFMC) has revised this estimate to 400-4,000 t.

A commercial trap fishery for this species subsequently developed in the Hawaiian Islands, and in 1984 the WPRFMC began the process of developing a fishery management plan for the *Heterocarpus* shrimp resources of the region. Landings from the Hawaiian fishery exceeded 135 t in 1983 but have declined sharply since, although commercial interest in the resource remains great (WPRFMC fn. 3). Recent research surveys in Hawaii have now more clearly defined this species' depth, temporal, and geographic distributions (Oishi 1983; Hawaiian Divers 1983[4]; Gooding 1984), although the life history of *H. laevigatus* remains largely unknown. The only substantive biological studies to date were

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completed in the Marianas (including Guam) and Fiji (Wilder 1977; King 1983; King and Butler 1985; Moffitt and Polovina[5]).

Evidence also exists to show that this species is highly susceptible to trapping (Ralston 1986) and, according to commercial fishermen, depletion of the resource has occurred over certain fishing grounds in Hawaii (S. Barrows[6]). Because estimates of the shrimp's productive capacity which are currently available are preliminary at best and a fishery has developed rapidly, this study set out to examine aspects of the life history of the Hawaiian stock of *H. laevigatus* to obtain information useful in developing a basis for management of the fishery.

METHODS

All sampling was conducted by commercial fishing vessels owned by the Hawaiian Shrimp Company (*Easy Rider*, *Mokihana*, and the *Easy Rider Too*) over the 16-mo period from August 1983 to November 1984. During this time, six 35-60 d cruises were completed and samples were obtained during 9 of the 12 calendar months (Table 1). Fishing was conducted throughout much of the Hawaiian Archipelago, from Gardner Pinnacles south to the Island of Hawaii (Fig. 1). Samples were collected at all of the seven main islands (Hawaii, Kauai, Lanai, Maui, Molokai, Niihau, and Oahu) and from Necker, French Frigate Shoals, and Gardner Pinnacles in the Northwestern Hawaiian Islands.

All shrimp were caught during overnight sets of baited pyramidal traps, which measured 1.5 × 1.8 m with a funnel opening at the top center. Fishing was targeted between depths of 500 and 700 m,

TABLE 1.—Temporal and geographic distribution of *Heterocarpus laevigatus* samples (FFS = French Frigate Shoals).

Year	Month	Location	Sample size
1983	Aug.	Oahu	79
1983	Sept.	Oahu	26
1983	Oct.	FFS	188
1983	Nov.	FFS	1,942
1984	Jan.	Oahu	285
1984	Mar.	Niihau, Kauai	530
1984	April	Hawaii	631
1984	May	Lanai, Maui, Molokai	1,389
1984	June	Necker	842
1984	Sept.	Gardner Pinnacles, FFS, Necker	1,438
1984	Nov.	Necker	18

although some catches were made in both shallower and deeper water because of the trap drift. The best catch rates were found in areas of hard rough bottom; otherwise, all sampling sites were to all appearances similar.

Systematic subsamples of the catch were taken from every other trap on every second fishing day by randomly scooping approximately 0.9 kg (2 lb) of shrimp from traps prior to emptying. Samples were placed in double bags with tags recording date, location, depth, and condition, and were then frozen and packed for transfer to the laboratory. There all shrimp were identified to species; sexed; examined for embryos on the pleopods; measured to the nearest 0.1 mm for carapace length (CL), carapace width (CW), and total length (TL); and weighed to the nearest 0.1 g on a top loading scale. The data were then keypunched and stored for analysis.

Size-frequency distributions of *H. laevigatus* were analyzed by the regression method of Wetherall et al. (in press) to estimate maximum size (L_∞ of the von Bertalanffy growth equation) and the ratio of total instantaneous mortality rate (Z) to von Bertalanffy growth coefficient (K). Additionally, the growth coefficient of *H. laevigatus* was estimated by following the progression of size modes evident in three large samples taken: 1) 24 October to 6 November 1983, 2) 24 April to 11 May 1984, and 3) 3 September to 6 November 1984. Sample sizes of $N = 2,021$, 1,991, and 1,438 were obtained in these respective samples, accounting for 74% of all shrimp measured in the study. Modal progression of size distributions was determined by the ELEFAN I computer program of Pauly (1982).

RESULTS

A total of 7,368 *H. laevigatus* were measured and examined for CL, sex, and the presence of eggs (Table 1). Of these 3,956 were females (32.6% of which were ovigerous) and 3,412 were males. This corresponds to an overall male to female sex ratio of 1:1.16, departing significantly from equality ($P < 0.0001$). Measurements of TL, CW, and weight were obtained from 5,920 of the shrimp sampled.

Due to an imbalance in sampling, the effects of location and time on the distribution of *H. laevigatus* could not be completely separated. We therefore assume that all samples were drawn from statistically homogeneous locations in order to isolate and examine temporal and depth effects. The strength of this assumption is based largely on our personal observations and those of fishermen that seasonal change seems to account for most major population
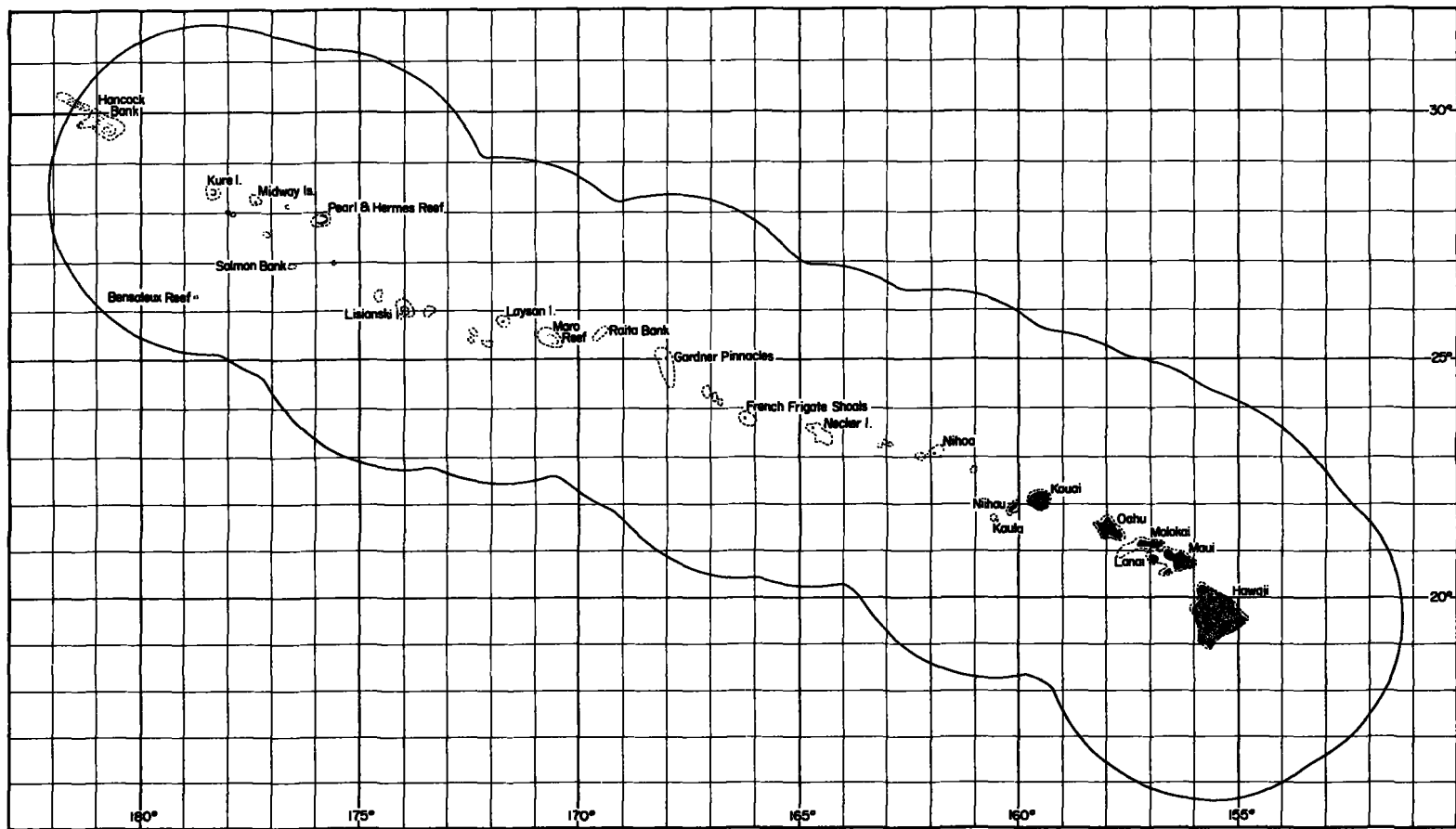
FIGURE 1.—Map of the Hawaiian Archipelago showing sampling locations. Note that the circumscribed area delimits the U.S. fishery conservation zone and that one degree of latitude equals 111 km.

variations in Hawaii, as well as evidence from the Mariana Archipelago which shows that populations of *H. laevigatus* are affected to a greater degree by temporal factors than geographic ones (Polovina[7]).

Morphometrics

The results of performing functional regressions (Ricker 1973) on the three linear size measurements (CL, CW, TL) are given in Table 2. Estimates of slope and intercept are provided for all possible permutations of these variables. Separate analyses for males (M), females without eggs (FØ), and females with eggs (FE) were not performed because all have similar gross morphologies (but see King and Moffitt 1984). As expected, the data were well described with a linear fit.

The relationship between weight and CL was examined by analysis of covariance (BMDP 1977) to determine whether the M, FØ, and FE subgroups have different weight-length relationships. Results showed all three were characterized by differing slopes in the regression of $\log_e$ (weight) on $\log_e$ (CL) ($F = 86.46$, df $= 2, 5912$, $P \ll 0.0001$). Parameter estimates with standard errors and other regression statistics are presented in Table 3 for each of the three subgroups. Note that the reduced r^2 of the

FE group is due to a substantial reduction in the range of CL over which the data were fitted. The results of performing functional regressions of $\log_e$ (weight) on $\log_e$ (CL) are also given.

During the analysis an anomalous bimodal distribution of weight at length emerged. The bimodality was not due to sexual class (M, FØ, or FE) and clearly diminished to a unimodal weight distribution as CL increased from 15 to 40 mm. We have no explanation for these data.

Reproductive Biology

The reproductive season of *H. laevigatus* was estimated by plotting the percentage of ovigerous females relative to total females against the month sampled. For the data which overlapped 1983 and 1984 no interannual difference was evident (i.e., the timing of reproduction was similar), so the data were pooled by month between these years. The results are presented in Figure 2 where the data have been further aggregated into 2-mo "seasons". For each the percentage of females bearing eggs is plotted with its 95% confidence interval and associated sample size given above.

The data show an increased incidence of ovigerous females from August to February (>30% of females). In particular over 50% of all sampled females carried eggs from October to January. Relatively few shrimp were caught with eggs during the period from April to July (<10%). Moreover,

TABLE 2.—Parameter estimates of functional regressions on linear size measurements. All measurements in millimeters and all sample sizes n = 5,920.

Dependent variable	Independent variable	Slope	Inter-cept	Correlation coefficient
Total length	Carapace length	2.864	10.182	0.963
Carapace width	Carapace length	0.613	−5.562	0.964
Carapace length	Total length	0.349	−3.536	0.963
Carapace length	Carapace width	1.630	9.098	0.964
Carapace width	Total length	0.214	−7.737	0.902
Total length	Carapace width	4.673	36.153	0.902

TABLE 3.—Functional and predictive length-weight regressions for *Heterocarpus laevigatus*. The natural logarithm of weight in grams is fitted to the natural logarithm of carapace length in mm. The standard errors of the slope (b) and intercept (a) are given by S_b and S_a respectively.

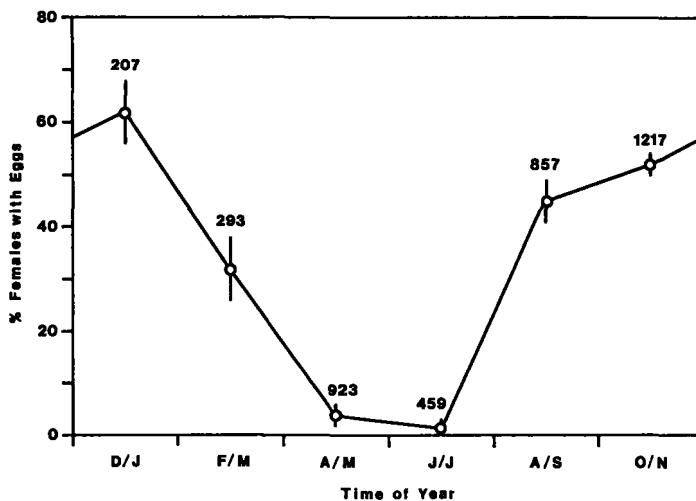|		Slope	Intercept	S_b	S_a	n	r^2
Males	Predictive	2.755	−6.809	0.0176	0.0629	2,788	0.8976
	Functional	2.910	−7.358	—	—	—	—
Females without eggs	Predictive	2.605	−6.252	0.0185	0.0671	2,202	0.8999
	Functional	2.745	−6.757	—	—	—	—
Females with eggs	Predictive	1.815	−2.986	0.0550	0.2114	928	0.5401
	Functional	2.470	−5.498	—	—	—	—

FIGURE 2.—Seasonal incidence of ovigerous *Heterocarpus laevigatus* females in the Hawaiian Islands. Vertical bars represent 95% confidence intervals and sample sizes are presented above. Site locations vary.

when the analysis was restricted to mature females only (see next section) the seasonal pattern of egg-bearing was unchanged. From these results we conclude that in Hawaiian waters *H. laevigatus* reproduces during the fall and winter seasons (August-February).

The size at maturity of female shrimp was determined by aggregating the female data into 5 mm CL classes and plotting the incidence of ovigerous females against CL class (Fig. 3). Only samples obtained during the reproductive season were included in the analysis. As before, the overall percentage
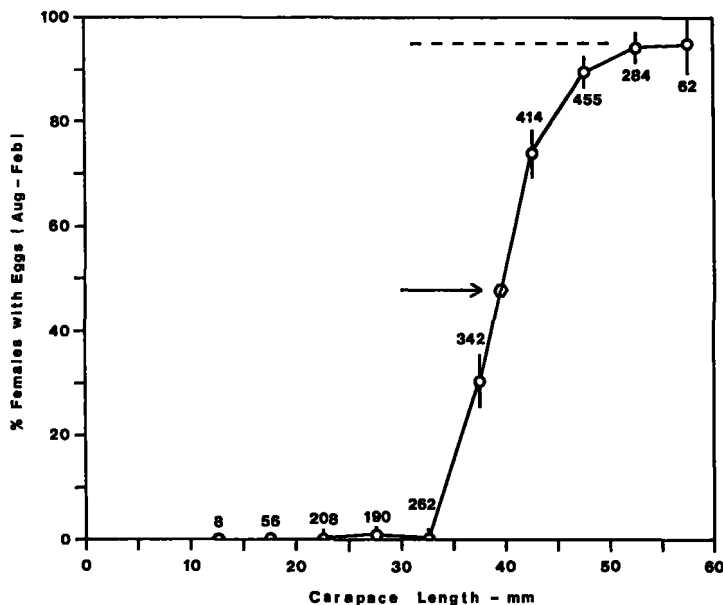

FIGURE 3.—Size at maturity for female *Heterocarpus laevigatus* sampled during the reproductive season. Vertical bars represent 95% confidence intervals and sample sizes are presented above.

with 95% confidence limits and sample sizes are provided.

The data show that the 55-60 mm CL class encompassed the largest shrimp observed. Virtually all (95%) females >50 mm CL that were sampled during August-February bore eggs. Conversely, up to 35 mm CL no more than 1% of the shrimp examined were ovigerous. The figure shows further that at a CL of 40 mm the percentage of ovigerous females is one-half its maximum value, with 48% of all sampled females bearing eggs. We conclude that females become sexually mature at this size (Gunderson et al. 1980). We have no data on maturation in males.

The data presented in Figure 4 show the sex ratio of shrimp as it depends on size (CL mm). Plotted are the percentage females, with 95% confidence intervals and sample sizes, against 5 mm CL size classes. The data clearly show that H. laevigatus maintains a relatively uniform sex ratio from 10 to 45 mm CL, but that females predominate in the largest length categories (45-65 mm CL).

Because some studies (Clarke 1972; Wilder 1977) have indicated that Heterocarpus females may experience mass mortality after egg bearing, we examined the relationship of sex ratio to season (Table 4). Presented for each 2-mo sampling period are the number of females and total number of shrimp sampled, the proportion which are female, and the standard error of the proportion. The results show

that an unusually high fraction (0.72) of the shrimp sampled during the peak of the reproductive season (December-January) are female. Note that the incidence of females in trap samples declines significantly to a value of 0.45 in April-May as the breeding season wanes. At first inspection these data support the contention that females experience increased mortality after bearing eggs, i.e., that H. laevigatus may be semelparous.

TABLE 4.—Sex ratio of *Heterocarpus laevigatus* by month sampled. The standard error of the proportion is given by S_p.

Month	Number of females	Proportion of females	n	S_p
December-January	207	0.72	285	0.026
February-March	293	0.55	530	0.022
April-May	923	0.45	2,020	0.011
June-July	459	0.54	842	0.017
August-September	857	0.55	1,542	0.013
October-November	1,217	0.56	2,148	0.011

Spatial Distribution

The relationship between the sex ratio of H. laevigatus and sampling depth is provided in Table 5. These results demonstrate that the relative abundance of the two sexes is not independent of depth ($\chi^2 = 165.6$, df = 16, $P < 0.001$). As depth increases (440-760 m) there is a significant decline in the percentage of females in our samples ($P = 0.05$).
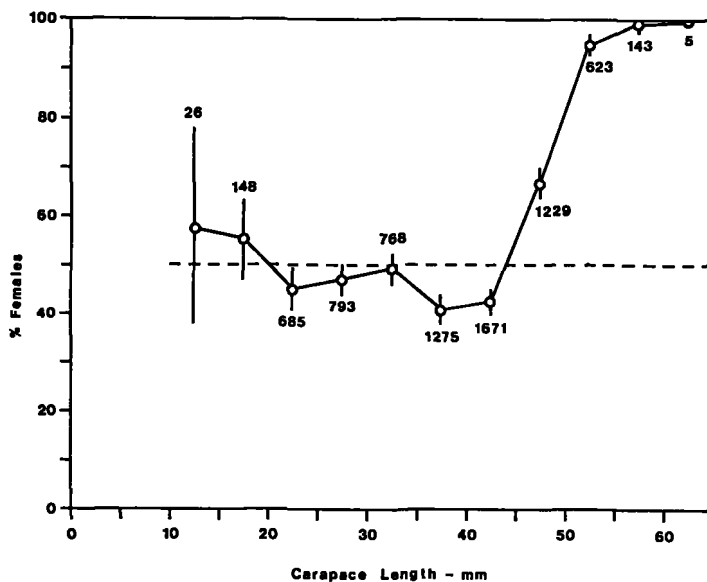

FIGURE 4.—Sex ratio as a function of carapace length. Vertical bars represent 95% confidence intervals and sample sizes are presented above.

The results presented in Table 5 also show the distribution of mean size (CL mm) by depth (m) for all *H. laevigatus* caught, and for the M, F∅, and FE subgroups. For all shrimp combined, average size decreases slightly with increasing depth fished. The trend for decrease in size with increasing depth is not evident in the M subgroup. However, the F∅ class demonstrates a strong relationship of decreasing mean CL with depth. For the FE category the decline is much less apparent, if at all. Thus the overall decline in mean CL of all shrimp combined, is clearly due to an overriding influence of females without eggs. We interpret these trends, or lack thereof, to indicate that young (i.e., small) females may move from deep to shallow water as they mature.

There is some evidence that the depth distribution of *H. laevigatus* changes with reproductive activity (i.e, season). Figure 5 presents the depth distributions for reproductively competent (>40 mm CL) male and female shrimp, classified into samples taken outside (March-July) and during the reproductive season (August-February). Note that depth distributions of both male and female shrimp are

TABLE 5.—Sex ratio and size of *Heterocarpus laevigatus* by depth (M is for males, F∅ for females without eggs, and FE for females with eggs). S_p is the standard error of the proportion.

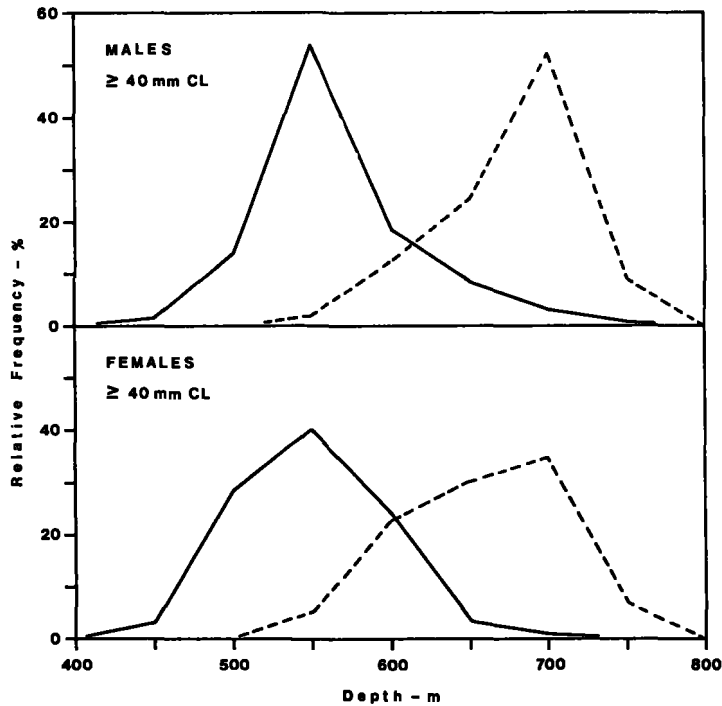| Depth (m)	Number of females	N	Proportion of females	S_p	Carapace length			
					All	M	F∅	FE
440	41	71	0.58	0.059	40	34	43	48
60	9	11	0.81	0.116	39	36	40	—
80	65	141	0.46	0.042	38	33	42	49
500	155	230	0.67	0.031	42	34	45	49
20	287	430	0.66	0.023	43	40	45	46
40	419	943	0.44	0.016	37	35	40	49
60	193	487	0.39	0.022	37	36	38	45
80	280	500	0.56	0.022	39	35	42	47
600	282	498	0.56	0.022	38	35	38 ·	46
20	284	463	0.61	0.023	39	35	34	48
40	325	581	0.55	0.021	38	37	32	47
60	109	210	0.51	0.034	37	34	35	44
80	95	167	0.56	0.038	39	37	35	48
700	90	222	0.40	0.033	36	36	31	43
20	399	738	0.54	0.018	39	38	32	47
40	68	126	0.53	0.044	40	37	33	48
60	14	46	0.30	0.068	34	34	28	42

FIGURE 5.—Seasonal distributions of large (>40 mm) male and female *Heterocarpus laevigatus* by depth. The dashed line represents the spawning season distribution (May-February) and the solid line represents the distribution during the nonspawning season (March-July).

shifted 150 m deeper when the females are ovigerous. Although the data are not corrected for what may have been differences in fishing effort by depth, it is true that fishing was targeted to depths of maximum shrimp abundance. Based on these findings, and the results presented in Table 5, our data are consistent with a hypothesis of gradual movement of small females from deep to shallow water, with mature shrimp moving between depths of 550 and 700 m in synchrony with the ovigerous cycle of females.

Growth and Mortality

Clarke (1972) and King (1983) have suggested that *Heterocarpus* spp. may breed once and die. Indeed the results already presented in Table 4 may be considered consistent with the hypothesis that at least female *H. laevigatus* are semelparous. To further address this question we examined the size structure of male and female shrimp classified as follows: 1) during the latter half of the reproductive season (January-February) and 2) immediately following the reproductive season (March-July). If postreproductive mortality of shrimp was severe, a decrease in the relative abundance of large, breeding adults would be expected as the reproductive season waned.

The results presented in Figure 6 conflict with this expectation, where it is apparent that the proportional representation of large reproductive individuals (>40 mm CL) is actually greater imme-
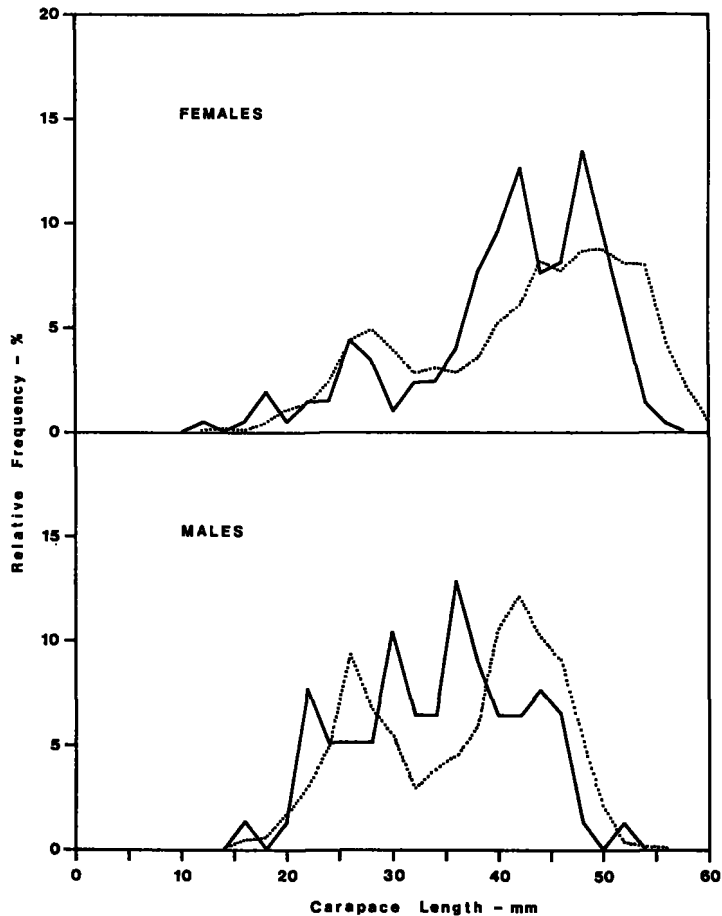

FIGURE 6.—Relative size-frequency distributions of male and female *Heterocarpus laevigatus* during the peak and postreproductive seasons. The solid line represents the peak season (January-February), males $N = 78$, females $N = 207$; the dashed line is based on data collected immediately after the peak season (March-July) males $N = 1,717$, females $N = 1,675$.

diately following than during the latter half of the reproductive season.

The total sample CL-frequency distribution of males and females combined was analyzed by the regression method of Wetherall et al. (in press) to estimate L_∞ and Z/K. When all shrimp are pooled ($N = 7,368$), an estimate of $L_\infty = 61.7$ mm CL results. Further, the ratio of total mortality rate to von Bertalanffy growth coefficient (Z/K) is estimated to be 2.6. Calculations were repeated for separate male and female subgroups, where it was found that $L_\infty = 57.9$ and 62.5 mm CL and $Z/K = 4.3$ and 2.9 for males and females, respectively. These results indicate that males generally grow to a smaller size than females.

The results of analyzing the progression of CL size modes in frequency distributions of male and female *H. laevigatus* provided preliminary estimates of $K = 0.35$ yr^{-1} for males and 0.25 yr^{-1} for females. The former result must be viewed with caution, however, because two "solutions" were detected by the computer search algorithm (Pauly 1982) which differed little in fit. One of these, $K = 0.70$ yr^{-1}, we believe to be unjustifiably high in light of the minor difference (8%) between the L_∞ of males and the L_∞ of females obtained from the regression analysis. Note that estimates of K and L_∞ typically show a strong inverse correlation (Gallucci and Quinn 1979). These results, in conjunction with the estimates of Z/K for male and female shrimp presented earlier, provide the basis for preliminary estimation of total mortality rate. We estimate $Z = 1.51$ yr^{-1} for males and 0.73 yr^{-1} for females, corresponding to annual survivorship fractions of 22% and 48% per year, respectively. These data indicate that males grow faster while experiencing a substantially greater total mortality rate than females.

DISCUSSION

Earlier it was assumed that, aside from depth, all shrimp samples were drawn from locations which are dynamically homogeneous; i.e., the behavior of shrimp populations through time does not vary from site to site. This is clearly a restrictive and simplifying assumption and is without doubt the major limitation on the results presented here. Nonetheless, it was a necessary simplification for us to analyze the commercial fishing data upon which this study was based. Consequently, we view those results which rely upon this assumption as tentative and in need for further validation.

Examination of the seasonal trend in the relative abundance of ovigerous females showed that in Hawaii over 50% of *H. laevigatus* females bear eggs from October to January, with a peak between August and February. Wilder (1977) found a similarly timed but more narrowly defined breeding season for *H. laevigatus* in Guam, where the percentage of ovigerous females in trap catches reached a maximum during December, but was not particularly high in any other month. Clarke (1972) reported that *H. ensifer* in Hawaii also reproduces in the winter. The breeding season of these shrimps is unusual among Hawaiian crustaceans and fishes, which typically reproduce during the spring and summer and uncommonly during the winter (Watson and Leis 1974; Lobel 1978; Uchida et al. 1980; Uchida and Tagami 1984; Walsh 1984).

Our data also indicate that in Hawaii sexual maturity of female ono shrimp occurs at approximately 40 mm CL, a size similar to that reported by King (1983) for shrimp from Fiji, Vanuatu, West Samoa, and Tonga and by Moffitt and Polovina (fn. 5) for samples from the Marianas. Based upon the estimated parameters of the von Bertalanffy growth equation derived here, this corresponds to an age of first maturity of 4 yr. Although we have no data on the maturation of males, we believe they probably mature earlier and at smaller size, perhaps at age 3 when they are 37-38 mm CL. Such a result is consistent with the findings of Moffitt and Polovina (fn. 5) who found that male *H. laevigatus* in the Marianas mature at a smaller size than do females.

Wilder (1977) speculated that both *H. ensifer* and *H. laevigatus* in Guam are protandrous hermaphrodites, as did Clarke (1972) for Hawaiian populations of *H. ensifer*. However, the results presented in King and Moffitt (1984) tend to contradict this conclusion. These authors studied the morphometry and sexuality of five deepwater pandalids, including *H. laevigatus*, in Fiji and the Marianas. Using the relative length of the appendix masculina expressed as a proportion of CL, they found no tendency toward protandrous hermaphroditism. Moreover, the sex ratio reported in their study was approximately 1:1.

Our results also indicate that for Hawaiian populations of *H. laevigatus*, and we speculate for most tropical pandalids, a sex transition does not occur. Wenner (1972) has termed the pattern exhibited in Figure 4 the standard sex ratio pattern, as distinguished from one of reversal. Due to the large numbers of females in small size classes, these data are generally inconsistent with a protandric hermaphroditic life history, as has been hypothesized by previous workers on *Heterocarpus* spp. (Clarke

1972; Wilder 1977). King and Moffitt (1984) also argue for dioecy in this species based upon relative changes in the morphology of the appendix masculina.

Evidence now exists to suggest that the sex ratio of *H. laevigatus* undergoes a seasonal change (Table 4), although the reasons for this are at present unknown. A biological alteration in population structure of this order seems unlikely. Rather, the relatively high catch of females during the December-January period may be due to seasonal changes in catchability or vulnerability of one or both sexes to the traps. Alternatively, the spatial dispersion of *H. laevigatus* may depend on sex. If males and females are spatially segregated, the high proportion of females in the December-January sample may have been due to small sample size ($N = 207$).

We have also shown that sex ratio depends strongly on the depth sampled (Table 5), with diminishing representation of females as depth increases. This spatial heterogeneity between the sexes may be due to directed movements. Based on size trends of females we conclude that they recruit to deeper water and subsequently migrate to shallower water. We have no evidence for similar movement of males.

Studies by King (1983) on Pacific *Heterocarpus* spp. showed cyclic migrations in these shrimps, suggesting that depth distribution may change seasonally, with an annual migration up and down the slope of the sea floor. The data presented in Figure 5 indicate that mature *H. laevigatus* in Hawaii do migrate seasonally, demonstrating distinct shifts in the depth distributions of both sexes during the reproductive season. Because this result is confounded by what may be a location effect, however, we view them as preliminary and in need of further confirmation. King (1983) also reported that *Heterocarpus* spp. were found in stomachs of tuna in Fiji, indicating perhaps some type of vertical migration in the water column.

King (1985), based on work completed in Fiji, examined the question of iteroparity and semelparity in several genera of pandalid shrimp (*Plesionika, Saron, Parapandalus,* and *Heterocarpus*). Based on the difference between length at sexual maturity and maximum length, he concluded that shallow-water species (e.g., *H. ensifer*) are semelparous. He states that deepwater *Heterocarpus* spp. "have an extended reproductive lifespan, the length of which may be taken to indicate the number of spawnings." We conclude, based on the relative size-frequency distributions of males and females during peak and postreproductive seasons, that both sexes survive well after reproducing—evidence in favor of itero-

parity. Although a high mortality of shrimp following the breeding season would be evidence consistent with a semelparous life history, it is not a sufficient result to prove it. This is because each female, before dying, could have sequential multiple clutches during the October-February ovigerous period. Nonetheless, good survival of *H. laevigatus* females after carrying eggs (Fig. 6) is indicative of iteroparous reproduction.

The regression technique of Wetherall et al. (in press) produced estimates of the ratio of mortality to growth coefficient of 2.9 and 4.3 for females and males respectively. Moffitt and Polovina (fn. 5), using similar methods, estimated $L_\infty = 55.2$ mm CL and $Z/K = 2.5$ for combined male and female samples of *H. laevigatus* from essentially unfished stocks in Guam and the Marianas. Ralston (1986) also reported that the Z/K ratio of an unexploited population of *H. laevigatus* at Alamagan in the Marianas was about 2.0. The differences between estimates may therefore relate to differences in levels of exploitation. Moreover, the higher mortality rate of male shrimp when compared with females (1.51 versus 0.73 yr^{-1}) may explain the somewhat biased sex ratio in favor of females.

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