

DISTRIBUTION AND YIELD OF THE DEEPWATER SHRIMP *HETEROCARPUS* RESOURCE IN THE MARIANAS

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ABSTRACT

A shrimp trapping survey was conducted at 22 islands and banks in the Mariana Archipelago during a 2-year field period. Three species of deepwater shrimp were found in abundance at various depths: *Heterocarpus ensifer* at 366-550 m, *H. laevigatus* at 550-915 m, *H. longirostris* >915 m. *Heterocarpus laevigatus* was the largest and most abundant of the three and has the greatest economic potential. Estimates of the unexploited biomass of this species by bank were calculated from estimates of catchability, relative abundance, and habitat area. An archipelago average of the unexploited trappable biomass was estimated to be 0.8 t/nmi². Evaluation of length-frequency distributions produced estimates of asymptotic length (L_{∞}) of 55 mm carapace length, instantaneous growth constant (K) of 0.3 yr⁻¹, and instantaneous total mortality (Z) of 0.75 yr⁻¹. A recommended yield of 162.0 t/year (0.2 t/nmi² per year) for the entire archipelago was calculated using the Beverton and Holt yield-per-recruit equation based on minimum spawning stock considerations. Of this yield, 85% would come from the southern islands (e.g., Guam and Saipan), 13% from the northern islands (e.g., Pagan and Anatahan), and 2% from the western seamounts (e.g., Arakane Reef and Pathfinder Reef).

The Mariana Archipelago in the western Pacific Ocean stretches from Guam in the south at lat. 13°N to Farallon de Pajaros (also called Uracas) in the north at lat. 20°N (Fig. 1). Within the approximately 270,000 nmi² area of the 200 mi zone around the archipelago are two political entities—the Territory of Guam and the Commonwealth of the Northern Mariana Islands (CNMI)—and three geological formations—the southern island chain, the northern island chain, and the western seamount chain (Karig 1971). The purpose of this study was to assess the standing stock and sustainable yield of the deepwater pandalid shrimp resources in the Marianas.

Pandalid shrimp catches account for about 9% of the world shrimp landings or about 155,000 t in 1982 (FAO 1984). About 98% of this catch is of a few species of the genus *Pandalus* trawled at depths of 70-240 m in the cold-water areas of the North Atlantic, North Pacific, and Bering Sea. The next largest pandalid fishery is the trawl fishery for *Heterocarpus reedi* conducted at depths of 155-424 m in the waters off Chile and Peru (Holthuis 1980). The landings from this fishery were 3,450 t in 1982 (FAO 1984). In recent years, pandalid shrimp resources with commercial potential have been identified from deepwater trapping surveys conducted at depths of

200-1,200 m in the central and western Pacific (Clarke 1972; Wilder 1977; King 1980, 1981a, 1981b; Moffitt 1983). The primary component of these catches has been species of the genus *Heterocarpus*, including *H. laevigatus*, *H. ensifer*, *H. sibogae*, *H. longirostris*, and *H. gibbosus*. Trawling for these species has produced poor results (Struhsaker and Yoshida 1975) which may be due to the depths involved, the rough bottom surrounding the Pacific islands, or behavioral characteristics of the shrimp. In Hawaii a rapidly expanding commercial trap fishery has been established with 1983 annual landings of about 135 t. Catches of 1,350 t have been projected for the near future by the Western Pacific Regional Fishery Management Council (WPRFMC 1984). This projected yield has not materialized and does not appear to be forthcoming since the larger shrimp trapping vessels have left the fishery for economic reasons. Commercial ventures in Guam and the CNMI have been sporadic and short lived; landings of 0.3 t were reported in 1982, the last year that the resource was fished.²

SAMPLING GEAR AND METHODS

Shrimp trapping operations in the Mariana Archi-

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²Western Pacific Fishery Information Network data on file at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

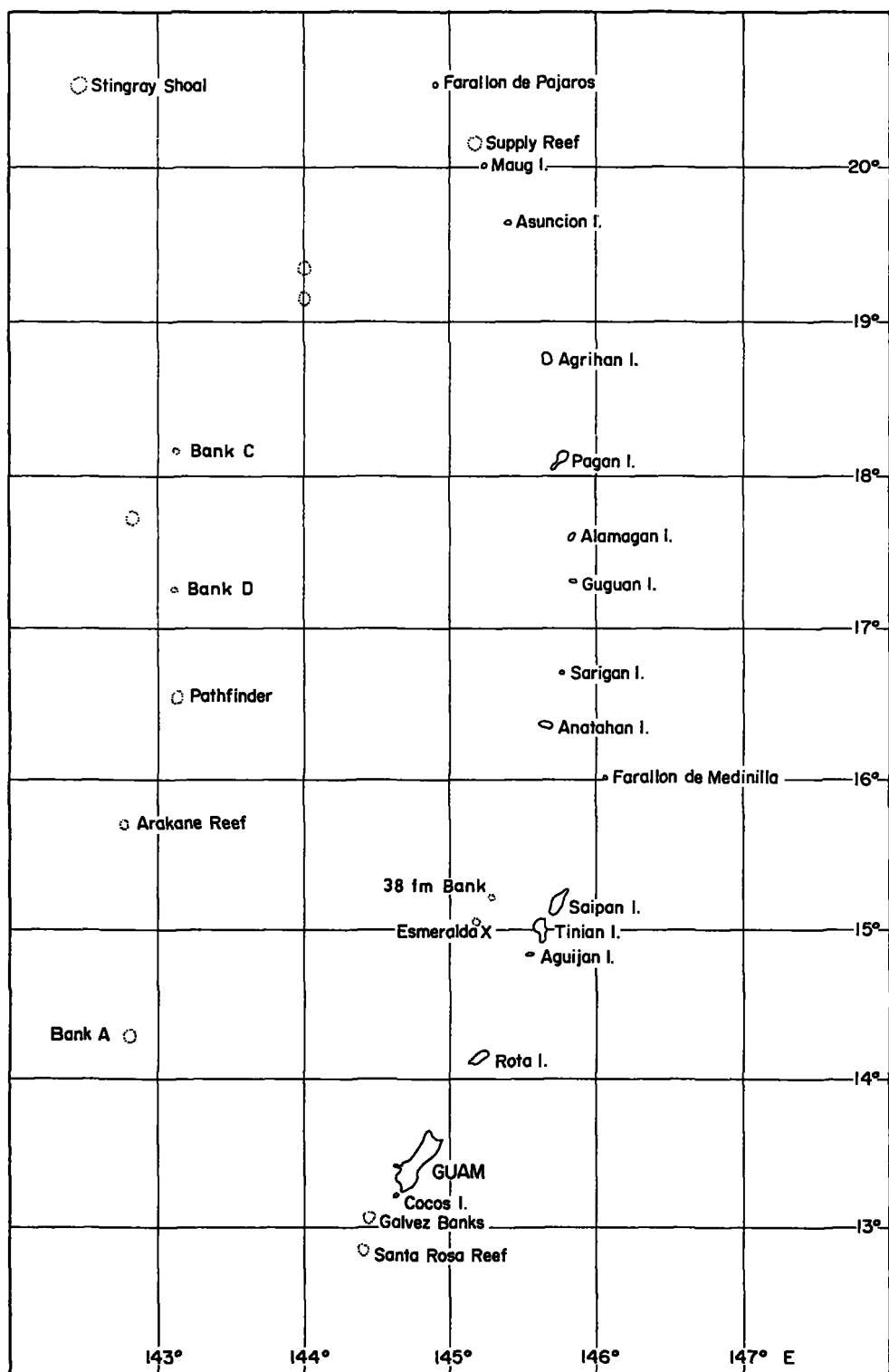


FIGURE 1.—Chart of the Mariana Archipelago.

pelago were conducted on seven cruises of the NOAA ship *Townsend Cromwell* (TC) between April 1982 and August 1984 and one charter cruise of the University of Guam vessel *Pesquedot* (PQ) in August 1984. The standard gear used consisted of strings of five canvas-covered, half-round shrimp traps set about 40 m apart. The traps were constructed of a reinforcing bar frame (about 90 cm long, 65 cm wide, and 45 cm high) wrapped with 2.5 × 1.3 cm mesh, 18-gauge welded wire. An entry cone with an opening of approximately 10 cm was located at each end of the trap. A figure of this general trap design is shown in Gooding (1984). The ground lines attaching the traps together and the main lines attaching the ground line to the surface buoys were of 13 mm polypropylene line. Strings were usually set in the afternoon and retrieved the following morning. Normal soaking times ranged from 15 to 24 hours. Traps were baited with Pacific mackerel, *Scomber japonicus*.

Ordinarily, subsamples of 100 specimens of each of the three major species of *Heterocarpus* (*H. laevigatus*, *H. ensifer*, and *H. longirostris*) were saved each day from each depth sampled. Two sampling sites, Esmeralda Bank and Pagan Island, were visited on each of six *Cromwell* cruises and large subsamples of 400 *H. laevigatus* were saved on each visit. All specimens were returned to the laboratory where the carapace length, sex, and reproductive condition were recorded. The areas of suitable habitat for *H. laevigatus* at each island and bank location was estimated from charts using a computer aided planimeter.

In this study, the yield assessment approach described by Polovina and Ralston (1986) was employed. A systematic survey of 22 islands and banks gave information on the depth range of the primary species and their relative abundance by area. An intensive fishing experiment produced an estimate of catchability using the Leslie method (Ralston 1986). This information combined with an estimate of the area of suitable habitat for each island or bank was used to estimate available biomass by location. Estimates of growth were obtained by application of Elefan I (Pauly 1982) to a site specific time series of length-frequency data. The ratio of mortality to growth and asymptotic length was estimated from a large length-frequency sample (Wetherall et al. in press). Equilibrium yield as a function of fishing mortality was determined from the Beverton and Holt (1956) yield-per-recruit equation as the product of yield per unexploited trappable biomass and the trappable recruited biomass estimate obtained from the systematic sampling and intensive fishing (Polovina and Ralston 1986). Estimates of recommended yield from the equilibrium yield equation were obtained based on marginal yield and minimum spawning stock biomass considerations.

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RESULTS³

Throughout the course of this survey a total effort of 2,508 trap-nights was expended at 527 shrimp trapping stations. The total catch of pandalid shrimp was 5,188 kg for an overall catch rate of 2.07 kg/trap-night. Over 99% of this catch was composed of *H. ensifer*, *H. laevigatus*, and *H. longirostris*. A complete list of shrimp species taken during this study is given in Table 1.

TABLE 1.—List of shrimp species taken (C = common, F = frequent, R = rare).

Species	Frequency	Depth of abundance (m)
Pandalidae		
<i>Plesionika serratifrons</i>	C	90-270
<i>Plesionika longirostris</i>	C	180-360
<i>Plesionika ensis</i>	F	450-630
<i>Plesionika martia</i>	R	360-450
<i>Heterocarpus ensifer</i>	C	360-540
<i>Heterocarpus gibbosus</i>	R	360-450
<i>Heterocarpus sibogae</i>	R	630
<i>Heterocarpus lepidus</i>	F	540-720
<i>Heterocarpus laevigatus</i>	C	540-810
<i>Heterocarpus dorsalis</i>	F	630-900
<i>Heterocarpus longirostris</i>	C	>900
<i>Heterocarpus tricarinatus</i>	R	900
Ophiophoridae		
<i>Acanthephyra eximia</i>	F	810-990
Aristaeidae		
<i>Plesiopenaeus edwardsianus</i>	R	630-810

DEPTH AND SIZE DISTRIBUTION

A plot of catch per unit effort (CPUE) versus depth for the three major species (Fig. 2) shows that they inhabit different depth strata. *Heterocarpus ensifer* is the shallowest dwelling of these species. The maximum catch rate for this species was 0.17 kg/trap-night at a depth of 366 m (200 fathoms). Unfortunately, 366 m was the shallowest depth targeted throughout most of the survey. A small amount of effort was expended in the 137-274 m (75-150 fathoms) depth range on cruises TC-84-02 and PQ-84-01. *Heterocarpus ensifer* catches in this depth range were negligible (only five shrimp in 37 trap-nights). *Heterocarpus laevigatus*, the most abundant shrimp taken in our survey, was caught

³Portions of this section are also presented in Polovina et al. 1985.

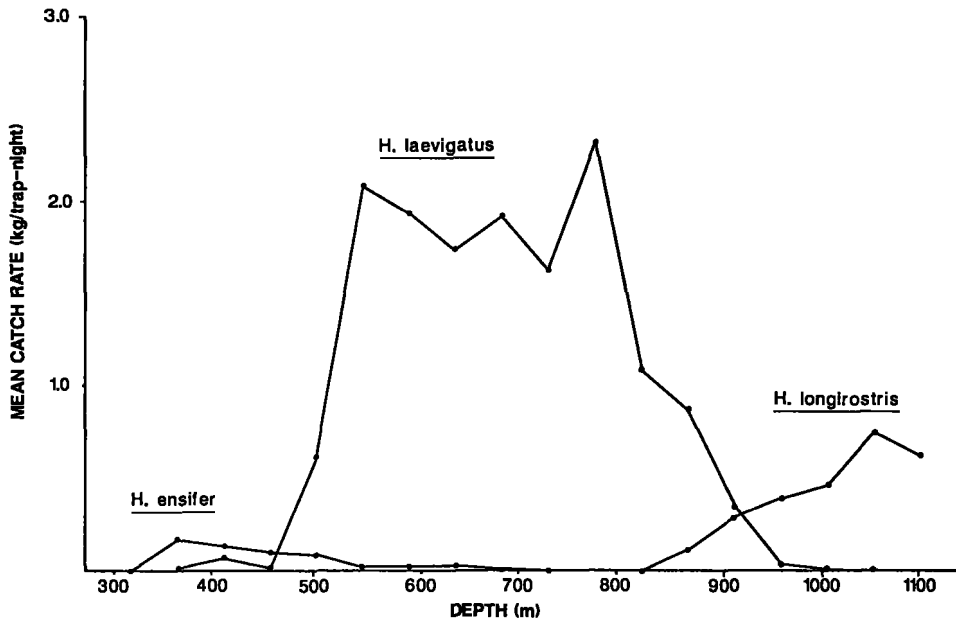


FIGURE 2.—Catch rate of three species of *Heterocarpus* by depth.

in large numbers at depths between 549 and 777 m (300 and 425 fathoms). A maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. *Heterocarpus longirostris* was the deepest dwelling of the *Heterocarpus* species taken, ranging from 823 m (450 fathoms) down past 1,097 m (600 fathoms), which was the greatest depth targeted in this study. Maximum catch rates of *H. longirostris* were obtained at 1,052 m (575 fathoms), but the deeper end of this species' range was not sampled and, as with *H. ensifer*, it is uncertain that the depth of maximum catch rate obtained here is indicative of depth of maximum abundance.

Heterocarpus ensifer was the smallest of the three major species taken. Carapace lengths of 3,401 individuals ranged from 11 to 38 mm with a mean of 26.4 mm. *Heterocarpus laevigatus* was the largest species taken. The mean carapace length was 38.2 mm and the range was 13 to 61 mm ($N = 16,405$). The mean carapace length of *H. longirostris* was similar to that of *H. laevigatus* ($\bar{x} = 37.5$ mm), but the size range of 1,443 individuals was more restricted (20 to 50 mm). The mean size of *H. longirostris* taken in this study is probably higher than the mean of catchable shrimp of this species for all depths. We set traps only in the shallower end of this species' depth range (<1,143 m) where the population is dominated by females that grow to a larger size than the males.

It has been suggested that the size of shrimp

varies with depth, i.e., larger shrimp occur within the range of maximum abundance while smaller individuals were found in shallower or deeper water (Clarke 1972; Wilder 1977). This type of distribution was not observed for any of the three major species of *Heterocarpus* in the Marianas. Linear regressions of mean carapace length with depth by sex were computed for each of the three species. A significant decrease in carapace length with increasing depth was obtained for *H. longirostris* females, although the full depth range of this species was not sampled. In all other cases, no significant change in size with depth was observed (Table 2).

Wilder (1977) reported high male to female ratios of 3-4 to 1 for *H. ensifer* and *H. laevigatus* taken around Guam. He also stated that small individuals were nearly all males and large individuals almost all female. This was not true for the shrimp examined in this study. The overall sex ratios (ex-

TABLE 2.—Results of mean carapace length by depth regressions for three species of *Heterocarpus* by sex.

Species	Sex	Regression coefficient	R^2	Probability
<i>H. ensifer</i>	Male	0.008	0.41	0.06
	Female	0.002	0.03	0.64
<i>H. laevigatus</i>	Male	-0.007	0.26	0.06
	Female	-0.017	0.16	0.16
<i>H. longirostris</i>	Male	-0.004	0.02	0.83
	Female	-0.04	0.67	0.02

pressed in percent males) for the three major species were 52.8% for *H. ensifer* ($N = 3,302$), 55.2% for *H. laevigatus* ($N = 12,555$), and 24.2% for *H. longirostris* ($N = 1,408$). These ratios tended to hold true for all size classes except the very largest of each species which were indeed nearly all females. Sex ratios did differ by depth showing that the two sexes tend to occupy different areas. In all three major species, females were more abundant at the shallower end of the depth range and males at the deeper end (Fig. 3). This relationship is much more obvious for *H. laevigatus* and *H. longirostris* than for *H. ensifer*. For *H. longirostris*, this may explain the small percentage of males taken in this study since the deeper end of the depth range of this species was not sampled.

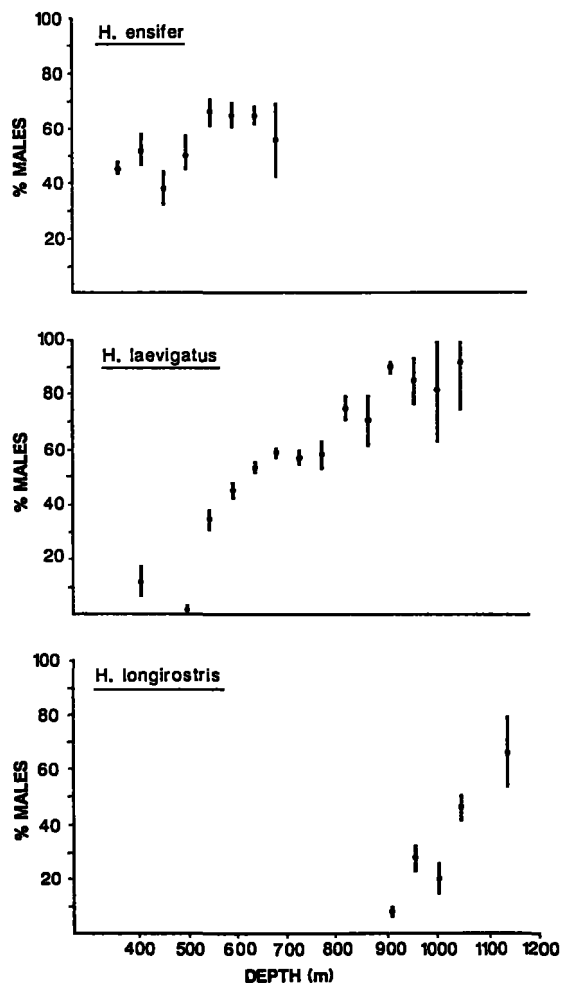


FIGURE 3.—Sex ratio by depth for three species of *Heterocarpus* with 95% confidence limits.

REPRODUCTION

Pandalid shrimp are typically considered to be protandrous hermaphrodites. This is indeed the case for the *Pandalus* species taken in the subarctic areas (Butler 1964). In these species the shrimp spend the first few years of life as functional males, transforming into functional females for the last year or two of life. Clarke (1972) and Wilder (1977) suggested that the tropical *Heterocarpus* shrimp also are protandrous hermaphrodites. The sex ratios obtained in our studies, particularly the near even ratio for the smaller individuals led us to believe that this was not the case. King and Moffitt (1984) examined males of several species of *Heterocarpus* and *Plesionika* for relative growth of the appendix masculina on the second pleopod (a secondary sex characteristic). If these species were indeed protandrous hermaphrodites, the relative size of the male appendage should decrease with increasing carapace length (as the shrimp transforms from male to female). This was not so for any of the tropical pandalids examined. Instead, the relative size of the male appendage increased with increased carapace length indicating maturation as a male. The Marianas data for the ratio (R) of the appendix masculina to the appendix interna versus carapace length (CL) was fit to the logistic model with three parameters, a , b , and c (Gunderson et al. 1980). Table 3 lists the parameters obtained when fitted to the model

$$R \times 100 = \frac{a}{1 + e^{-b(CL-c)}}$$

The fit to the nonlinear regression for *H. longirostris* was not particularly good due to the lack of small males in our collection. When the data for this species are fit to a linear regression, however, the slope of the regression is positive indicating relative growth of the secondary sexual characteristics

TABLE 3.—Parameter values for the nonlinear regression of the relative length of the appendix masculina versus carapace length.

Species	a^1	b	c^2
<i>Plesionika longirostris</i>	106.83	0.75	11.67
<i>Heterocarpus ensifer</i>	80.35	0.43	15.05
<i>Heterocarpus laevigatus</i>	104.97	0.29	28.09
<i>Heterocarpus longirostris</i>	158.32	0.05	19.36

¹Asymptotic value for the ratio of the lengths of the appendix masculina and the appendix interna.

²Carapace length at the inflection point at 50% of the asymptotic ratio.

with increasing size (regression coefficient = 1.64, $r^2 = 0.52$).

Based on the assumption that the relative growth of the appendix masculina correlates directly with maturity, we chose the point where this appendage is 90% of its asymptotic value to define the length at maturity for males. The 90% level was used instead of 50% of the asymptotic value, as used for the females below, because the 50% point would be where the males are 50% mature, not where 50% of the males are mature. Using this definition, the carapace length at maturity (L_M) for males of *H. ensifer* is 20.2 mm and that of *H. laevigatus* is 35.7 mm. For *H. longirostris*, the length at maturity is estimated at 31 mm.

The length at maturity of females is perhaps more important in assessment work since the females are directly responsible for the production of recruits to the population. For this study we used the presence of eggs (berried) as the indicator of maturity. The length at maturity is defined as the size where 50% of the females are mature (Gunderson et al. 1980). When using the presence of eggs as the measure of maturity, the sample must be restricted to females collected during the time of year that egg bearing can be expected. For *H. laevigatus*, the breeding season is relatively discrete (November to February), whereas for *H. ensifer* and *H. longirostris* there are peaks in December and May (Fig. 4). Data for each species were fitted to the same non-linear regression model used for the males. Asymptotic values for percent berried by carapace length are 66% for *H. ensifer*, 92% for *H. laevigatus*, and 55% for *H. longirostris*. The carapace lengths associated with values equal to one-half of the asymptotic values are the L_M for the various species. These are 23.9 mm for *H. ensifer*, 42.7 mm for *H. laevigatus*, and 37.4 mm for *H. longirostris*.

YIELD ASSESSMENT

The assumptions and methods of yield assessment used in this study are presented in Polovina and Ralston (1986) and Wetherall et al. (in press). Because *H. laevigatus* yielded the highest catch rates and because it is generally regarded as having superior market acceptability, most of our fishing effort targeted this species. Hence estimates of total biomass and sustainable yield for the pandalid resource are restricted to this species.

GROWTH AND MORTALITY

Estimates of asymptotic size (L_∞) and the ratio

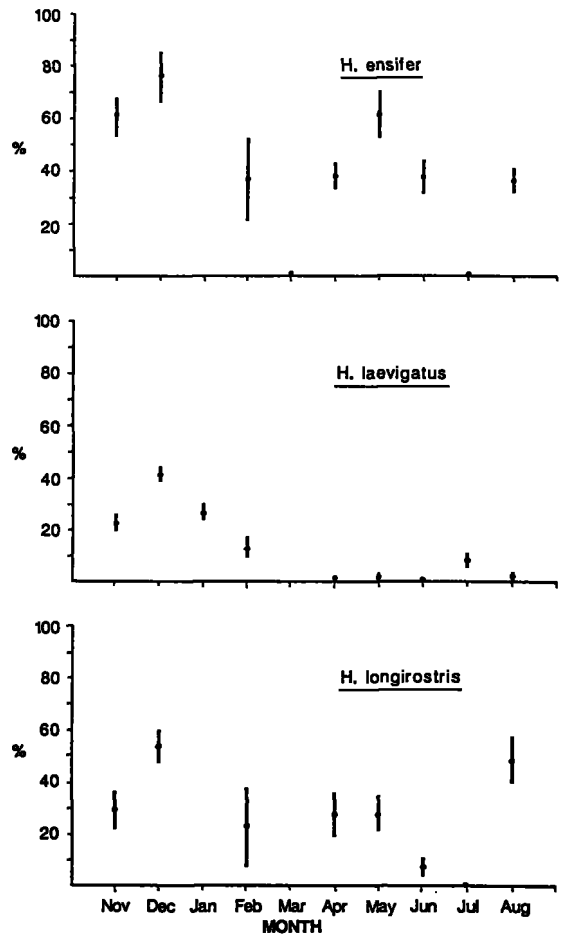


FIGURE 4.—Percentage of females bearing eggs by month for three species of *Heterocarpus* with 95% confidence limits.

of instantaneous total mortality to the instantaneous growth constant (Z/K) were obtained by examining the descending limb of the length-frequency distribution using the regression method based on the Beverton and Holt (1956) model (Wetherall et al. in press). Table 4 lists the values of L_∞ and Z/K for males, females, and pooled sexes for each of the three major species. As anticipated, L_∞ values for females are larger than those for males of the same species. Estimates of length at recruitment to the exploitable population (L_R) were obtained by applying the method of Gulland (1969) to the ascending limb of the same length-frequency distributions. *Heterocarpus ensifer* is recruited into the fishery at a carapace length of 23 mm, *H. laevigatus* at 29 mm, and *H. longirostris* at 34 mm.

By fixing the L_∞ value at the estimates obtained from the large length-frequency sample and using

TABLE 4.— L_{∞} and Z/K estimates for the three major species of *Heterocarpus* by sex from length-frequency data.

Species	L_{∞}	Z/K
<i>Heterocarpus ensifer</i>		
Males	34.5	2.6
Females	37.5	3.0
Sexes combined	36.6	2.9
<i>Heterocarpus laevigatus</i>		
Males	51.3	2.1
Females	55.4	1.9
Sexes combined	55.2	2.5
<i>Heterocarpus longirostris</i>		
Males	41.0	1.7
Females	48.1	1.9
Sexes combined	48.6	2.2

Elefan I (Pauly 1982) to fit the von Bertalanffy growth curve to the time series data for *H. laevigatus* collected at Esmeralda Bank and Pagan Island, the growth constant K can be estimated. When applied to the sexes separately, multiple estimates were obtained for each category ranging from 0.19 to 0.31 yr⁻¹. The inconsistency of these estimates within area and sex groupings was most likely due to the small sample size. When sexes were pooled, however, K was estimated at 0.30 yr⁻¹ for both areas. Estimates of the age at recruitment and maturity were obtained by solving the von Bertalanffy equation for the particular carapace lengths estimated above. For female *H. laevigatus*, with a $L_R = 29$ mm, the $T_R = 2.0$ years, and with $L_M = 43$ mm, the $T_M = 4.5$ years. With a K estimate of 0.3 yr⁻¹ and Z/K of 2.5, an estimate for Z of 0.75 yr⁻¹ is obtained. Because there is no fishery for *H. laevigatus* in the Marianas, Z is equivalent to natural mortality (M).

UNEXPLOITED BIOMASS

Because standard trapping techniques were used throughout our study, CPUE values from various locations could be used as a measure of relative abundance. The unexploited biomass of the *H. laevigatus* resource for each area is then calculated as the product of the area of suitable habitat and relative abundance divided by the coefficient of catchability ($q = 0.001945$ trap-night⁻¹) estimated from the Alamagan Island intensive trapping operation (Ralston 1986). Although the catch rate from the western seamounts is about twice that of the southern island chain, the fiftyfold greater area of suitable habitat around the southern islands more than compensates for the low catch rates in producing a higher biomass estimate for the southern islands (Table 5).

TABLE 5.—Catch rates, habitat areas, and unexploited biomass estimates for *Heterocarpus laevigatus* by location.

	Catch rate (kg/trap-night)	Area (nmi ²)	Biomass (t)
Northern Banks			
Maug	1.88	3.83	3.7
Asuncion	2.11	5.93	6.4
Agrihan	1.96	12.39	12.5
Pagan	2.17	16.19	18.0
Alamagan	2.18	11.43	12.8
Guguan	2.52	5.60	7.2
Sarigan	1.45	4.55	3.4
Anatahan	2.36	10.89	13.2
38 Fathom Bank	2.12	6.37	6.9
Esmeralda Bank	1.35	2.03	1.4
Mean =	2.01	Total = 79.21	85.5
Southern Banks			
Farallon de Medinilla	0.97	88.55	44.2
Saipan	2.06	213.99	226.5
Tinian	1.81	73.80	68.4
Aguijan	1.61	39.36	32.6
Rota	1.02	197.31	103.6
Guam	0.48	44.24	16.2
Galvez and Santa Rosa	1.78	50.77	84.5
Mean =	1.39	Total = 708.02	576.0
Seamounts			
Bank C	2.07	2.71	2.9
Bank D	2.72	2.71	3.8
Pathfinder	2.79	2.71	3.9
Arakane	2.83	2.10	2.1
Bank A	1.43	3.33	2.4
Mean =	2.37	Total = 13.56	15.1

EQUILIBRIUM YIELD

With the values for K , L_{∞} , M , and T_R , the Beverton and Holt yield-per-recruit equation can be used to compute the ratio of equilibrium yield to unexploited recruited biomass (Y/B) as a function of fishing mortality (F) (Polovina and Ralston 1986). Because the shrimp resource in the Marianas is not fished, the estimates of the biomass for each bank represent the unexploited trappable biomass (B), and hence, the product of Y/B and B gives the equilibrium yield as a function of F (Table 6). As F increases, the equilibrium yield increases rapidly for low levels of F . The relationship between F and the equilibrium yield estimated from the Beverton and Holt yield-per-recruit equation assumes that recruitment is unchanged as F increases and does not take into account any economic considerations. Ideally a spawner-recruit relationship is needed to account for changes in yield because of the changes in recruitment which might occur as F increases. However, in the absence of a knowledge of the spawner-recruit curve, two approaches can be used to estimate recommended yield. One approach esti-

TABLE 6.—Equilibrium yield of *Heterocarpus laevigatus* and relative spawning stock biomass as a function of fishing mortality (F).

F	Total yield (t)	Relative spawning stock biomass
0.1	56.2	0.70
0.2	95.6	0.51
0.3	124.2	0.37
0.4	145.4	0.27
0.5	161.6	0.20
0.6	174.1	0.15
0.7	184.1	0.11
0.8	192.0	0.09
0.9	198.5	0.07
1.0	203.8	0.05

mates the recommended yield from the yield-per-recruit derived yield equation as the yield which corresponds to that level of effort where an increase in one unit of effort will increase the catch by 0.1 of the amount caught by the very first unit of effort (Gulland 1983, 1984). This effort is denoted as $F_{0.1}$ and the corresponding yield as $Y_{0.1}$. The value of $F_{0.1}$ for *H. laevigatus* in the Marianas is 0.8 and $Y_{0.1}$ is 192 t annually (Table 6) from areas within the depth range of 500-825 m.

A second approach to estimate recommended yield uses a computation of the spawning stock biomass. With an age estimate of the onset of sexual maturity, the spawning stock biomass for a level of F relative to the spawning stock biomass, in the absence of fishing, can be computed from the Beverton and Holt yield-per-recruit equation (Polovina and Ralston 1986). This relative spawning stock biomass can be used to determine the maximum value of F before a substantial decline in recruitment occurs. The recommended yield can then be estimated as the yield from the constant recruitment yield curve which corresponds to that maximum value of F . This is a conservative approach because it does not incorporate any density dependent compensation, i.e., size at onset of sexual maturity does not decrease as density decreases. The relationship between the relative spawning stock biomass and recruitment is not known for *H. laevigatus*, but it has been suggested that as a lower bound the relative spawning stock biomass should not be reduced below 20% of the unexploited level if a substantial reduction in recruitment is to be avoided (Beddington and Cooke 1983). When F is 0.5, the relative spawning stock biomass is estimated to be 20% of the unexploited level, and the equilibrium yield at this level of fishing is estimated at 162 t annually (Table 6) for the depth range of 500-825 m. To be conservative, the lower yield estimate of 162 t annually from the Mariana

Archipelago will be used. Given the habitat area from 500 to 825 m, this yield is equivalent to 0.20 t/nmi². An approximate variance for this yield, and hence an approximate confidence interval, can be computed from a Taylor series expansion of the yield estimator if it is assumed that the variance of the yield estimate is due primarily to variances in bank CPUE and catchability. The yield at each bank is computed as

$$\text{Yield} = (\text{CPUE}/q)(\text{Area})(Y/B).$$

Thus the variance of the yield ($V(\text{Yield})$) can be expressed as

$$V(\text{Yield}) = (\text{Area})^2(Y/B)^2 V(\text{CPUE}/q),$$

$$= (\text{Area})^2(Y/B)^2$$

$$\times \left[\frac{V(\text{CPUE})}{q^2} + \frac{(\text{CPUE})^2 V(q)}{q^4} \right].$$

Estimates of $V(\text{CPUE})$ were obtained from the repeat sampling at each bank and ranged from 0.02 at Guam to 0.64 at Sarigan, while $V(q)$, estimated at 5.5×10^{-7} , was obtained from the intensive trapping work. The variance of the total yield was estimated as the sum of the individual bank variance. The 95% confidence interval, derived from the estimate ± 1.96 times the standard deviation of the estimate of total yield, resulted in a targeted yield range of 102 to 218 t (0.12 to 0.27 t/nmi²) per year. About 85% of this yield would come from the southern islands and banks, 13% from the northern islands, and about 2% from the western seamounts (Table 7).

DISCUSSION

Although trap design, depth fished, and species present undoubtedly affect catch rate, catch rates reported in other studies using differing trap designs in various areas fall within a fairly tight range of 1.2 to 6.6 kg/trap-night (Table 8). This indicates that the productivity of deepwater pandalids is relatively uniform throughout the tropical central and western Pacific, and the first estimate of recommended yield of 0.2 t/nmi² obtained from the Mariana Archipelago can be applied to other Pacific islands, though the relative importance of the various species may differ greatly from area to area.

In our study *H. ensifer*, *H. laevigatus*, and *H.*

TABLE 7.—Equilibrium yield for *Heterocarpus* shrimps in the 500-825 m depth range for a fishing mortality of 0.5.

Bank	Yield (t/yr)
Northern Banks	
Maug	0.9
Asuncion	1.5
Agrihan	3.0
Pagan	4.3
Alamagan	3.0
Guguan	1.7
Sarigan	0.8
Anatahan	3.1
38 Fathom	1.7
Esmeralda	0.3
Total	20.3
Southern Banks	
Farallon de Medinilla	10.6
Saipan	54.1
Tinian	16.3
Aguijan	7.8
Rota	24.7
Guam	3.9
Galvez and Santa Rosa	20.2
Total	137.6
Seamounts	
Bank C	0.7
Bank D	0.9
Pathfinder	0.9
Arakane	0.5
Bank A	0.6
Total	3.6
Archipelago total	161.5

TABLE 8.—Catch rates of pandalid shrimp in the tropical Pacific.

Area	Catch rate (kg/trap-night)	Source
Tonga	1.2	King 1981b
Samoa	1.4	King 1980
Fiji	1.5	King 1983
Hawaii (main islands)	1.5	Clarke 1972
Guam	2.1	Wilder 1977
Mariana Archipelago	2.1	Present study
Hawaii (NWHI)	2.5-3.5	Oishi 1983
Vanuatu	2.8	King 1981a
Hawaii (main islands)	3.5-5.0	Hawaiian Divers, Inc. 1983 (text fn. 4)
Hawaii (main islands)	6.6	Struhsaker and Aasted 1974

longirostris proved to be the major components of the catch within their respective depth zones. *Heterocarpus ensifer* was the shallowest dwelling and the least abundant of the three major species in the Marianas. Its range of abundance was 366 to 503 m (200 to 275 fathoms) and the peak catch rate was 0.17 kg/trap-night at 366 m. In Hawaii, *H. ensifer* appears to be the most abundant species. Average catch rates are between 1.5 and 6.6 kg/trap-night in a somewhat wider reported depth

of abundance of 274 to 600 m (Clarke 1972; Struhsaker and Aasted 1974; Gooding 1984). In the Southern Hemisphere; *H. ensifer* is not found in great abundance and is replaced in the 300 to 500 m depth range by a very closely related species, *H. sibogae* (King 1983).

Heterocarpus laevigatus is an important part of the catch throughout the central and western Pacific. In the Marianas, this was the most common species. Its abundance peaked between 549 and 777 m (300 and 425 fathoms) and the maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. In the Northwestern Hawaiian Islands (NWHI), the same standard half-round traps caught just under 1.0 kg/trap-night in an optimum depth range of 500 to 800 m (Gooding 1984). Commercial vessels using larger traps obtained catches of 2.5 to 5.0 kg/trap-night in the Hawaii area and found that the optimum depth range is shallower in the main Hawaiian Islands (530 to 622 m) than in the NWHI (640 to 732 m) (Hawaiian Divers 1983⁴; Oishi 1983; Gooding 1984). In the South Pacific, *H. laevigatus* is reported to be abundant at depths of 549 to 640 m and catch rates range from 0.4 to 1.1 kg/trap-night depending on the area studied (King 1983).

Before this study, *H. longirostris* had been known to science from only four specimens taken in the Indian Ocean (Moffitt 1983). In the Marianas, it occurs in sufficient quantity to suggest a commercial potential. *Heterocarpus longirostris* is probably present in many other areas in the Pacific but has not been found because its optimum depth range is below those sampled.

In the Marianas, sex ratio varied with depth for all three of the major species of *Heterocarpus*. For each species, a larger percentage of the catch is composed of females at the shallower end of the species' depth range. A similar distribution in Hawaii has been reported for *H. ensifer* (Clarke 1972) and *H. laevigatus* (Dailey and Ralston 1986).

Changes in the mean size with depth have been reported for *H. ensifer* and *H. laevigatus*. Wilder (1977) and Gooding (1984) reported increases in size with increasing depth for *H. ensifer* from Guam and the NWHI, respectively. Clarke (1972), on the other hand, found that a higher proportion of larger individuals in Hawaii occupied the depth of greatest abundance, while smaller individuals were found in shallower or deeper water. Gooding (1984) noted a

⁴Hawaiian Divers, Inc. 1983. Deepwater shrimp utilization study for Hawaii. Report prepared under NOAA Cooperative Agreement No. 80-ABH-00065 for the Southwest Region, Western Pacific Program Office, National Marine Fisheries Service, NOAA, 47 p.

decline in size (kilograms/individual) with increasing depth for *H. laevigatus* in the NWHI. In all of these studies, changes in sex ratio with depth were not taken into account. As we have shown, sex ratio does change with depth and the sexes do grow at different rates. The observed changes in size with depth may be due to changes in sex ratio rather than size-specific stratification. Dailey and Ralston (1986) examined the sexes separately and found that for *H. laevigatus* in Hawaii the carapace length of males and egg-bearing females displayed no apparent change with depth, whereas that of nonegg-bearing females showed a strong inverse relationship. In the Marianas, significant changes in mean carapace length with depth were not observed for either sex of the three species of *Heterocarpus*, except for female *H. longirostris* (Table 2). For this group, an inverse relationship was observed much like that found for nonegg-bearing female *H. laevigatus* in Hawaii (Dailey and Ralston 1986).

The estimates of growth parameters for *H. laevigatus* obtained in this study correspond well with those of other authors (Table 9). Using the regression method (Wetherall et al. in press), we estimated L_{∞} to be 51.3 mm CL for males, 55.4 mm CL for females, and 55.2 mm CL for the pooled population in the Marianas. Using the same method, Dailey and Ralston (1986) obtained estimates of 57.9 mm CL for males, 62.5 mm CL for females, and 61.7 mm CL for the combined sexes in Hawaii. Apparently, *H. laevigatus* grows about 7 mm larger in Hawaii than in the Marianas. King (1983), using the Beverton and Holt method, estimated $L_{\infty} = 57$ mm CL for *H. laevigatus* in Fiji.

Estimates of Z/K for *H. laevigatus* in the Marianas were 2.1 for males, 1.9 for females, and 2.5

for the sexes combined. In Hawaii, Z/K estimates of 4.3, 2.9, and 2.6 were obtained for the same categories, respectively (Dailey and Ralston 1986). The Z/K estimates for the combined sexes are nearly identical in the two studies. In our study, Z/K estimates for the two sexes were similar to each other and lower than that of the sexes combined, whereas in the Hawaii study they were very different from each other and both larger than that of the combined sexes. In our study, if we assume that instantaneous growth of the two sexes is similar, then mortality will also be similar and close to the 0.75 yr^{-1} value estimated for the pooled sexes. In the Hawaii study, Z/K estimates for males and females differed widely. Mortality estimates differed considerably as well, $Z = 1.51 \text{ yr}^{-1}$ for males and 0.73 yr^{-1} for females.

The K parameter for *H. laevigatus* in the Marianas was estimated as $K = 0.30 \text{ yr}^{-1}$ for the combined sexes (Table 9). Estimates of K for the individual sexes were ambiguous and inconsistent. King (1983) estimated K as 0.27 yr^{-1} for *H. laevigatus* in Fiji and Dailey and Ralston (1986) estimated K as 0.35 yr^{-1} for male and 0.25 yr^{-1} for female *H. laevigatus* in Hawaii. Because growth estimates for *H. laevigatus* are similar for the various areas studied, it is not surprising that estimates of age at maturity are also similar (Table 9). King (1983) reported the age at maturity for female *H. laevigatus* in the South Pacific as 4.6 years (40.5 mm CL). He further suggests that males mature at about 24 mm CL (age not calculated). Dailey and Ralston (1986) found that females in Hawaii mature at 40 mm or about 4 years. In the Marianas female maturity is estimated at 43 mm CL or about 4.5 years. Males mature earlier at 35.7 mm CL or about 3.0 to 3.5 years. Male maturity estimates by King (1983) and this study are based on the relative growth of the appendix masculina on the second pleopod. King appeared to have chosen 50% of the asymptotic value as the point of maturity much as the point where 50% of the female shrimp are bearing eggs is used to define maturity for females. We feel that 90% of the asymptotic value is a better estimate of male maturity and have used that point in our estimate for the Marianas.

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TABLE 9.—Asymptotic length (L_{∞}), instantaneous growth constant (K), length at maturity (L_M), and age at maturity (T_M) of *Heterocarpus laevigatus*.

Location	L_{∞} (mm)	K (yr^{-1})	L_M	T_M
Fiji				
(King 1983)				
Sexes combined	57	0.27		
Females			40.5	4.6
Males			24	
Hawaii				
(Dailey and Ralston 1986)				
Sexes combined	61.7			
Females	62.5	0.25	40	4
Males	57.9	0.35		
Mariana Archipelago				
(present study)				
Sexes combined	55.2	0.30		
Females	55.4		43	4.5
Males	51.3		36	3.5

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